Pine Forests

Utilization of their Products

V.N. Vorob′ev

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V.N. Vorob'ev
V.N. Sukachev Institute of Forests and Timber
Academy of Sciences, Russia
Siberian Division

Editor-in-Chief
I.V. Semechkin

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Introduction

Modern forest science, specially the organization and management of forest economy, has experienced great development, owing to the need in many cases for the application of unconventional methods of tackling practical problems. Typical examples of such a high level of researches are those conducted only in V.N. Sukachev Institute of Forests and Timber, Siberian Division, Academy of Sciences, USSR, in the field of timber development in conifers (Sudachkova 1977), theory of their resistance to various factors causing damage (Isaev and Girs 1975 and Girs 1967 and 1982), mathematical modeling of stock formation (Kuz'michev 1978), their polymorphism (Iroshnikov 1964, 1972, 1974, and 1975), reproductive activity (Nekrasova 1972 and Minina and Larionova 1979), ecological and typological aspects of taiga forest science (Polikarpov 1966 and 1981, Smagin 1980, and Nazimova 1975 and 1980), and others.

Such advanced investigations are essential in the sphere of theoretical principles of comprehensive utilization of forest resources (Pozdnyakov 1973 and 1975), especially of pine forests. It is generally acknowledged that their exploitation is not satisfactory largely due to an inadequate understanding of several aspects of organization and management of these forests.

The scientific aspects of resolving pine forest problems with a predominance of lumber industry approach of utilizing these most valuable forests of our country are vast. Among them, the most important are organizing the system (Motovilov and Shcherbakov 1963, Lebkov 1967, Semechkin 1971, and Semechkin and Vorob'ev 1980), its management (Polikarpov 1966, 1980, and 1981) and economic (Spiridonov 1966, Saeta 1971 and 1979, Parfenov 1979, and Vorob'ev, Saeta, and Kulikov 1978) principles.

These and similar aspects of scientific principles of organization and management of economy in pine forests have a close and direct bearing on the practice of forest exploitation while their foundation rests on the theoretical premises of a biological nature. In this respect, the theory of comprehensive utilization has not developed adequately. The investigations carried out by this author help formulate such a theory and advance many practical suggestions for solving the prevailing situation in the exploitation of pine forests. Considering that the main products responsible for their 4 popularity and outstanding economic importance are the nuts, timber, and resin, the biological aspects of relationship between regeneration, growth, and resin-formation have been studied in this monograph under normal conditions as well as under the conditions of experimental variation of root-leaf proportions. Great attention has been paid to genotypic, ontogenetic, eco-geographical, and other aspects.

The relationship between the productivity indexes of trees and stands with respect to growth, cone production, and resin development at intra- and interpopulation levels have been adopted as a basis for analysis. The detection of a positive statistical correlation between them together with the presence of appropriate genotypic and phenotypic deviations aided in formulating the principles for a differential approach to the comprehensive utilization of pine forests in the taiga region and adopting selection based on economically significant factors for creating specialized plantations yielding nuts, resins or timber.

The theoretical justification for this approach is evident in that it takes into consideration the variability of wooded plants but avoids the modern practice of applying statistical correlations between growth and development which are most prominent when using a single factor like the age of the stand that is well-controlled in different groups of forests.

The practical significance and utility of a differential management practice in taiga forests lie in that the resultant recommendations actually call for reorganizing the existing facilities and methods of economic activity by establishing a close relationship with comprehensive evaluation of pine stands. As the techno-economic conditions are evidently inadequate for upgrading the level of forestry in Siberia, the most probable solution to resolving the problems of pine forests lies in studying and improving these aspects.

The present work is the outcome of 20 years of integrated investigations carried out by the author aided by several specialists.

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CHAPTER I

Ecology of Siberian Stone Pine

The ecological studies of Siberian stone pine, like many other characteristics, began in the early '60s. Significant contributions to these studies were made by N.P. Polikarpov (Polikarpov and Nazimova 1963 and Polikarpov 1966 and 1981) and his co-workers. The climatic conditions for growth of pine in the mountainous environment were particularly extensively studied.

The ecological approach to the study of pine and other forests in the mountains of southern Siberia as well as aspects of zonation of forest vegetation (Smagin 1980 and Nazimova 1975 and 1980) helped in recognizing altitudinal zones of forest complexes exposed to diverse formation conditions and reflecting the major advancements of modern biogeocoenology.

During the same period, much work was carried out in the field of ecological aspects of the polymorphism (Iroshnikov 1964 and 1972–1974), growth (Sudachkova 1977), and reproduction (Nekrasova 1961, 1967, and 1972, Iroshnikov 1963, and Vorob'ev 1965, 1967, and 1974) of Siberian stone pine. Several ecological concepts of the Siberian stone pine as a timber species underwent a change. It became evident that this pine is more photophilous and fast-growing than was hitherto understood.

The modern ecological description of Siberian stone pine depicts it as a stable and adaptable species, sensitive to the changes of growth conditions. This is confirmed from successful course of macrocyclic natural regeneration of pine forests under cover of deciduous and coniferous species. The favorable response of pine seedlings on being relocated outside the forest cover provided an adequate base for concentrating efforts in this direction for restoring pine plantations.

Our investigations have included several ecological aspects of comprehensive utilization of pine forests. The growth indexes of pine cited in this context have been evaluated on the basis of their importance for the processes of growth and cone production and as a characteristic of the area of investigation.

North-eastern Altay represents a convenient area for studying the ecological aspects. This area combines altitudinal zonation and latitudinal heterogeneity, and highly divergent growth conditions which influence the growth and regeneration of this species.

7 The major ecological studies were carried out in the high-altitude regions: Kyga in the southern part of Teletsk taiga, Uimen' in the central part and west of Teletsk lake, Kamga in the northern part of the lake, as well as in Sur'yaza in the basin of Chul'cha river (Fig. 1).

The itineraries covered the main pine massifs in Altay forest reserve and Gorno-Altay Experimental Forest Group: Sur'yaza, Bulandu-kol', Klyk, Malye Chili, Kochesh, Samysh, Tazhirvakh-Pyzha, Tazhirvakh-Evii, Uchal, Nyrna,

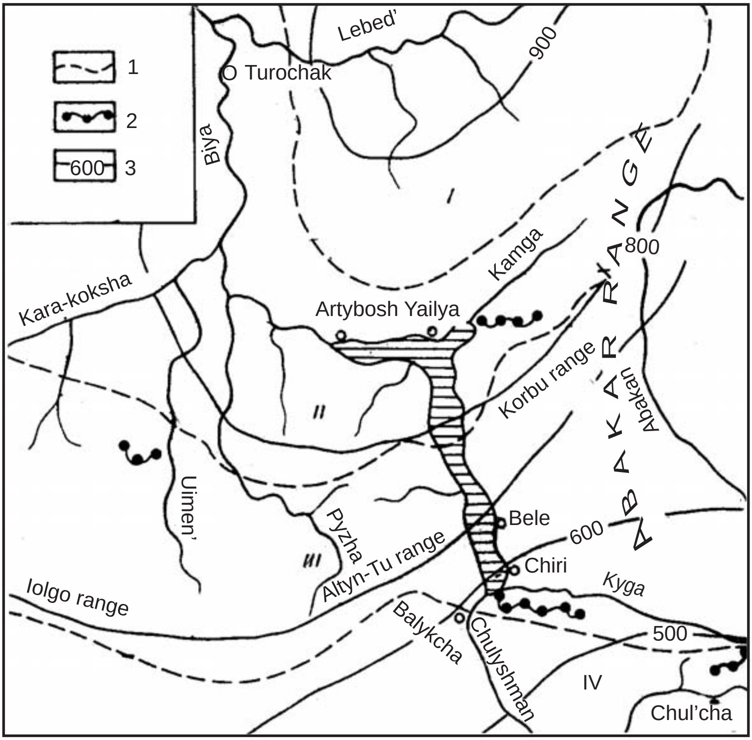

Fig. 1. Teletsk section of north-eastern Altay.
Regions: I—Biya-Lebed' fir, II—Koksha-north Teletsk pine-fir, III—Pyzha-south Teletsk fir-pine, and IV—Chulyshman-Chul'cha pine-larch. 1—Zone boundaries, 2—altitude profiles, and 3—annual precipitations.

and others. Several test plots were marked in sections considered most important from ecological or economical angle and the various aspects of the relevant problems were studied.

The *ecological factors* characterizing the growth conditions and reproduction of pine can be examined within the latitudinal and altitudinal profiles in north-eastern Altay and later the longitudinal aspects in some mountainous areas in southern Siberia.

Topography in a mountainous country plays a leading role in the
8 distribution of light, heat, and moisture. Among the topographic types identified by S.S. Voskresenskii (1962) in Altay, those most commonly found in its north-eastern region are: low-mountain erosion, midmountain erosion, and high-mountain glacial reliefs. In such a succession, their predominance varies within the latitudinal profile of north-eastern Altay which represents in general a cross-section of the northern megaslope of the western part of mountains of southern Siberia. As the first two types prevail mainly within the forest belt of mountains, they have been studied in greater detail.

Low-mountain topography is characterized by broad valleys and gently sloping ranges intersected by a close network of small rivers. The effect of exposure on the distribution of vegetation here is feeble since the dominant altitudes are 600–1000 m above sea level. Low-mountain topography is more typical of the north-western part of Altay-Sayan province and of Lebed' river basin and lower courses of Kara-Koksha river within north-eastern Altay.

Midmountain erosion topography is the most prevalent type in north-eastern Altay as also more than half of the territory within the mountainous area of southern Siberia (Mikhailov 1961). This type of topography is closely associated with the spread of pine forests (Krylov and Rechan 1965). One of the characteristic features of this topography is its steplike profile. In Altay, it is seen in the northern part of Teletsk taiga where it plays an important role in moisture distribution and in precipitation cycles of different types. In the southern part of Teletsk taiga, mountain sections are characterized by steep and steady ascent to altitudes of 1400–1600 m and a level surface appears only thereafter. The area of this level surface is quite extensive and the bulk of subalpine pine forest massifs is concentrated here.

On the whole, the topography of this territory promotes diverse conditions for the redistribution of light, heat, and moisture, thanks to a multiplicity of its forms. It facilitates an increased flow of atmospheric precipitations and excellent incidence of light and heat, particularly south of north-eastern Altay.

Soil. The soil characteristics of the region under consideration have been extensively dealt with in the literature (Zolotovskii 1938a, B.F. Petrov 1952, Lebedinova 1952, Gorshenin 1955, Gradoboev 1958, Brysova and Korotkov 1961, and Kovalev and Trofimov 1965). The soil cover and the corresponding type of topography and climate quite completely reflect the latitudinal heterogeneity of the region and the altitudinal distribution of vegetation. Mountainous soddy-podzolic deeply podzolized soils prevail in Lebed' river region where the climate is most humid. In the northern part of Teletsk taiga where precipitations are few, the soil cover is represented by mountain-taiga brown soddy and coarse humus soils. Mountain-taiga, soddy-podzolic and mountainous gray forest soils together with brown soils are seen in the south.

Latitudinal heterogeneity of soil cover is confirmed by the nature of its altitudinal variations. While the vertical soil section in the southern part of
9 Teletsk taiga has been more fully described as comprising, top downward, zones of mountain-tundra, mountain-meadow, and mountain-forest soils with podzolic, brown forest, and gray forest subzones in the latter, the northern part almost entirely falls in the zone of mountain-forest soils because of its lower altitude.

An important condition for the growth and cone production of Siberian stone pine is the water and aeration regimes of soils. In the mountains, their dependence on the structure of horizons, total atmospheric moisture, steepness of slopes, temperature regime, and snow thawing seasons is particularly noticeable. In the river valleys, at places where soils are underlain by pebble formations, water and aeration regimes are most favorable and pine shows maximum growth. Ascending into the mountains, the total moisture rises but, at the same time, the steepness of slopes also shows increase. The latter factor makes for a sharp increase of drainage and checks swamping processes. Such conditions prevail essentially in the mountain-taiga subzone.

In the upper part of the mountains where pine forests are mostly confined to the level surfaces, the rate of surface and internal drainage is reduced. Thus, there is soil swamping on many northern slopes. In the exposed portions on the south, these processes are restricted and aeration conditions are better. Differences are also caused by dissimilar light conditions. As a result of these factors, tall grass pine forests confined mostly to areas exposed to light bear characteristics of good growth and development while dwarf birch and lichen-type forests on the northern slopes have low vegetative and seed output.

Light. The study of this factor in the eco-geographical context has so far not received adequate attention. An exception is the work carried out at V.N. Sukachev Institute of Forests and Timber in western Sayan (Sadovnichaya and Chebakova 1978).

It has been estimated that the horizontal surface of the Earth receives 1.2–1.3 cal/cm^2-min. As its inclination varies, the incidence of radiation too varies. For a given incidence of sunlight (30°), a level surface may receive 0.6 cal/cm^2-min and a surface inclined at 45° 0.84 cal/cm^2-min out of the total radiation (1.2 cal) (Sklyarov 1960). For maximum incidence of light, the optimum steepness of slope falls in the range 25–45°.

The duration of solar radiation from the foothills to the summit, and from south to north, varies: light decreases toward the polar boundary but increases toward a similar limit in the mountains.

In north-eastern Altay, specially in its humid regions, differences of light incidence along the profile are evidently not so marked and more light is perceptible only in the uppermost portions of mountains. Toward the south, as a result of reduced total precipitations, light and the quantum of direct radiation vary more as a whole and specially in the upper parts of the profile. In this context, the conclusion drawn by E.A. Sadovnichaya and N.M. Chebakova (1978) is particularly important: radiation factors depend on the wetness of the territory and, in this respect, the radiation index of dryness represents a good index for marking the boundaries of altitude zones. According to the data of the above investigators, this index falls sharply toward the upper part of mountains and the total direct radiation and the total overall radiation also decrease in the period of active vegetative growth of plants.

It is therefore important to understand the significance of abundant light and the quantum of direct radiation.

K. Rubner (1960) for example considers that the forest boundary in the Alps is largely determined by the duration of solar radiation, with not the atmospheric temperature but insolation heat, i.e. direct solar radiation, playing the main role.

The application of this principle to the Russian conditions will show that the pine boundary traverses at 1700 m above the sea level in the northern part of Teletsk taiga where precipitations are the highest (900 mm/year) and hence light is less. The boundary rises by 300 m to the south of this region due to reduced precipitation (600 mm). In central and south-western Altay which receive even less precipitation, pine forests rise to altitudes of 2200–2400 m (Razlivalov 1960 and G.V. Krylov 1961).

A.A. Malyshev (1965) cites similar data but somewhat differently for the Caucasus. According to him, photosynthesis and plant growth processes in the high-altitude conditions are largely determined by the temperature of plant tissue which depends on the direct action of insolation than on atmospheric temperature. S.L. Pumpyanskaya (1961) for example explains that the leaf temperature of some high-altitude plants at a height of 2400–2500 m was 14–19° more than the ambient temperature. At an altitude of 1300 m, this difference is no longer noticeable.

Thus, high-altitude plants develop within and around themselves their own microclimate which differs significantly from the ambient conditions.

Such a utilization of direct radiation may be regarded as one of the forms of adaptation of mountain plants to the severe conditions of survival.

Under conditions of plains and in the low mountains, diffuse radiation plays the main role as it is better absorbed by the plants while direct rays are reflected (Ivanov 1953). This reflection depends on the atmospheric temperature, i.e. the higher the atmospheric temperature, the more complete is the reflection of direct radiation. When the temperature is inadequate, as noticed for example in the upper parts of mountains, reflection decreases. In all probability, it is this ratio of atmospheric temperature and insolation heat that explains the transition of the dominant role of one type of radiation over another.

Heat. The nature of heat regime in the mountains is unusually complex because of its dependence on the orographic structure of the locality and has not been well documented for want of adequate studies. For example, meteorological stations in north-eastern Altay are located mostly in the valley of Biya river and Teletsk lake and hence provide an idea of only the general tendency of climatic variations (Table 1).

11 In the foothills of Altay (Biya and Kyzyl-Ozek), the atmospheric temperature is high and its sum for the period $t > 10°$ goes up to 2000°. Ascending into the mountains, this value falls but only up to the northern part of Teletsk lake since it again rises toward south under the influence of warm and dry winds from the inner regions of Mongolia (Alisov 1956). The relative penetration of air masses bearing the characteristics of a given climate is facilitated from the northern side of Biya river valley and from the south from Chulyshman river. These valleys, including the lake graben, constitute a unique system of atmospheric circulation (Vorob'ev 1974a and Selegei 1976).

Heat availability falls sharply with ascent into the mountains, causing significant differences with high-altitude sections (Table 2). The sum of

11 Table 1. Variation of atmospheric temperature (°C) from the foothills of northern Altay to the inner regions of its north-eastern border

Station, m above sea level	July	Annual	$\Sigma t > 10°$
Biya, 194	19.2	1.1	2140
Kyzyl-Ozek, 331	18.0	1.0	1910
Turochak, 332	17.5	– 0.3	1770
Artybash, 438	16.2	1.2	1610
Yailya, 441	16.2	2.8	1630
Bele, 450	16.9	3.6	1800

12 Table 2. Change of atmospheric temperature (°C) along Kyga profile (m above sea level, zone-wise) for 1962–1964

Monthly mean								Variation through		Σ t >	
May	June	July	Aug.	Sept.	May–Sept.	Oct.–April	Jan.–Dec.	5°	10°	5°	10°
Black soil subzone, Kyga station, 660											
7.8	12.5	15.0	14.4	7.0	11.2	–6.0	1.4	May 10 Aug. 7 150	May 24 Aug. 30 97	1800	1400
Gorno-taiga subzone, Ayu-kol' station, 1200											
5.2	11.2	13.2	12.2	4.3	9.2	–7.0	–0.3	May 18 Sept. 20 125	May 25 Aug. 25 90	1400	1100
Subalpine subzone, Ernikovaya station, 1800											
2.6	8.8	11.2	10.6	2.4	7.1	–8.6	–2.2	May 23 Aug. 28 97	June 7 Aug. 22 76	980	800
M. Kolyushta station, 2000											
1.3	8.1	10.8	10.4	1.9	6.5	–9.5	–2.8	May 25 Aug. 25 90	June 10 Aug. 20 70	870	630

temperatures representing the main conditions of plant growth in the upper parts of mountains decreases by more than half and the duration of vegetative period falls by almost 60 days.

The degree of atmospheric temperature drop with the rise in the hypsometric level of a given locality depends on the general climatic conditions (Buchinskii 1950). Thus, for example, while the thermal gradient over the vegetative period is 0.35 in the southern part of Teletsk lake, it is 0.44 more to the south (Zolotovskii 1938b). This makes for a more continental type of climate on the southern compared to the northern aspect. *Water.* A similar study of total precipitation within a longitudinal profile would show more significant variation than temperature (Table 3). Thus, in the forest-steppe part of Altay (Biya), the annual precipitation does not exceed 500 mm (does not reach even 300 mm in the vegetative period). These values rise sharply in the foothills (Kyzyl-Ozek) and the precipitation in July alone amounts to 100 mm, thus ensuring a high level of moisture availability in the territory. The main variations of its value leading to zonal differences of vegetation occur from north-west (Lebed' river basin) to south

12 Table 3. Variation of total precipitation (mm) from the foothills of northern Altay to the interior of its north-eastern border

Station	July	May–Sept.	Annual
Biya	75	290	522
Kyzyl-Ozek	110	462	725
Turochak	111	466	828
Yailya	133	590	850
Chiri	90	460	560
Balykcha	68	300	402

(Balykcha station). The distribution plan of precipitation (see Fig. 1) plotted by us for the foothills taking into consideration the maps of V.B. Shostakovich
12 (1931) and A.P. Slyadnev (1960) as also the nature of disposition of mountain ranges, variations of vegetation, and direct meteorological observations in the mountains provides a better idea of relations between precipitation and the type of vegetation.

Precipitation increases at higher altitudes in mountains (Table 4). In the midmountains, for example, its sum is double that in the foothills. This rise continues even further, with the maximum recorded at an altitude of 1600–1800 m (Malyshev 1948).

The total precipitation also depends on the overall climatic features of the given locality. In the anticyclonic regions, in the upper half of the profile, the total precipitation falls and maximum value shifts to a much higher level than in the cyclonic regions (Malyshev 1965). Corresponding differences in the moisture level on top of mountains in the southern and northern parts of Teletsk taiga provide excellent conditions for the growth and development of pine in the former and inferior conditions in the latter.

13 Table 4. Variation of total precipitation (mm) along Kyga profile for 1962–1964

Month	435	1250	Month	435	1250
	m above sea level			m above sea level	
May	45	55	Total for		
June	102	183	season (May–Sept.)	316	634
July	69	191	Annual total		
August	48	121	(Jan.–Dec.)	451	905

The variation of snow cover supplements the information on the moisture reserves in the mountains. Within north-eastern Altay, its depth increases from the foothills to the northern part of Teletsk taiga, falling thereafter under the influence of the warm Mongolian winds and reduced precipitation, especially the winter precipitation. The variation of the duration of the snow period proceeds similarly. Rising into the mountains, the amount of winter as well as summer precipitation increases (Table 5). In the extremely snowy winters, as for example in the 1965/1966 winter, snow reserves attain high values, specially in the mountains.

13 Table 5. Variation of snow cover along Kamga profile (m above sea level) (numerator 1964–1965, denominator 1965–1966)

Thickness of snow cover, cm										Dates of formation and thawing of snow cover	Snow cover duration, days
Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June		
Kamga station, 600											
–	4	8	73	100	90	90	43	5	–	Oct. 10–May 5	206
–	10	35	117	110	115	135	108	10	–	Oct. 22–May 17	206
Shaltan station, 1000											
–	17	27	90	112	100	105	82	40	–	Oct. 5–May 15	221
–	7	58	135	154	175	195	150	50	–	Oct. 10–May 25	226
Korbulu station, 1600											
10	45	55	136	162	144	148	140	100	40	Sept. 25–June 15	263
–	30	88	152	180	210	250	235	200	17	Oct. 10–June 15	247

On the whole, the distribution of winter precipitation along the altitudinal profile is uneven. Bulk of it is concentrated in the latter half of the altitudinal profile. According to the available information, the altitudinal gradient of snow cover thickness in the lower part of mountain-taiga subzone is 9 cm and in the upper 12 cm; in the subalpine zone, it is 3 cm (Sobanskii and Selegei 1975).

14 The greater snow thickness in the mountains with a cyclonic climate helps maintain positive temperatures in the soil almost throughout the entire forest belt (Table 6).

Biotic factors. The most important are the interrelations of pine with the animal and plant life. The influence of animals is essentially seen in the

14 Table 6. Variation of soil temperature (°C) along Kamga profile, month-wise

Station, m above sea level	Soil temperature at depth 0.6 m									
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.
Yailya, 441	1.7	1.1	0.7	1.2	7.3	11.8	15.2	7.5	3.4	2.2
Shaltan, 1000	2.5	2.0	1.7	1.7	3.3	8.5	11.3	4.9	3.4	2.9
Boloto, 1300	3.3	2.6	3.1	3.8	3.8	7.5	12.2	5.6	4.4	3.7
Korbulu, 1600	1.1	0.9	0.6	0.7	0.5	–	–	2.3	1.6	1.3

period of ripening of cones and seeds. By eating or pilfering cones and seeds, animals inflict direct losses on the forest economy. More than all others, the slender-billed nutcracker causes maximum damage (Kalyaev and Krinitskii 1961). Nevertheless, the animal life inhabiting the pine forests brings forth many advantages. While some of it comprises the main source of game, the nutcracker promotes the natural regeneration of pine forests.

The interrelations between pine and other woody species also play a significant role. Many Russian and Soviet investigators have dealt with the various aspects of this problem mainly from the study of the vegetation in north-eastern Altay. This has resulted in the classification of forest types (G.V. Krylov 1957, Brysova and Korotkov 1961, and Krylov and Rechan 1965) and their zonation based on forest vegetation (G.V. Krylov 1957 and Krylov and Rechan 1965) and geobotany (Kuminova 1960). The scientists at the Altay State Forest Reserve made intensive studies of the features of vegetation and climate of the region. M.V. Zolotovskii (1938a), L.P. Brysova and I.A. Korotkov (1961) worked on forest-vegetation and geobotanical zonation of Teletsk taiga. They divided the Teletsk part of forest reserve into northern, central, and southern zones, and described the soil cover and forest types. A.I. Kalyaev and V.V. Krinitskii (1961) studied the fruiting of Siberian stone pine for the above classification of the territory. They could not complete their studies due to the closure of the forest reserve and the zone boundaries were marked later (Vorob'ev 1967).

The following modified zonation of the territory under consideration has no independent objective but to form a basis for analyzing the conditions and consequences of pine growth in this region (see Fig. 1).

Biya-Lebed' pine-aspen-fir region. The main vegetation in this region is in Lebed' river basin and the upper course of Biya river. Its south-eastern
15 boundary runs along the waterdivide with the Teletsk lake basin. Descending

onto the left bank side of Teletsk taiga along Torot mountain range, it emerges onto Azha cape and, ascending northward, closes the region of Biya ridge. This line almost wholly coincides with the boundaries of Biya-Lebed' foothill-forest region drawn by A.V. Kuminova (1960).

The climate of the region is characterized by maximum humidity and bears a distinct cyclonic character. The increase of humidity is promoted by a predominance of low-mountain relief and the south-eastern waterdivide range of mountains, the latter restraining many cyclones from entering from the north and north-west into the valley of Lebed' river.

The forests of this region described by B.N. Klopotov (G.V. Krylov 1961) as early as in 1909 represent a typical black soil taiga mainly comprising fir. The latter are disposed mainly in the lower and middle regions of mountains. Pine predominates in the sharp sections of topography and in the ridges between the rivers. Birch and aspen form a prominent combination in the river valleys.

The forest types are represented by fir forests with forbs, broad-grass, fern, and grass-swamp groups (Krylov and Rechan 1965). Similar groups are noticed among pine forests. In the background of large-scale clearing of Altay deciduous forests, the pine forests of this region represent remnants of most productive and valuable plantations from the viewpoint of breeding.

Koksha-north Teletsk pine-fir region occupies the northern part of Teletsk taiga and lower course of Kara-Koksha river. Korbu mountain range forms the southern boundary of the region within the right bank portion of the lake and represents the second barrier which restrains a significant amount of precipitation. The distribution zone of precipitation falls along such concave-parallel lines of mountain ranges (see Fig. 1). Korbu mountain range simultaneously serves as the boundary between the northern and southern parts of north-eastern Altay as well as the boundary of predominance of fir and pine. On the left bank, the boundary runs along the northern waterdivide of Malye Chili river, encompassing from the south the basins of Koldora, Samysha, and Iogacha rivers; later, it traverses along the basin of Kochesh river in Pyzha taiga and reaches Kara-Koksha river through the midcourse of Pyzha and Uimen' rivers.

The climate of the region is also cyclonic although the rainfall here is less than in Biya-Lebed' region. The temperature regime is moderate, specially in the region of Kamga profile described below with a typical section in the zone of predominance of pine-fir taiga (Table 7).

The climatic conditions of the region (combination of moderate temperatures and high humidity) are favorable for the growth of fir which covers much of the area here with up to three pine trees in its composition. Ascending into the mountains, fir extends almost up to the forest boundary.

16 Table 7. Physical characteristics of forest stands (m above sea level) in Kamga profile

No. of test plots	Zone	Quality index, forest type	Composition	Density	Age, years	Height, m	Diam., cm	Reserve m^3/ha
Black soil subzone, 450								
8	1	I	$2P_{I}$	0.12	400	34	88	65
		Sorrel-fern	$8P_{II}$	0.30	220	31	56	248
			6B	0.15	70	23	32	46
			4F	0.08	70	19	22	24
	2		+P	0.01	80	11	14	4
Gorno-taiga subzone, 1000								
6	1	II	10P	0.50	250	31	56	370
	2	Green moss-reed grass	10F	0.30	110	17	16	60
			Stray P	0.01	90	13	14	3
Subalpine subzone, 1650								
5	1	V[a]	$8P_{II}$	0.32	350	16	61	85
		Bitter root-tall grass	$1P_{I}$	0.05	590	15	81	12
			$1P_{III}$	0.04	220	13	48	9
	2		$7F_{I}$	0.11	110	11	19	15
			$1P_{IV}$	0.01	110	12	32	2
			$2F_{II}$	0.08	85	8	14	6

Note: B—birch, P—pine, and F—fir.

16 This region differs little from Biya-Lebed'. Another characteristic feature of vegetation here is the complexity and mixed ages of stands (see Table 7).

At present, Kokshin-north Teletsk region is the main area of forest exploitation, the main source being the pine forests but the resources have been considerably depleted, specially in the north-western part.

Pyzha-south Teletsk fir-pine region is the main area of pine growth. Its southern boundary coincides with that of north-eastern Altay and runs along the waterdivide of Chul'cha and Kyga rivers, along Altyn-Tu and Iolgo mountain ranges. These mountain ranges representing the last barrier in the path of cyclones divide the northern Altay regions with predominant dense coniferous forests and the southern regions where open coniferous forests predominate.

The forest belt in Kyga region attains maximum extent: black soil pine forests are disposed at altitude of 430–1000 m, mountain-taiga forests at

1000–1600 m, and subalpine forests at 1600–2000 m (Table 8). While the altitudinal profile in the preceding region could be called "fir type", here, it could be called "pine type".

17 Tall grass-fern type pine forests with well-developed timber and grass-shrub zones are seen in the river valleys. Pine proportion in the forest canopy

17 Table 8. Physical characteristics of forest stands on Kyga profile

No. of test plots	Zone	Quality index, forest type, m above sea level	Composition	Density	Age, years	Height, m	Diameter, cm	Reserve, m³/ha
Black soil subzone								
2[a]	1	I	$3P_{I}$	0.15	300	35	80	90
		Tall grass, 450	$7P_{II}$	0.44	210	32	58	296
	2		9F	0.36	130	17	25	90
			1B	0.03	90	20	39	10
			Stray P	–	90	12	10	2
4	1	I	$3P_{1}$	0.10	390	34	80	90
		Reed grass-tall grass, 870	$7P_{II}$	0.30	190	30	56	210
	2		9F	0.70	110	18	21	198
			1B	0.20	90	15	20	30
			Stray P		–100	15	16	5
Mountain-taiga subzone								
8[a]	1	II	10P	0.76	270	29	67	470
	2	Green moss-fern, 1250	10F	0.35	130	19	21	103
			Stray P	–	130	13	13	4
21	1	IV	10P	1.10	160	22	40	467
		Bilberry, 1450	Stray F	1.05	70	12	14	11
11[a]	1	IV	$10\ P_{I}$	0.65	390	20	48	229
		Bilberry, 1650	$10P_{II}$	0.10	210	14	24	33
	2		P_{III}	0.02	130	7	9	2
Subalpine subzone								
12	1	V[a]	$10P_{I}$	0.30	400	18	48	3
		Green moss-dwarf birch, 1350	$10P_{II}$	0.40	210	3	24	107
13	1	V	10P	1.15	210	17	37	340
		Bitter root-tall grass, 1800						
14	1	V[a]	10P	0.30	120	4	16	90
		Bitter root-tall grass, 1950						

Note. B—birch, P—pine, and F—fir.

is more than in the northern valleys, trees increasingly taller and stouter, 18 with well-developed crowns. A.V. Kuminova (1960) described such pine forests as nemoral forests.

The mountain-taiga pine forests are characterized by a predominance of pine in the upper half of the subzone. As this section is confined more to a break in hypsometric profile from the steep ascent to the levelled area, bergenia and whortleberry types of forests are seen here.

The subalpine pine forests are more predominant. They represent far more area than in the regions described above, type composition more diverse, and stands with diverse physical structures are found here. Bitter root-tall grass type pine forests are most widely spread and provide a park-like landscape to the locality. Green moss-dwarf birch types predominate on the northern slopes. Stands of both the types are generally of V-V^{a} classes, of different ages, while a few attain a high density. In the thinned stands, pine trees are very few, with crowns bent down almost to the ground.

The above description of vertical zonation is characteristic of Teletsk part of the region. In the west, in Pyzha river basin, pine forests are mainly represented in the mid- and high-mountains, their stands are of uniform age and of pure composition, smaller diameter, and the number of trunks per unit area is high. Uimen' profile is a typical section (Vorob'ev 1974a). It is largely a duplication of Kyga profile with respect to vertical zonation and structure of stands. The above data are adequate to recognize the test plots 19 with stands similar to those of Kyga: Kyga, 2^{a}—Uimen', 1; later, 4 and 2, respectively; 8^{a} and 3; 21 and 6^{a}; 13 and 8.

At the same time, Uimen' profile is close to that of Kamga since the boundaries of vertical subzones in them almost coincide. The intermediate position of Uimen' profile reflects the features of transition from one to another type of vertical zonation.

Pyzha-south Teletsk region on the whole is more completely represented by pine-type forests (Krylov and Rechan 1965). Green moss, specially reed grass-green moss, wood fern-green moss, etc. types represent the most widely distributed groups here.

Chulyshman-Chul'cha pine-larch region falls in south-eastern Altay and occupies predominantly the right bank portion of the slopes of Chul'cha river (G.V. Krylov 1961). According to S.P. Rechan (Krylov and Rechan 1965), this territory falls in Chulyshman spruce-pine-larch region.

The climate here is drier than in the other regions described before. Its continental character is manifest in a very sharp variation of temperature during day. The effect of microclimatic conditions is even more perceptible. Thus, while in the northern regions, exposure reveals no specific influence on landscape distribution, forests here are markedly confined to certain slopes. Pine forests are concentrated toward shaded sides while larch forests are attracted to the brighter side.

Forests are grouped mainly in two subzones: lower subzone with larch (1200–1600 m above sea level) and the upper with pine-larch (above 1600 m). Forests of the lower subzone cover the steep slopes of Chul'cha river valley while those of upper subalpine subzone occupy the levelled area within which can be distinguished isolated hillocks and ridges between the internal network of small rivers.

Valleys in the upper reaches of the main tributaries of Chul'cha river (Sur'yaza river) are quite clear and broad. They are surrounded outwardly by a belt of larch forest consisting of sparse main canopy with profuse undergrowth of larch in pockets, clearances, and around glades. The midportion of slopes is covered by mixed pine-larch and larch-pine forests, with pine predominating in the undergrowth; larch is sparse and underdeveloped in the undergrowth. Trees in the main canopy are affected by rot and often damaged by fire. As early as in 1938, M.V. Zolotovskii concluded that larch was being displaced there by pine and the region tended to be transformed into a pine forest.

An analysis of the stand characteristics made in collaboration with I.A. Korotkov helped draw several conclusions (Table 9). Firstly, the predominance of green moss-cowberry types with both pine and larch in their formation is striking. Pure pine forests are represented by berry-moss and larch types. The physical characteristics of stands are considerably inferior than in forests in the northern regions falling at the same altitudes. Trees are predominantly small-sized, with average age under 200 years, and quality index often only 20 V^a. The seed-bearing portion of the forest is generally 30–50% while the total number of trees is large. Crowns are poorly formed and the small-sized portion of the stand is fast vanishing.

The region is quite interesting from the viewpoint of pine cone production since the conditions for its growth here are less favorable than in the regions described above; nevertheless, pine penetrates here significantly. In this context, an important question is the extent of self-seeding of pine under these conditions and the possibility of its further advance into the larch zone.

The above description of the regions can be supplemented with some general information. Considering the territory of north-eastern Altay as a whole, it can be divided into subzones roughly as follows: black soil subzone about 30%, mountain-taiga 50%, and subalpine 20%. On the whole, pine covers 47% of the territory, fir 18%, and rest of conifers 3%; deciduous, mainly, birch 32%. The density variation of plantations is rather insignificant in the subzones. Significant variations are observed in their productivity. Thus, in
21 the black soil subzone, the average quality index is II, 8, in the mountain-

20 Table 9. Physical characteristics of forest stands in Sur'yaza profile

No. of test plots	Quality index, forest type, m above sea level	Composition	Density	Age, years	Height, m	Diameter, cm	Reserve, m³/ha	Trees, No./ha
			Larch forests					
1	V	8L	0.90	190	17	26	300	480
	Green moss-	2P					50	180
	cowberry, 1600							
4	V^a	8L	0.72	180	14	18	170	400
	Green moss-	2P					40	340
	cowberry, 1550							
6	V	9L	1.10	150	20	24	320	800
	Green moss-							
	cowberry, 1600	1P			16	16	40	280
			Pine forests					
2	V^a	9P	0.60	300	16	29	260	500
	Green moss-	1L					30	100
	cowberry, 1650							
3	V	6P	0.75	218	16	23	150	350
	Green moss-	4L					100	220
	cowberry, 1630							
5	V^a	8P	0.50	340	11	18	100	470
	Larch forest,	2L					20	200
	1670							
7	V	10K + L	1.20	160	13	23	230	880
	Berry-moss,							
	1800						15	40

Note. P—pine, L—larch.

taiga III, 2, and in the subalpine IV, 2. The average age is 180 years, with the much older forests concentrated in the black soil and subalpine subzones.

When analyzing the growth conditions of Siberian stone pine in the mountains, a comparison of the various climatic indexes within the longitudinal segment of southern Siberian mountains would be of interest. It is not intended to provide complete details of variations but to indicate the overall trend of climatic changes and structure of pine forests and provide comparison with the ecological segments examined above. Keeping this in mind and the need to bring as close as possible the objects compared to the conditions of our region, the longitudinal segments in which investigations on pine, specially its cone production, were carried out more completely were chosen as reference points. On this basis, the following regions were selected:

North-eastern Altay—investigations of A.I. Kalyaev and V.V. Krinitskii (1961) and our own investigations (1962–1982);

Western Sayan—Dzhebatsk-Borussk region after D.I. Nazimova (1975) (Iroshnikov 1963a);

Eastern Sayan—north-western regions in Mana river basin (Iroshnikov 1963b) and north-eastern regions in Belaya river basin (Krest'yashin 1966); and

Trans-Baikal—south-western regions in Krasnyi Chikoi river basin (Zubarev 1961, Kozhevnikov 1963, and Sitnikov 1964).

As in north-eastern Altay, midmountain *topography* predominates in the eastern mountains of southern Siberia (Mikhailov 1961). However, pine forests mostly tend to be confined to the extensive ridges, slopes, and flat ascents in the somewhat levelled lower portion of the macroslopes, thus rendering them more accessible for exploitation than in Altay or in western Sayan. The following forests fall under such topographic conditions: Mana pine forests in eastern Sayan (Iroshnikov 1963b), Belaya pine forests at the border of eastern Sayan and mid-Siberian plateau (Povarnitsyn 1944, and Krest'yashin 1966), Krasnyi Chikoi pine forests in western trans-Baikal (Zubarev 1961, Novosel'tseva and Utkin 1963, and Kozhevnikov 1963), and others.

Daylight increases perceptibly toward the east of Altay-Sayan system. In western trans-Baikal (Kozhevnikov 1963), for example, the average duration of sunshine amounts to 72% of the maximum possible value but does not exceed 59% in the upper parts of Altay mountains and that too in the least humid regions (Kosh-Agach).

Atmospheric *temperature* regime changes such that heat availability in the vegetative season increases from west to east (Table 10). This, however, is not the same in the different altitudinal segments of mountains. Temperature rise toward east is mainly noticed in the lower part of mountains, less marked in the midportion, and least in the upper portion for the same height. As a result, the lower and upper portions of the megaslope of southern Siberia are less homogeneous than the midportion in which the bulk of mountain pine forest massifs are located. 22

The variability of atmospheric temperature decrease along the altitudinal profile forms the basis of these variations. In the western, less continental regions, the thermal gradient does not exceed 0.5° and is distinctly higher in the eastern parts. As a result, the heat availability in the higher parts of mountains in the east changes more sharply than in the west.

It is significant that the variation of atmospheric temperature regime is the same along the longitudinal section of the northern megaslope of southern Siberian mountains (from west to east) and the latitudinal section (from north to east in north-eastern Altay region). The similarity of these profiles

22 Table 10. Variation of mean atmospheric temperature within the longitudinal profile of mountains of southern Siberia (July)

Region	Station, m above sea level	Temp. gradient	Part of mountains		
			lower	middle	upper
North-eastern Altay (Vorob'ev 1965)	Yailya, 441	0.35	16.2	13.6	11.5
Western Sayan (Protopopov 1965)	Ermakovskaya, 300	0.50	18.8	14.3	11.3
Eastern Sayan (L.I. Malyshev 1965)	Irkutsk, 480	0.50	17.5	13.9	10.9
Trans-Baikal (Novosel'tseva and Utkin 1963)	Krasnyi Chikoi, 766	0.75	17.4	14.2	9.7

Note. Temperature is given for the lower portion of mountains at the level of the base stations (long-time mean data); for the midportion (1200 m) and upper portion (1800 m), it has been calculated from the thermal gradient (a gradient lower than shown in the reference cited has been adopted for trans-Baikal).

suggests that, to some extent, these represent a duplication of the same type of ecological series.

Such a pattern can be equally relevant to the variation of the quantum of *precipitation.* It should, however, be understood that the fall of atmospheric humidity and soil moisture toward east is not as sharp as it appears at first sight. In the region of Teletsk lake, for example, the annual rainfall exceeds 800 mm while at Ermakovsk village (western Sayan) it drops to 474 mm (Protopopov 1965) and does not exceed 400 mm in the south-western Chita province (Novosel'tseva and Utkin 1963). At the same time, in the east, the warm season receives up to 95% of the annual total precipitation but is not more than 60–70% in the west. Moreover, in the trans-Baikal, about 30–60% of the total precipitation is recorded in July–August (V.M. Zhukov 1959). The monsoon coincides with the maximum thawing of the permafrost, ultimately causing excessive soil moisture and increasing the flow of rivers. The poor rainfall here prolongs the duration of clear and cloudless days
23 resulting in a large quantum of solar radiation, specially in the upper part of mountains. To some extent, it compensates for the deficiency of heat, which was discussed above.

This profile as a whole represents a transition from regions with distinct cyclonic climate in the west to anticyclonic climate in the east. Similar climatic variations are characteristic of the latitudinal profile of north-eastern Altay from north to south.

The similarity of the profiles under comparison is also seen in the nature of variations of woody vegetation. Within north-eastern and particularly south-eastern Altay, black soil pine-fir forests predominate in the northern cyclonic regions covering the lower portion of the megaslope; in the southern regions, under the influence of anticyclones and located in the midportion of megaslope, pine forests admixed with fir predominate. Even more southward, in south-eastern Altay, pine forests are found together with larch forests. In general, a similar variation of woody vegetation occurs within the longitudinal profile of southern Siberian mountains from west to east. This similarity to some extent is responsible for the transition from a predominance of forests of mixed ages to nominally same-aged forests due to the predominant role of pyrogenetic factor in these directions and is responsible for a more frequent succession of stands under conditions of an anticyclonic compared to cyclonic environment. The importance of the biotic factor, i.e. the presence of fir in the humid and larch in the relatively arid regions, also acts in a similar manner within the profiles studied.

The broad spectrum of conditions for the growth of Siberian stone pine in the mountains and plains necessitates establishing the distribution range to different extents of detail and the homogeneity of the territory so as to organize and manage a differential economy. The zonation and the plan of economic groups of Siberian pine forest types drawn by the Institute of Forests and Timber have taken into consideration these problems. An essential difference in the case of mountains is the combination of the above-discussed longitudinal heterogeneity of pine growth conditions which forms the basis for recognizing some parts of the range into independent regions and vertical zonation representing their internal content (Polikarpov 1966 and Vorob'ev 1974). The altitudinal and zonal types of forest complexes (Smagin 1980) have come to be regarded as an integrated system.

Many such altitudinal and zonal complexes have now been recognized in southern Siberian mountains: subtaiga-forest steppe, mountain-black soil, mountain-taiga, and subalpine-taiga complex under bald peaks (Nazimova, Polikarpov, and Cherednikova 1981). Each of these complexes should adopt an appropriate system of forest management (Polikarpov 1966 and 1981) based not only on a consideration of eco-geographic characteristics of pine growth but also its bio-ecological properties as a woody species. A study of the different growth aspects of Siberian stone pine under standard as well as experimental conditions would be of interest.

CHAPTER II

Cone Production and Growth of Siberian Stone Pine

The relationship between growth and reproduction of higher plants depends on several factors and has been studied for long (Tumanov and Gareev 1951 and Tsel′niker and Semikhatova 1957). Such studies on woody plants, including pines, have lagged behind those on herbaceous plants in quantitative as well as qualitative terms. Enough to say that there is no single monograph nor adequate number of original publications in spite of the fact that the relations between growth and cone bearing in woody (specially coniferous) plants are important for crop control. While this problem is quite satisfactorily handled in the case of herbaceous plants grown for foliage or fruits, by intense and short-term modification of metabolism for activating the regenerative processes, this procedure faces many difficulties in the case of conifers due to the prolonged life span.

In this context, it has been suggested that the theoretical principles of regulating sexual reproduction in woody plants should be related to establishing the optimal correlations between regenerative and growth processes in the background of their prolonged life span.

The results of our earlier investigations (Vorob′ev 1974b) also point to the usefulness of such an approach. It has been demonstrated in experiments with the tapping of pine trees that a one-sided approach to crop control by creating favorable conditions for cone production temporarily holds no promise because it leads ultimately to a weakening of growth and, later, of regenerative processes. It is therefore necessary to find such relationship between growth and cone production which would help in realizing a moderately high but adequately stable crop over a prolonged period. It is this aspect that holds, in our view, the maximum theoretical and practical interest (Vorob′ev and Vorob′eva 1980).

In the plan of relations between growth and cone production, a study of the effect of the extent of reproductive activity on the growth of shoots and later their condition during cone production is important. Its dependence on the extent of preceding growth of shoots has been demonstrated on Scotch pine (Pravdin 1950), English oak (Minina 1954 and Polozova 1957) as well as in apple tree (Tsel′niker and Semikhatova 1957, Chilikina 1965, and Kolomiets 1966). It has been shown that a certain optimum level of shoot growth is essential for it to bear fruit. At the same time, the duration in which this optimum is achieved is also important since flower primordia begin to form in the background of weakened apical growth (Bucovac 1963, Batjer et al. 1963 and 1964, Verzilov 1974, and Minina and Lanionova 1979) or its cessation (Tseluiko 1964).

The area of leaf surface is also important. According to the observations of Z.Z. Gareev (1970), flower buds in apple form at the center of dense leaf rosettes: if the growth of rosette is poor, the bud remains vegetative.

A number of studies have also investigated the influence of cone production on the current growth of trees. It has been shown in particular that the growth of trunk diameter decreased in the year of crop maturity in deciduous (Holmsyaard 1955) as well as coniferous species (Danilov 1953, Eklund 1956, Eis et al. 1965, Kuz′mina 1968, Zviedre and Vanags 1975, and Chalupka et al. 1975, 1976, and 1977). However, these investigators have not examined the consequences of this reduction on subsequent cone production and the growth of crown metameres.

The variation of shoot growth under the influence of seed production represents the overall result of the effects of sex development and further development of regenerative processes. The importance of sex development for shoot growth was reported many times in literature (Makarov 1954, Orlenko and Syromyatnikova 1958, Dzhaparidze 1965, Kochanovskii 1968, and Lapa 1971). In the case of pines, differences in the morphometric characteristics of shoots and male and female specimens have been demonstrated (Pravdin 1950 and Minina 1975). In the case of English oak, a positive correlation has been established between female sex development and apical shoot growth (Polozova 1957 and Minina and Polozova 1962). This phenomenon was later confirmed for Scotch pine (Minina 1960 and 1975 and Kozubov 1974) and Siberian stone pine (Pravdin 1963 and Nekrasova 1967 and 1972). It has also been demonstrated that the weight of needles in a female shoot of Scotch pine is more than in a vegetative shoot (Osetrova 1975).

The growth of shoot diameter is ensured at first by the division and elongation of cells in the primary meristem of cone. With the completion of linear growth, the factor of cell division in the zones of secondary meristems—cambium and phellogen—as well as the rate of differentiation of phloem and xylem acquire increasing importance. A study of the cambial activity in different woody species showed that the rate of cambial division, and not the duration of its functioning, is more important for increase in diameter

(Lobzhanidze 1961). The size and thickness of cells are associated with the ecological and other growth conditions (Wodzicki 1960 and 1971). Among the latter may evidently be placed sex development and nutrition of reproductive shoot.

Information on the dependence of the cambial activity of shoot on its sex are found in the literature. For example, in balsam fir, removal of reproductive buds reduced the cambial growth (Little et al. 1974). In the axis of year-old shoots of Siberian spruce, the diameter ratio of individual tissues depended on whether the buds are vegetative or reproductive 26 (Skupchenko 1979). The large diameter of female shoots compared to the vegetative shoots in Scotch pine (Pravdin 1963, Nekrasova 1972, and Varnell 1976) and stone pine (Nekrasova 1967) should evidently be regarded as a result of the combined effect of sex development and nutrition of reproductive organs. Conclusive evidence is lacking on the role of each of these factors as also on the effect of nutrition alone on diameter of one- and two-year-old cones and its constituents in the growing shoot (Vorob′eva and Vorob′ev 1982).

Contrary to the influence of sex development, nutrition of reproductive organs in the year of seed maturity reduces the number of buds, leaf size, and shoot growth in paper and yellow birch (Gross 1972) as well as in common Douglas fir (Ebell 1971), affects the seasonal dynamics of storage and consumption of dry matter in the leaves of English oak (Eremich and Minina 1960), and reduces the needle weight in balsam and silver fir (Morris 1948 and Rehfuess 1970). These changes are important because the reduction of photosynthetic reserves in the leaf system, as demonstrated on the example of yew and Scotch pine, would result in a subsequent reduction in autumnal growth of shoots (Giertych and Maciej 1970, Splittstoesser 1971, and Olifonboba et al. 1973).

According to T.P. Nekrasova (1972), the growth of one-year-old cones in pine with the reproductive cycle extending into two vegetative seasons enhances the apical growth of shoots formed while that of two-year-old cones reduces it (Kobranov 1907 and Nekrasova 1972). However, as in the case of the increase of shoot diameter, these investigators did not differentiate the effect of sex development and its magnitude from that of nutrition of cones and seeds. A study of the role of these factors individually showed that the growth of one- and two-year-old cones and their quantum did not exert any significant influence on the growth of female shoot length (Vorob′eva and Vorob′ev 1982).

A study of the physiology of reproductive activity of woody plants promotes understanding the role of cone production in shoot growth.

From this viewpoint, the influence of crop along with other factors was studied by modifying the content of plastic and hormonal agents (Zahner et al. 1964, Richardson 1964, and Brown 1970 and 1974) as also by increasing

the flow of assimilates. The importance of the latter as a factor integrating the physiological processes in plants was demonstrated in foreign (Halbshaw 1973 and Chatterton et al. 1980) and Russian (Turkina and Pavlinova 1981) studies. However, the importance of growing fruits is not restricted to changing the extent of nutritional requirements and corresponding control of their transport. Active involvement of fruits in the metabolism of the organism as a whole is supported by recent evidence. The flow of carbohydrates, for example, in acropetal and basopetal
27 directions has been demonstrated in the ripening uva (Durmishidze and Bernashvili 1973). It is also known that fruits at different stages of growth represent the source of auxins (Rakitin 1976) while fertilized ovules become sources of gibberellins (Luckvill 1964). On the whole, the growing fruits modify the amount and ratio of plastic and hormonal compounds in the tissues of vegetative organs. These compounds determine the direction and rate of conversions of the most important compounds, specially carbohydrates.

The effect of reproductive organs on carbohydrate content was studied essentially in fruit-bearing plants. It has been demonstrated on the example of apple trees that, in a crop year, the content of plastic substances in buds, bark, and wood is more than in the same organs in a barren year (Chindler 1960). In shoot metameres (leaves and pith) with fruits in summer and autumn, the content of sugars is much higher than in shoots without fruits (Poul 1970). The growth of reproductive organs alters not only the quantity but also the pattern of carbohydrate storage and its transport from the leaf system (Kazaryan and Gevorkyan 1974, Kazaryan and Mnatsakanyan 1974, Kazaryan and Arutyunyan 1966, Brown 1973, and Bradbury and Hofstra 1977). Correlations were established between the intensity of this transport and the rate of utilization of plastic substances in the consuming organs (Anisimov et al. 1976); a relative freedom for the utilization of metabolic products within the shoot and absence of their regular flow between different shoots were also established (Jacques 1972 and P.I. Yushkov and V.I. Yushkov 1974).

Unlike in the fruit-bearing trees, the status and conversion of carbohydrates in the reproductive shoots of pine have been less studied. A comparison of the dynamics of mono- and oligosaccharides in the period of intense growth in needles and pith of growing and female shoots of Siberian stone pine did not reveal quantitative differences (Nekrasova 1967 and 1972). According to the data of this author, the course of reproductive processes is manifest only in a reduction of carbohydrate content in the female growing shoots during crop maturity (latter half of July-August). The ratio of oligo- to monosaccharides in the reproductive shoots (male and female) of Siberian stone pine is higher than in the growing shoots throughout the growing season and specially during the period of vertical growth

(Vorob'eva 1974). The storage of oligosaccharides at the end of growing season in female shoots compared to vegetative shoots has been noticed in Scotch pine (Osetrova 1975).

Information is not available on the variation of the qualitative composition of carbohydrates and their quantity in shoots of Siberian stone pine under the influence of nutrition of one- and two-year-old cones in the period of active vertical growth of axis. Nevertheless, the duration and intensity of material conversions determine the biochemical cycles of metabolism and corresponding changes in the subcellular structures. The direction of these changes in the apical bud determines the further growth and seed production. It has been demonstrated that in conifers the bud formation coincides with the period of active elongation of the growing shoot (David et al. 1971). Evidently, changes of composition and quantity of 28 nutrients as well as the rate or magnitude of shoot growth in the period under consideration are reflected on the course of processes occurring in the bud. A knowledge of the direction and extent of these variations as well as their influence on bud formation is essential for solving the problems of reduced periodicity of cone bearing. Thus, one of the problems studied in this book concerns the morphological and physiological parameters of shoot growth in Siberian stone pine under the influence of sex development as well as nutrition of one- and two-year-old cones individually and collectively.

In relation to the study of the reproductive phase of ontogeny of conifers, attention was drawn to the growth and characteristics of its commencement in young Siberian stone pine trees. Information on ecological and genetic characteristics of the ratio of growth and cone production of shoots was also collected.

In all these cases, investigations involved a study of the ratio of growth and cone production in order to use this information for crop control, theoretically rationalize the comprehensive utilization of the main produce of pine forests (nuts and timber), and organize specialized plantations based on the principles of optimal combination of outstanding features.

Cone Production and Shoot Growth

Morphological Characteristics of Process Relations*

Sex development in shoots. Seed output of woody plants largely depends on the form and structure of the reproductive part of crown. The extent of the latter, in turn, depends on the quantitative ratio between shoots of different

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*N.A. Vorob'eva and S.N. Goroshkevich collaborated in the preparation of this section.

sexes. The problem of seed output from any viewpoint thus inevitably involves the problem of sex development (Minina 1974). While discussing this subject, attention was chiefly devoted to the importance of growth in determining the sex of shoots.

The investigations showed correlation between the sex determination of shoots with the growth activity. It has been established, specially in the case of conifers, that younger branches of lower orders are predominantly female and older branches of higher order conversely male (Nekrasova 1961 and Pravdin 1963). In these directions, shoot growth decreases with respect to all the parameters, with phytohormones playing a definite role. According to E.G. Minina (1974), the high activity of auxins and insignificant content of gibberellins are characteristic of female tissues; the male tissues exhibit a typical direct relation with the content of gibberelin-like bodies (GLB).

These patterns are generally also characteristic of Siberian stone pine. Following a study of some specimens, a specific model of relation between
29 growth and sex of shoots was evolved in order to use its parameters for objective control of growth as well as reproductive processes.

The arrangement of shoots of different sexes in a common age series and order of branching reveals the relation of their sex development with the ontogenetic growth curve (Fig. 2). A characteristic feature was the increased growth of shoots of primary branches even at the commencement of their development. Female sex development which is initially unstable due to inadequate growth and physiological immaturity of shoots is typical for these conditions. After passing through the peak of maximum growth, shoots assume a typical feminine appearance and optimal growth parameters: length 7–18 cm and

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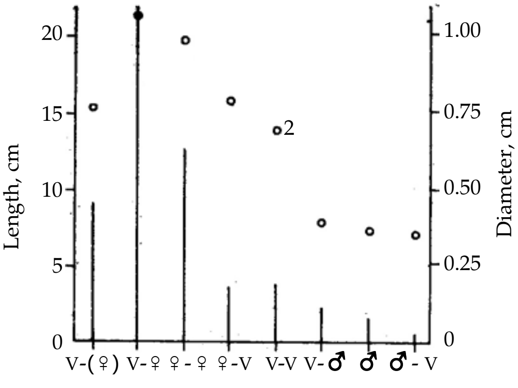

Fig. 2. Ontogenetic model of relation between growth and sex of shoots: 1—length and 2—diameter of growing axis.

diameter 0.9–1.1 cm. The cessation of the formation of primordia due to the aging of shoots or increase of the order of branching is preceded by a slow-down of the linear growth of shoots up to 25% of their maximum value at the commencement of development.

The cambial activity of shoots exhibits a different behavior. A characteristic feature is the delayed slow-down of growth energy, mainly on transition of shoots from growth activity to male sex development. As a result, the range of female sex development with respect to the cambial activity of shoots is broader than male organs. It is also evident from the model depicted that the cambial activity of shoots remaining at a high level (0.8–1.1 cm) can ensure the formation of female primordia even when apical growth is significantly below the average annual growth level.

30 The weight of needles and axis changes sharply conforming to the linear variations of shoots (Table 11). Suffice to say that, on the slowing down of (♀-V) female sex development of pine shoots in the black soil subzone, the weight of needles falls compared to the period of its maximum activity

30 Table 11. Main morphometric characteristics of female and lateral shoots (according to subzones)

Shoot type and its characteristics	Type of female shoots					
	V-♀		♀-♀		♀-V	
	black soil	sub-alpine	black soil	sub-alpine	black soil	sub-alpine
			Female shoots			
One-year-old						
axis, gm	21.0	12.5*	13.0	3.0*	2.0	1.0*
needles, gm	37.0	13.0	14.5	7.0*	9.0	3.0*
length, cm	25.0	12.5	12.5	5.2*	4.0	2.8*
diam., cm	1.0	1.0	1.0	1.0	0.6	0.6
Two-year-old						
axis, gm	36.0	11.0*	17.5	6.0*	2.0	1.5
needles, gm	44.0	19.0*	21.5	12.5*	8.0	6.0
diam., cm	1.3	1.2	1.2	1.3	0.8	0.8
			Lateral shoots			
One-year-old						
axis, gm	2.1	0.9*	1.4	0.3*	0.4	0.1*
needles, gm	9.3	2.4*	3.3	1.1*	1.6	0.3*
Two-year-old						
axis, gm	3.1	1.0*	1.4	0.7*	0.3	0.1*
needles, gm	9.1	3.0*	5.0	2.3*	1.3	0.8*

Note. Here and later, in the tables, significant differences between the variants compared have been asterisked (*).

(♀-♀) by 1.6 times and of axis by 6.5 times. These changes are particularly marked in two-year-old shoots which are known to be the main source of cone nutrition. Here, the nutrient consumption for crop maturity and for maintaining the optimum level of growth of young needles and shoot axis is so significant that the weight of two-year-old needles falls by more than 2.7 times below the standard value. Compared to the weight of shoots at the commencement of cone bearing, their reduction amounts to 5.5 times.

In the background of these changes, not only a slight drop of the diameter of shoot axis, as stated before, but also a relatively steady "specific" weight of needles (10 bunches of brachy-blasts) are striking. This index decreases considerably only on a significant weakening of female sex development.

Insofar as lateral shoots are concerned, weight variations of axis and needles proceed according to the type of female shoots but in a much sharper form. This suggests that the state of reproductive activity of central shoots is reflected primarily on the lateral formations. A study of their condition has an important bearing on regulating the seed productivity of trees since the periodic involvement of the bulk of such shoots in reproductive activity, in our view, determines the high yield more than the concentration of energy for cone production of a relatively small number of central female shoots.

When evaluating the growth of lateral shoots, the latter were divided into permanently (♀-♀) and periodically (V-♀) reproductive and vegetative shoots (V-V).

An analysis of their apical and cambial growth showed that in case of formation of female primordia, the activity of growth processes increases (Fig. 3). Apical growth remains almost at the level of the annual growth of typical female shoots while cambial growth initially lags before approaching the maximum value. If in the first 1–3 years, there is no formation of primordia, the growth of lateral shoots (initially apical, later cambial) falls sharply. On the whole, the growth rate of central female shoots and variously developed lateral sexual shoots vary significantly, specially in their cambial activity (Fig. 4). Its definite importance for female sex development is traced by comparison with the apical growth of shoots. In the central female shoots, the ratio of cambial to apical growth at 1–2 years of age considerably exceeds the corresponding index for lateral shoots, thus establishing the conditions for the development of female sex. Later, the ratio of shoot growth in thickness and length stabilizes at a relatively static level: in central female shoots in the range 1.5–2% and in lateral shoots at 1–1.5%.

The weight of needles of lateral shoots duplicates the size variations of axis according to the characteristics of their sex development. The weight of

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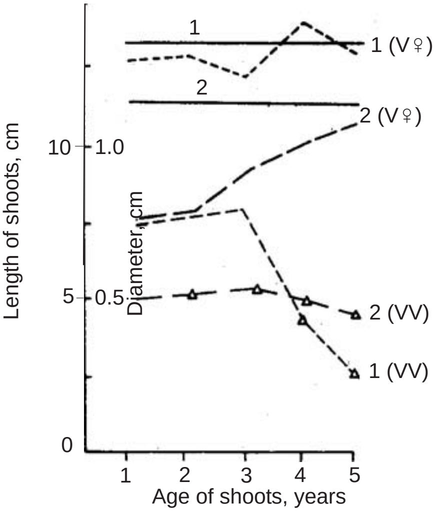

Fig. 3. Growth variations of lateral reproductive (V-♀) and vegetative (V-V) shoots relative to their age:
1—apical, 2—cambial. Straightlines on top—average values of the growth of typical female shoots. Triangles here and later denote significant deviations from the variant compared.

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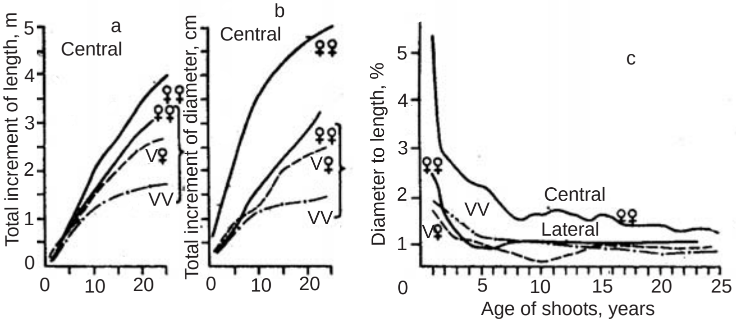

Fig. 4. Growth and its relation (c) in shoots of different sex types relative to their age: a—apical, b—cambial.

needles in shoots beginning to bear seed by five years is the same as in typical female central shoots; shoots without primordia at the commencement
32 of growth have needles weighing 80% less by the same period.

Thus, while on one hand, the initial level of optimal growth of a part of lateral shoots (not less than 0.75 cm in diam. and 10 cm long) determines their female sex development, the formation of primordia on the other hand stimulates the further growth processes. In this background, the effect of formation of female primordia in the productive years is particularly important. The massive onset of cone production of lateral shoots in these periods promotes the growth of female reproductive stage, i.e. the formation of productive crowns of trees. In the nonproductive years, the bulk of lateral shoots does not experience the impetus for sex development and remains as vegetative shoots. Efforts to stimulate sex development should therefore be made first for improving the growth of most developed lateral shoots and later for inducing the formation of female primordia. In this direction, the practice of decapitating a part of lateral buds and shoots holds promise. However, the trimming of leading shoots or restricting the growth of crowns in general leads to a temporary but significant loss of a part of the seed output of the trees and to subsequent restoration of the original parameters of reproductive stage. Such results were recorded in our trials as well as in several other studies (Alekseev 1979 and Beloborodov 1979).

A poor growth of some lateral shoots excludes female sex development and greatly restricts male sex development. In the latter case, evidently the position of shoots in the crown and the type of branching play a decisive role. A comparison of vegetative lateral shoots from the upper part of the crown and typically male shoots from the central portion reveals their nominal similarity with respect to growth indexes but a sharp difference in their regenerative development (Table 12).

32 Table 12. Main morphometric characteristics of vegetative and male shoots

Shoot component and its characteristics	Type of shoots		
	V	♂	♂-V
	Year-old		
Axis			
length, cm	1.18	1.25	0.17*
diam., cm	0.51	0.45	0.40*
weight, gm	0.28	0.25	0.13*
Needles			
weight, gm	1.28	1.40	0.76*
	Two-year-old		
Axis			
diam., cm	0.56	0.54	0.47*
weight, gm	0.25	0.32	0.17*
Needles			
weight, gm	1.61	1.70	0.88*

The evidence presented shows that, for male sex development too, there is an optimum growth below which the appearance of male cones bears a periodic character. Shoots of this type have maximum size with respect to the parameters of annual growth and needle weight. As in the case of female shoots, the most significant growth changes in male shoots are associated with the progressive weakening of apical activity. Subsequent worsening of cambial growth impedes the male sex 33 development of shoots.

The foregoing discussion suggests that the optimum growth of male shoots is restricted to maximal and minimal values. Their variations under the influence of one or the other conditions affect the productivity of pollen regime of trees, thus confirming the cyclic occurrence of this phenomenon, importance of growth in it, and the need to maintain it at an optimum level. In the latter case, it should be borne in mind that special measures are needed for optimizing the female and male sex development of trees. In this context, a study of the different aspects of the dynamics of shoot growth describing the range of their parameters and relation with the level of reproductive activity is of special interest.

Apical growth. The effect of reproductive organs on apical growth of shoots has been considered to involve two main components—evocation of apex (inducing female primordia) and development (growth and nutrition) of one- and two-year-old cones.

The importance of the latter factor for shoot growth has not been completely understood. T.P. Nekrasova (1972) for example considered that the development of strobili stimulates the linear growth of central and lateral shoots in Scotch pine. The evidence presented on this subject, however, projects a more complex picture of the above phenomenon than it appears at first sight. It is only evident that the central shoots are significantly longer than lateral. Insofar as the role of strobili in the linear growth of shoots is concerned, their stimulating effect on central shoot has not been confirmed since the differences between the length of shoots with and without strobili were insignificant. The positive role of strobili is evident only during their development on lateral shoots but the primary cause of this relation—evocation of apex or the current effect of strobili—in this case is not clear.

The author studied these aspects in Siberian stone pine in time, i.e. taking into consideration the extent of preceding and current cone production of shoots. In the background of different combinations of crops, it has been found that strobilus development on central female shoots does not exert a significant influence either on the dynamics of their apical growth or on the end parameters. The growth of shoots in all cases—with strobili fully preserved or fully fallen—remains unchanged.

The positive association between the presence of strobili and lateral shoot growth in Scotch pine, in all probability, is a consequence of the formation of female primordia. Such a correlation has been demonstrated by E.G. Minina (1975) on the example of Scotch pine and examined by the author in Siberian stone pine by analysis of evidence on shoot sex development. The following evidence points to the same conclusion, suggesting additionally that the formation of female primordia, their numbers, and subsequent linear growth of shoots, are determined simultaneously and depend appropriately on ecological factors (Table 13). On the whole, apical shoot growth is evidently largely associated with the development processes, age, and stage of their branching than with the subsequent development of strobili. 34

34 Table 13. Linear growth of female shoot relative to the preceding stage of formation of primordia

No. of reproductive organs (primordia)/shoot	Shoot length as % of growth in preceding year	No. of observations
0	79.6 ± 4.2	17
2.5 ± 0.1*	93.3 ± 2.7*	22
4.5 ± 0.1*	112.2 ± 5.7*	28

Note. Strobili and cones absent.

Unlike the latter, the ripening of cones in Scotch pine reduces the length of one-year-old shoots by 10–28% (Kobranov 1907 and Nekrasova 1972). In Siberian stone pine, in our view, the nutrition of the current crop of cones restrains the growth of central female shoots but does not lead to significant changes in their seasonal length (Fig. 5).

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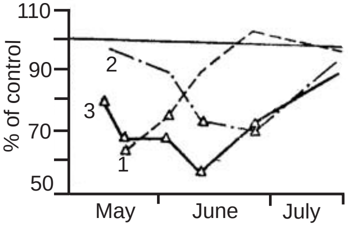

Fig. 5. Apical growth of female shoots with one-year-old (1), current year (2), and two successive (3) crops.

The period of restrained shoot growth noticed occurs in the latter half of June, i.e. the period of maximum activity of reproductive processes (pollination of female strobili of one generation, intense growth of cones, and fertilization of ovules of another generation).

The noticed growth lag under favorable ecological conditions is compensated in July which thus explains the absence of significant variations of shoot length by autumn. Under adverse growth conditions or in case of a bumper crop, this lag may evidently reduce the length of the growing shoot. Examples of such effects will be examined in the subsequent data. In the present case, it is not as much the ultimate result that is important as the mechanism of influence of reproductive processes on growth shoots. As demonstrated before, the latter results in redistribution and "control" of the intensity of growth and reproductive processes in the affected periods of growth.

The adverse effect of two-year-old cones on growth is manifest at the start of the growth of shoots of the following year. When there is no current crop, growth lag is compensated fairly rapidly. When there are two successive crops, the period of reduced shoot growth extends to the end of July.

Thus, the activity of apical growth and the length of central female shoots are independent of the presence or loss of strobili. Insofar as the effect of cones is concerned, their ripening restricts the growth of shoot length in the period of activity of reproductive processes in June but, under optimum ecological conditions, does not result in any significant variation of ultimate length. The extent of apical shoot growth is positively associated with the level of preceding formation of female primordia. The extent of manifestation of this association may vary under different ecological conditions, ontogenetic state of shoots, and other factors.

Cambial growth. The radial growth of shoot axis is determined by a combination of activity and duration of cambial activity together with rate of cell differentiation as well as the magnitude of specialized zones. Fluctuations of parameters of cambial tissue in the vegetative period due to different rates of above processes are a characteristic feature of conifers (Bannan 1955 and Wilson 1964).

In Scotch pine, the maximum cambial activity in one-year-old shoots coincides with the period of completion of linear growth (Antonova and Shebeko 1979). There is poor transition of xylem cells from the cambial zone into the zone of ontogenetic development during this period (Klimas 1969). By the end of July, cambial activity is practically complete and specialization of the cells formed proceeds essentially thereafter (Antonova and Shebeko 1979).

In the growing shoot of pine, the maximum activity of cambial cell differentiation is noticed in the latter half of June. Compared to xylem, the formation of phloem in this period proceeds faster. Such an increase in the frequency of mitoses of cambial derivatives adhering to bast in the middle 10 days of June has been reported in larch (Lebedenko 1970). The increased growth of xylem in pine continues to the end of July. By this period, the shoot diameter attains almost 1 cm, i.e. an average of 70% of its final size.

The reproductive activity of shoots does not affect the overall dynamics of above phenomena but, as in the case of apical growth, advances the period and intensity of individual tissue formation.

Under the influence of strobili, e.g. the diameter of the young shoots increases due to the activity of the growth of phloem and xylem tissues (Fig. 6). The growth activity of xylem is not uniform at all stages of development of strobili. Their growth before formation of strobili promotes the size increase of cambial zone with simultaneous inhibition of xylem formation. The formation of strobili activates xylem formation and the size of cambium
36 decreases. It is also significant that, before formation of strobili, the growth of cambium is noticed all along the shoot length. The presence of crop intensifies the effect of strobili only in the apical portion. After formation, strobili exert their influence only in the lower and middle portions of shoot. Changes in the apical segment appear insignificant.

Nutrition of cones initially activates xylem formation in the growing shoot and later, with the increasing stresses of regenerative processes, retards this process (see Fig. 6). The lag in xylem formation commences from the upper part of shoot axis. In the presence of strobili, it is more evident; nevertheless, by the end of growing season, growth lag is compensated in all cases by its subsequent activation.

Similar tendencies have been noticed in the variation of phloem size. Its growth in May is increased primarily at the base and midportion of shoot but weakened in June. Unlike xylem, growth lag of phloem begins from the base of shoot axis, subsequent compensation corresponding to

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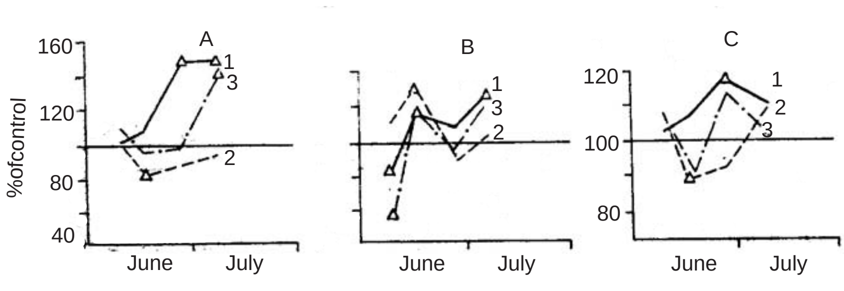

Fig. 6. Cambial growth of one-year-old female shoots under the influence of: 1—strobili, 2—two-year-old cones, and 3—presence of (1) and (2) together. A—xylem, B—cambium, and C—phloem.

it. The extent of lag is more in the presence of strobili than in their absence.

The cambial zone during the period of growth lag of xylem and phloem enlarges significantly. In the absence of strobili, this proceeds more noticeably in the midportion of shoot but in the upper portion as they grow simultaneous with two-year-old cones. The contrasting tendencies of size variations of xylem, phloem, and cambial zone in the period under study suggests that this inhibition occurs due to reduced intensity of differentiation of cambial cells. The commencement of the compensation of the growth lag of xylem and phloem is accompanied by a reduction of cambial zone; its subsequent rise, in July end, in all probability, is associated with the commencement of a new lag of phloem growth.

Consequently, the nutrition of two-year-old cones, without affecting the diameter of the axis of growing shoot, varies significantly in the different periods of growth intensity of tissues. Initially (May), the formation of phloem and xylem tissues is intensified under the influence of two-year-old cones but retarded in the period of active growth (latter half of June). Depending on the ecological conditions and crop size, the shoot growth parameters may be restored by autumn or remain suppressed. The presence of strobili increases the range of these changes.

The formation of xylem tissues is closely associated with the amount of differentiating cells. The contrasting influence of strobili and two-year-old cones on the extent of cambial zone, xylem growth, and number of cells can be quite clearly perceived in Fig. 7. Similar tendencies are noticed in the variations of their cross-section but they are not significant. Under the combined influence of strobili and two-year-old cones, the role of the latter predominates on xylem growth.

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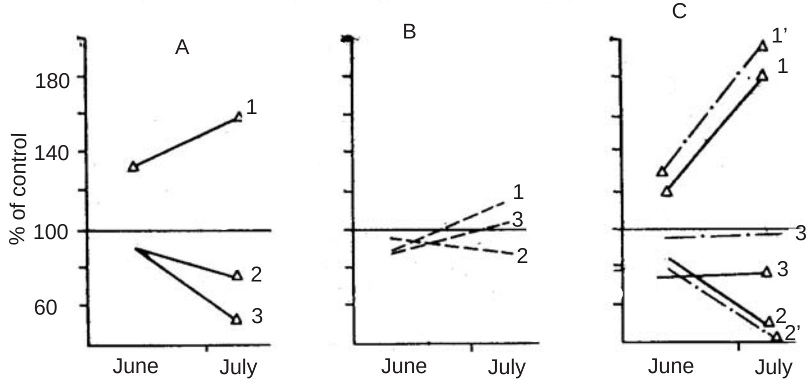

Fig. 7. Growth of cells in the axis of one-year-old female shoot under the influence of: 1—strobili, 2—two-year-old cones, and 3—combined presence of (1) and (2). A—number, B—cross-section, and C—xylem cell size. 1′–3′—cell size in cambial zone.

It is known that the induction of cell division in the cambium and their further differentiation in a growing shoot are controlled by the presence of complexes of indolyl acetic acid (IAA) and gibberellic acid (GA) (Wareing et al. 1964). The ratio of hormone groups and their correlation with a definite state of growth in the shoot, in turn, influence the direction of further bud sex development (Verzilov 1974). It may therefore be assumed that size variations of cambial zone and xylem, which arise in the young shoot under the influence of strobili and cones, provide the preconditions for changes in the subsequent course of growth and cone bearing in the female shoot.

The above influence of two-year-old cones is also reflected on the growth of shoots in the ensuing year. It may be seen in Fig. 8 that the growth of
37 phloem and xylem is impeded from the beginning of growing season and its compensation or even some acceleration (in the absence of current cone crop) begins from mid-June, i.e. after anthesis.

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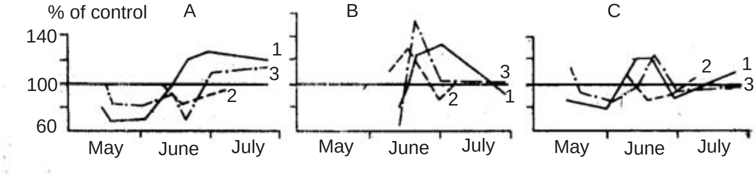

Fig. 8. Cambial growth of one-year-old female shoots under the influence of: 1—preceding, 2—current, and 3—two successive crops. A—xylem, B—cambium, and C—phloem.

In the presence of two successive crops, growth lag of phloem, specially xylem, also begins early and extends until July. In this case, as under the influence of only the current cone crop, the activation of regenerative processes in the second half of June is accompanied by a sharp retardation of xylem growth and corresponding rise of phloem and cambial zone of the growing shoot. On the whole, when many crops are present, the current quantum of cones exerts the main influence on shoot growth. It is manifest for two years
38 after which it is compensated under favorable growth conditions, even in the presence of a new crop.

Content of dry matter. The intensity of accumulation and amount of dry matter, primarily in the elements of growing shoots, is important as an index of the prevailing metabolism and adequacy of nutrient reserves for progressive growth and cone bearing of plants. The available evidence suggests that nutrition of two-year-old cones, independent of the presence or absence of one-year-olds, without influencing the dynamics and final accumulation of dry matter in one- and two-year-old shoot, changes the

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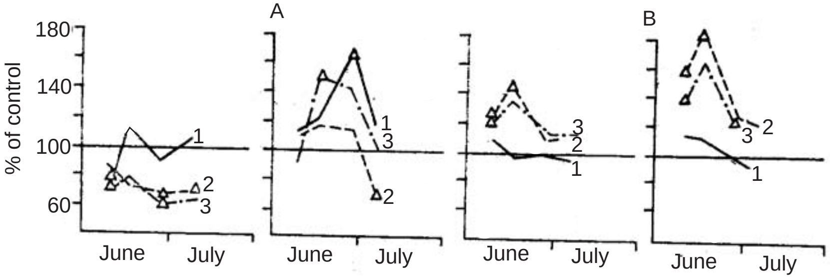

Fig. 9. Weight of needles (A) and axis (B) of one-year-old (left) and two-year-old (right) female shoots under the influence of:
1—strobili, 2—two-year-old cones, and 3—simultaneous presence of (1) and (2).

extent and intensity of growth in different methods of plant development. (Fig. 9).

The weight increase of two-year-old shoot axis is most perceptible in the preparatory period and in the course of fertilization of ovules. Here, evidently, the need for intense transport of nutrients to the growing seeds is particularly important. With the transition of two-year-old cones from active growth to seed maturity, the extent of accumulated dry matter decreases in year-old shoot axis to the initial value while remaining somewhat above it in two-year-olds. These changes combine in the first stage with lag of shoot growth and in the second stage with its activation. The effect of strobili in this background is insignificant.

The ratio of maturing cones also dominates the dynamics of dry matter content in the needle. Their nutrition significantly reduces the weight of the young needle and leads to impaired conditions for future crop formation. The presence of strobili, as in the first case, does not exert any significant influence on the weight of needles of young shoots.

Unlike the foregoing discussion, in two-year-old needles which represent the main source of nutrition to the maturing cones (Dikman and Kozlovskii 1973), their growth determines the main pattern of dry matter accumulation. However, when strobili are absent, this process is not as active as in their presence. Strobili in the latter case stimulate the accumulation process. After anthesis and fertilization, the accumulation rate of dry matter in two-year-old needles decreases to a level characteristic of shoots which are temporarily
39 devoid of reproductive organs.

The observed tendencies of dry matter content are seen not only in the central female shoots but also, in a more distinct form, detected in the lateral shoots, thus suggesting the significant influence of reproductive organs on their condition. Since lateral shoots under favorable conditions begin massive cone production, identifying trees with abundant crop, followed by a study of their condition, as pointed out before, is of great interest. This probably is the reason for the cessation of their cone production after such abundant crops. It is associated with a significantly reduced accumulation of dry matter by the young needles which form the base for the growth of the future shoot and nutrient for the subsequent cone crop. If the observed reduction in central shoots can be compensated to some extent by other factors, it would exert a decisive influence in poorly developed lateral shoots in determining their future growth. Nevertheless, even in relation to the central shoots, the nature of influence of the prevailing cone crop should be borne in mind. When the cone crop is large, it can through this means clearly influence the subsequent course of growth and cone bearing of shoots. The consequences of an abundant crop are felt at least in the ensuing year (Fig. 10).

40 In two-year-old shoot axis, dry matter accumulation in the absence of current crop is delayed up to mid-July. In new shoot axis, this occurs throughout the period of intense growth. Significantly, in the presence of two successive crops, that of the preceding year is of decisive importance. In its presence, the temporary stimulating effect of current crop on the accumulation of dry matter in the axis is not observed. The utilization of

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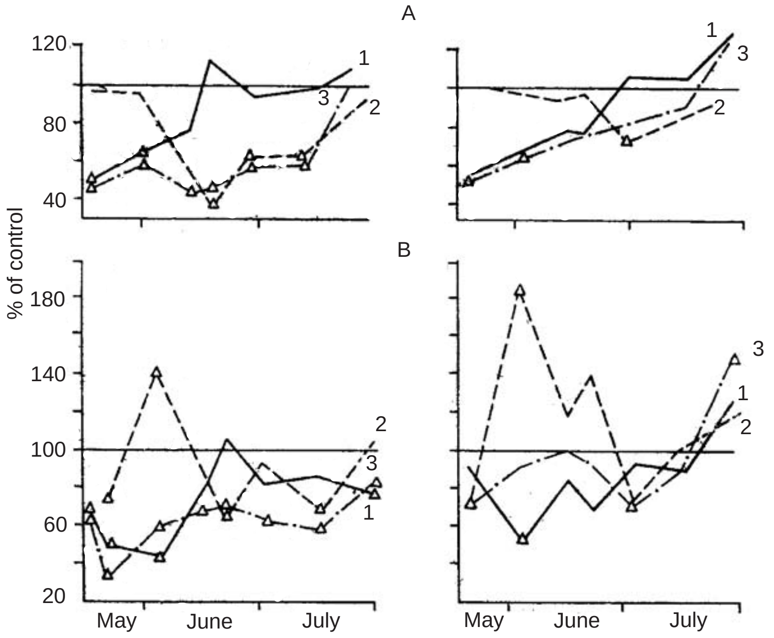

Fig. 10. Weight of needles (A) and axis (B) of one-year-old (left) and two-year-old (right) female shoots in the presence of:
1—preceding, 2—current, and 3—two successive crops.

reserves then attains utmost importance and extends not only to the needle as in the case of current crop but also to the axis.

The preceding crop also adversely affects the dry matter content in the needles of one-year-old shoots. Moreover, in this case, its role is aggravated by the presence of current crop. As a result, in the presence of two successive crops, the reduction of dry matter accumulation in the young needles is prolonged and significant.

Crop size. Neither the material studied so far nor the available literature have explored aspects that reflect on the influence of the quantum of reproductive organs on shoot growth. There is also no simultaneous analysis of the effect of the entire complex of factors studied on this process. These aspects are important for understanding the causes of crop cyclicity and the possibility of narrowing the range of their fluctuations so as to maintain a relatively steady yield of seeds.

In this context, evidence is presented below on the effect of the quantum of strobili and ripening cones on apical and cambial shoot growth as well as on the dry matter content of axis and needles.

The response of shoot growth to the quantum of reproductive organs is primarily associated with the presence and active utilization of nutritional sources. In pines, as pointed out before, the utilization of reserves in the early spring when the photosynthetic activity is poor is of much importance. At this time, the nutrition of ripening cones reduces the dry matter content of two-year-old needles (Fig. 11). Further, there are no differences due to the varying number of cones, i.e. the effect is essentially of the presence of the crop. In June, in spite of the fact that this inflow of assimilation product increases, the dry matter content of the needles of two-year-old shoots bearing cones does not rise. This too points to the utilization of needle metabolites for crop growth.

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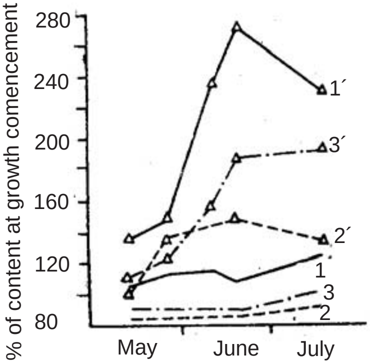

Fig. 11. Dry matter content of two-year-old needles and axis (broken line) of female shoots in the:
1—absence of, presence of 2—moderate, and 3—heavy crop of cones.

In the axis of two-year-old shoots, the dry matter content, unlike in needles, increases invariably, i.e. in the presence or absence of cones. The 41 role of heavy crop in this case is reflected in a smaller accumulation of dry matter in the shoot axis.

Variations of dry matter content of needles and shoot axis suggest that cone crop in Siberian stone pine, like the growth of new organs in Scotch pine (P.I. Yushkov and V.I. Yushkov 1974), forms primarily by expending the reserve matter of two-year-old needles. Shoot axis reserves are evidently utilized to a smaller extent. Moreover, shoot axis as a transport system may partly consume for its own growth nutrients passing through its tissues for the needles. The magnitude of the assimilates supply to the reproductive organs is known to correlate with their consumption (Anisimov et al. 1976), i.e. the flow of transported metabolites in the shoots bearing varying number of cones, varies. This may explain the differences in the growth of one- and two-year-old shoots with different reproductive loads which can be interpreted as the amount of cones or strobili on a shoot.

Observations on the growth of young female shoots confirm the conclusions drawn earlier about the reduced weight of the needles under the

41 Table 14. Growth of one-year-old female shoot in the absence (1), presence of moderate (2), and heavy (3) crop of cones

Growth phase, date of observation	1	2	3
	Length of axis, cm		
Intense, June 10	13.1 ± 1.5	12.9 ± 1.2	12.8 ± 0.1
Latent, July 24	15.3 ± 1.0	17.2 ± 1.7	15.5 ± 1.5
End of growing season, Oct. 16	17.4 ± 2.5	17.1 ± 2.0	17.7 ± 1.5
	Diameter of axis, mm		
Intense, June 10	10.2 ± 0.4	9.4 ± 0.3	9.2 ± 0.4
Latent, July 24	10.8 ± 0.5	10.2 ± 0.7	10.4 ± 0.6
End of growing season, Oct. 16	10.9 ± 0.5	11.5 ± 0.6	11.6 ± 0.1
	Weight of axis, g		
Intense, June 10	10.7 ± 0.2	11.1 ± 1.2	13.1 ± 1.6
Latent, July 24	15.7 ± 2.9	15.4 ± 2.0	14.6 ± 1.8
End of growing season, Oct. 16	21.1 ± 2.7	17.9 ± 3.1	17.5 ± 4.0
	Weight of needles, g		
Intense, June 10	6.7 ± 0.5	5.5 ± 0.6	6.1 ± 0.4
Latent, July 2	23.0 ± 2.5	15.5 ± 1.4*	13.0 ± 2.0*
End of growing season, June 16	38.8 ± 3.5	21.2 ± 3.6*	24.2 ± 2.4*

influence of a crop (Table 14). There is, however, no positive association
with its quantum as also with the size of young shoot axis (weight, length,
and diameter). This does not mean, however, that the crop size has no
bearing at all on the formation of the new shoot. A study of its radial growth
structure shows that the nutrition of a large number of cones reduces cambial
activity at the commencement of growing season. Later, this growth lag is
compensated and, under optimal growth conditions, does not cause any
42 significant deviations of xylem size (Table 15). In two-year-old shoot axis, a
high crop level shifts the increased xylem growth to a much earlier period,
activates cambial activity, ultimately resulting in their larger diameter (mm):
1st variant 12.0 ± 0.6, 2nd variant 13.4 ± 0.5, and 3rd variant 15.5 ± 0.3 (on
Oct. 16).

The role of strobili in the growth of young shoots has its own characteristics. Since, as shown before, in the absence of a crop and at the

42 Table 15. Dynamics of cambial growth of female shoots (mm) in the absence of (1), presence of moderate (2), and heavy (3) crop of cones

Date of observation	1	2	3
One-year-old shoot			
Cambium			
June 10	0.36 ± 0.03	0.38 ± 0.02	0.26 ± 0.01*
June 18	0.36 ± 0.04	0.35 ± 0.02	0.24 ± 0.02*
June 24	0.37 ± 0.06	0.33 ± 0.01	0.39 ± 0.06
July 8	0.33 ± 0.02	0.34 ± 0.02	0.35 ± 0.03
Xylem with pith			
June 10	2.00 ± 0.23	1.98 ± 0.11	1.93 ± 0.09
June 18	2.30 ± 0.20	2.27 ± 0.18	2.17 ± 0.13
June 24	2.40 ± 0.23	2.20 ± 0.33	2.30 ± 0.16
July 8	2.65 ± 0.22	2.60 ± 0.13	2.50 ± 0.51
Two-year-old shoot			
Cambium			
June 10	0.27 ± 0.03	0.31 ± 0.03	0.31 ± 0.04
June 18	0.36 ± 0.03	0.38 ± 0.04	0.39 ± 0.06
June 24	0.33 ± 0.07	0.36 ± 0.06	0.46 ± 0.07
July 8	0.41 ± 0.10	0.42 ± 0.03	0.47 ± 0.11
Xylem			
June 10	0.39 ± 0.06	0.31 ± 0.03	0.48 ± 0.05
June 18	0.59 ± 0.07	0.50 ± 0.06	0.88 ± 0.09*
June 24	0.55 ± 0.07	0.60 ± 0.08	0.87 ± 0.08*
July 8	0.73 ± 0.09	0.74 ± 0.06	0.89 ± 0.10*

level of female primordia remaining as at the preceding level, the nutrition of strobili does not exert any influence on the weight of the needles and linear growth of axis of shoot formed, their high amount naturally does not change these parameters (Table 16). Unlike this, the axis diameter and weight increase under the above conditions. A comparison of the independence of the linear growth of cone-bearing shoots from the number of strobili and the data about the female shoots of Siberian stone pine being usually longer than growth shoots (Nekrasova 1961) once again confirms a much closer relation of the apical growth of shoots with the sex development processes than with the development of strobili.

43 Table 16. Seasonal growth parameters of one-year-old female shoots (mm) in the absence of (1), presence of moderate (2), and high (3) amounts of strobili

Index	1	2	3
Weight of needles, gm	21.2 ± 2.5	23.7 ± 3.2	24.5 ± 2.0
Length of axis, cm	17.8 ± 1.4	17.2 ± 2.3	18.8 ± 3.3
Weight of axis, gm	9.6 ± 0.8	10.4 ± 0.9	12.4 ± 0.7*
Diameter of axis, cm	1.30 ± 0.05	1.26 ± 0.07	1.58 ± 0.03*
Including xylem with pith	0.64 ± 0.04	0.65 ± 0.04	0.83 ± 0.03*

On the whole, the effect of reproductive organs on shoot growth reveals diverse relations between growth and reproductive processes. Thus, if apical growth and weight of shoot metameres correlates with the direction and extent of its sex development, cambial activity is largely associated with the nutrition of reproductive organs. Further, the role of strobili and cones is not the same since strobilus growth enhances and cone maturity depresses
43 cambial activity of axis of young shoot. The ultimate effect of their combined action is evidently largely associated not with the quantitative aspect of the reproductive activity of shoots but with its presence and ecological growth conditions. Under optimal conditions, the consequences of even heavy crops are compensated toward the end of growing season, opening up considerable possibilities to the growing trees for growth and cone production. At least, it is evident that under optimal pine growth conditions, its potential reproductive capacity is not fully realized. Its utilization, as seen from the foregoing discussion, should be related to a more significant shift of the metabolism of trees toward activization of reproductive activity of central as well as lateral female shoots.

Genotypic Characteristics of Process Relations

In the relation of growth and cone production, the genotypic features of shoots characterizing their potential for sexual reproduction are equally important. The heterogeneity of shoots with respect to these characteristics has not been adequately studied although such knowledge is essential for investigating the structure of the regenerative stage of the crown as also for an assured selection of graft material for organizing plantations for high yield or some other valuable properties.

The above role of the quantitative aspect of yield in shoot growth showed that its variation within a time frame depends largely not on the number of cones but on their overall presence, i.e. on the shift of female sex development. These conclusions at first appear at variance with the concepts on the adverse effect of crop size on the growth of trees and with the recommendations emerging from them on defloration of a part of reproductive organs to control the dynamics of cone production.

A detailed analysis of evidence reveals not only the above effect of crop size but also the mechanism of its operation. The latter, as demonstrated
44 before, leads to restraining the apical and cambial shoot growth in the period of maximum intensity of regenerative processes. Under favorable ecological conditions, toward the end of growing season, this effect is compensated by a corresponding growth spurt without any bearing on the ultimate shoot parameters. Genotypic characteristics of trees evidently play no less a role.

The available information shows that shoots with different cone output exhibit dissimilar behavior of apical and cambial growth. The importance of the above transition of shoots from vegetative to reproductive activity is evident (Fig. 12). A significant reduction of the growth of shoot length marks

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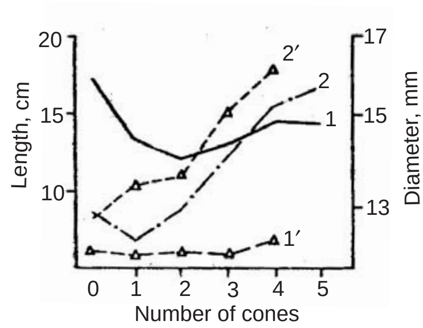

Fig. 12. Growth of female shoots relative to their reproductive activity and conditions of black soil and subalpine (1', 2') subzones: 1—apical and 2—cambial.

the commencement of its stable cone output while further differences between shoots with different productivities are less perceptible since in all cases their sizes are optimal. It is also understandable in this context that any change of reproductive load, with the exception of its total removal has little effect on the growth of shoot length. Keeping this in view, it is necessary to pay attention to the overall increase of shoot length with the rise of its productivity. The latter is important in that the shoots with a large number of cones show enhanced growth, i.e. have the same genotypic condition of optimal combination of characteristics which help in utilizing its properties for selection.

The cambial growth of shoots is also characterized primarily, although weakly, by a reduction of their diameter when the cones begin to be held stably from falling. A significant increase of this index with increasing productivity is an important feature of the growth of shoot thickness. This relation once again points to the dominant role of cambial activity of shoots for their reproductive activity and the advantage of selecting grafts from trees with most developed and productive shoots.

The heterogeneity of cone-bearing shoots on pine trees concerns not only their growth but also the structure of reproductive capacity (Fig. 13). Having examined in this background the ratio of regenerative and lateral primordia, it may be seen that their total number drops by the time the cones begin to be held stably. Subsequently, it increases with respect to the total content of primordia as well as the involvement of regenerative parts. In the background of these changes, the "physiological" drop of strobili decreases to a minimum with increasing growth and shoot productivity. From the
45 foregoing discussion, it is evident that not only the shoots of productive trees

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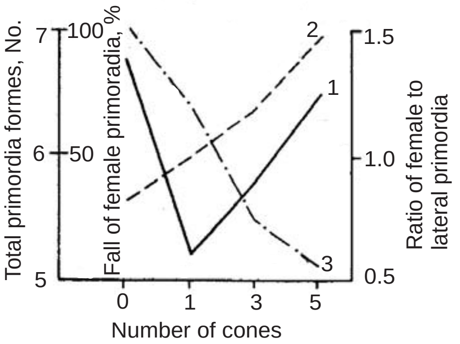

Fig. 13. Ratio of regenerative and lateral primordia in female shoots relative to their reproductive activity:
1—total number of primordia, 2—ratio of female primordia to the lateral, and 3—fall of strobili.

but also those with similar energy of formation of regenerative primordia but not utilizing it either in the period of embryonic growth (primordia of lateral shoots predominate) or at the commencement of postembryonic growth (fall of strobili at this stages touches 100%) meet the genotypic conditions for reproductive activity. The possible reason for it, specially for the fall of strobili, is the predominance of linear shoot growth. According to the available data, the mean annual increment of shoots at which reproductive primordia begin to be held is 13–14 cm. In this case, the ratio of diameter to length is evidently optimal since it exceeds the 5% limit as at the commencement of the age curve of the growth of female shoots (see Fig. 4). The predominance of lateral branching in these shoots and the high fall of reproductive primordia for reasons of growth or some other factors points, from this aspect alone, to the need to take into consideration the genotypic conditions of the characteristics of growth and cone production of shoots on trees.

Ecological Characteristics of Process Relations

The ecological characteristics of relations between growth and cone production of shoots include several aspects. Some of them will be studied when analyzing the cyclicity of processes. Many others can be discussed here on the basis of the preceding material.

It was shown in Fig. 12 that apical and cambial growth of shoots vary
46 differently relative to their productivity under subalpine subzone conditions. While in the black soil subzone, the linear growth of shoots responds to the appearance of cones and intensity of reproductive activity to the maximum limit required for selection according to a given characteristic, it remains practically unchanged in all cases in the subalpine zone. The optimum growth of shoots that is adequate under these conditions for relatively normal cone production varies around 6 cm a year.

Insofar as cambial growth is concerned, its behavior is the same as in the zone of optimum pine growth. This once again reveals the overwhelming importance of cambial activity of shoots for sexual reproduction. As evident from the preceding data, apical growth slows down at first suggesting, among others, the adaptation mechanism of woody plants to the high-altitude conditions (Vorob'ev 1979).

Data on the ontogeny of female sex development also lead to a similar assessment of the role of apical and cambial growth of shoots. Table 11 and Fig. 14 depict the main characteristics of the growth of female shoots in black soil and subalpine subzones. Their comparison reveals a natural drop of most growth parameters including shoot length and weight of axis and needles. The growth of lateral shoots suffers particularly significant variations.

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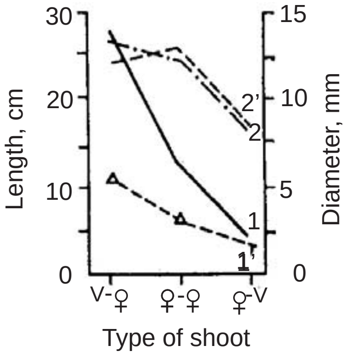

Fig. 14. Growth of female shoots relative to their ontogenetic development and conditions of black soil and subalpine (1′, 2′) subzones:
1—apical and 2—cambial.

But, as in the above case, in the subalpine subzone, the cambial growth of female shoots maintains from the appearance of cones to ontogenetic weakening practically the same parameters as in the optimal zone. The apical growth of shoots falls sharply in this background, confirming the pattern of its behavior detected before. However, this is not as important here as the significant dominance of the growth of shoot length in the optimal zone at the commencement of regenerative development of shoots. The presence of such growth "spurts" creates the background and establishes the need for considerable restriction in the growth of trees so as to generate conditions for accelerated appearance of cones. This also suggests the need for a differentiated approach not only to controlling the regenerative and growth processes but also their various aspects, specially the apical and cambial activity of shoots and trees.

Turning attention to the ecological aspects of growth-cone formation relations, their optimum conditions should be distinguished. Examples of the compensation of growth loss in heavy crop years in the optimum zone of pine growth, high linear growth of shoots accompanying a significant loss of strobili, and several other factors suggest that optimum growth and cone formation do not coincide: excellent growth conditions are found closer to the south and lower boundaries of pine distribution and for regenerative processes slightly farther away. For example, plantations for accelerated raising of timber, taking advantage of the growth potential of pine, should be planned close to the above boundaries in the mountains, specially in the
47 range 450–600, and for nut production 600–800 m above sea level.

The many morphological characteristics of growth and cone appearance on shoots examined above open up some typical relations. Among them, the mechanism of relations between regenerative and growth processes is very important. It would be interesting to analyze the apical and cambial growth of shoots for understanding this mechanism. It is to this area of problems that observations of physiological characteristics of shoots are addressed.

Physiological Characteristics of Process Relations*

Establishing the physiological characteristics of the growing shoot tissues in relation to the nutrition of one- and two-year-old cones is important for analyzing the mechanism of relations between growth and cone production. In this context, not only a quantitative assessment of nutrients, specially of carbohydrates, but also of the possibilities and activities of their utilization in the course of these processes is important.

It is known that the growth stage of two-year-old cones characterized by the fertilization of female gametophyte (Minina and Larionova 1979) matches in time with the phase of shoot emergence from the bud and the commencement of axis growth and elongation. In this period, the shoot axis represents a heterotrophic formation without distinct division into individual tissues. Its developmental parameters were therefore initially studied without division of phloem and xylem.

The nutrition of two-year-old cones in May enhances the starch content by 1.5–2% in the axis of female shoots but simultaneously reduces the total soluble carbohydrates, mainly of monosaccharides, by 4–5%. The content of saccharose and the activity of invertase remain practically unchanged while those of amylase decrease from 11 to 2 nm maltose/mg protein/min. The activity of amylase together with starch-synthesizing systems, according to N.E. Sudachkova (1977), determines the starch variations in pines. Without data on the extent of synthesis of this polysaccharide but on the basis of seasonal dynamics of starch and much information on the concentration of sugars, specially saccharose preceding the starch formation, it can be said that the increase of starch content under the influence of two-year-old cones is not due to its accelerated synthesis but weakening of hydrolysis. It is known that growth commencement in woody species is accompanied by the utilization of starch stored in the tissues of shoot and bud before the activation of growth processes. Consequently, nutrition of two-year-old cones in early spring reduces the utilization of reserve carbohydrates in one-year-old shoots.

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*This section was written together with N.A. Vorob'eva.

Since the availability of carbohydrates for successive metabolism is associated with the dissociation of complex carbohydrates, primarily 48 saccharose up to monosaccharides, the reduction of invertase activity—main enzyme for the hydrolysis of saccharose in the needle tissues—can be regarded as suggesting that crop nutrition also reduces the utilization of soluble carbohydrates.

The fixed value of saccharose and the reduction of monosaccharides in tissues of short axis make for a reduction of mono- to disaccharide ratio which is generally characteristic of conditions accompanying poor linear growth of shoots. As shown before, increased nutrition of cones actually reduces the rate of apical growth. Contrary to this, the radial growth of shoots increases in spite of reduced utilization of carbohydrates in the formation of cell structure. Evidently, this can be explained by the fact that, at this stage, shoot diameter is determined more by the number than size of cells. The increased rate of division of cambial derivatives compared to the activity of differentiation of young tissues has been noticed during this period in the shoots of pine, arborvitae, and larch (Bannan 1950, 1955, and 1962 and Lebedenko 1970).

Thus, the nutrition of two-year-old cones reduces the availability of stored and free carbohydrates to the growth process by reducing the activity of hydrolase during early shoot growth. As a result, the rate of apical growth of shoots falls at this stage.

The growth of two-year-old cones before ovule fertilization (June) enhances the starch and glucose contents in the phloem of one-year-old shoots for the same monosaccharide and saccharose, and a very low activity of amylase and invertase (Fig. 15). The activity of β-glucosidase varies significantly. It is known that the transport of carbohydrates to the shoots proceeds through the phloem in the form of saccharose. If its content in the transporting tissues is regarded as the result of its supply and subsequent utilization, it can be said that the presence of two-year-old cones does not disturb the balance of this ratio. At the same time, different aspects undergo some variation.

The increased content of glucose, one of the products of hydrolysis of saccharose in phloem together with the reduced activity of invertase suggests a weakening of its further utilization. The reduction of glucose level in the tissues during growing season is regarded as the result of the utilization of the glucose portion of saccharose during the synthesis of cell walls. It can therefore be said that the nutrition of two-year-old cones, along with reduced activity of hydrolase, reduces the possibility of utilizing monosaccharide in the growth processes.

At the same time, the unchanged saccharose level at reduced rate of hydrolysis and starch accumulation is an index of carbohydrate utilization in nonmetabolic reserves. The increased content of complex hydrocarbon

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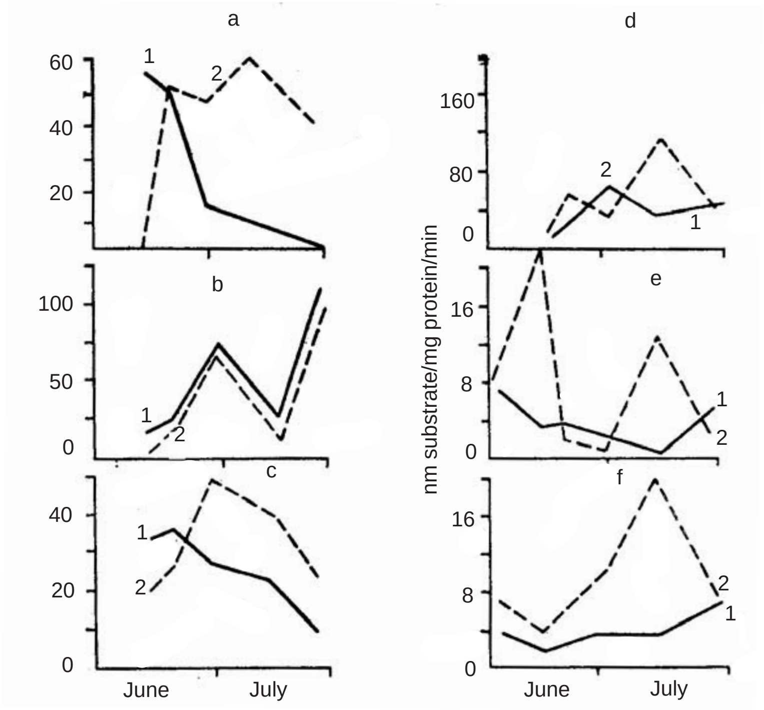

Fig. 15. Changes in the phloem of one-year-old female shoot in the presence of (1) and absence of (2) two-year-old cones.
Content of: a—glucose, b—saccharose, c—starch; activity of: d—β-glucosidase, e—invertase, and f—amylase.

compounds as a rule precedes the cell lignification process. The noticed
activization of β-glucosidase under the influence of crop is evidently a
49 manifestation of the response of the organism to the increased starch content.

Changes in the carbohydrate composition and hydrolase activity show that the nutrition of cones, without affecting the carbohydrate content of phloem, modifies the direction of their preferential utilization: reduction in the growth process and increase in the temporarily inactive nonmetabolic reserves. In other words, the nutrition of cones alters the possibility and conditions of carbohydrate utilization in the tissues of the axis.

During the post-fertilization period (July), the maturity of cones reduces the starch content in the phloem of the growing shoot and increases the amount of soluble carbohydrates, mainly monosaccharide, thus reducing the activity of invertase and amylase, and activizing β-glucosidase.

The simultaneous reduction of amylase activity and starch content suggests reduced rate of synthesis of the latter. The high level of monosaccharides and their content exceeding that of disaccharides, are noticed in the shoots in the period of active linear growth.

The reduced activity of invertase and amylase noticed all through the period of shoot growth as well as the absence of accumulation of saccharose suggests increased formation of protein-enzymes in the phloem tissues under the influence of nutrition of two-year-old cones. The activation of enzymes
50 promotes utilization of carbohydrates in the growth processes.

The above relationship of sugars with hydrolase activity of carbohydrate metabolism shows that the nutrition of two-year-old cones at this stage does not hinder the availability of carbohydrates to the growing shoot but activates their use in the growth processes by reducing the accumulation of nonmetabolic reserves.

The nutrition of two-year-old cones before the fertilization of ovules supports the tendency to maintain a much higher starch level and its further increase in phloem as well as xylem (Fig. 16). But, unlike in the preceding period of starch accumulation, there is a parallel increase of soluble carbohydrates, mono- and disaccharides, in the xylem. A period of predominance of starch precedes the accumulation of saccharose. Changes in the extent of increase of stored and free carbohydrates proceed at an insignificant level of amylase activity and similar invertase activity. In general, the low hydrolase activity of carbohydrate metabolism is natural for xylem since soluble carbohydrates enter it in the form of monosaccharides. In our case, the absence of hydrolytic activity combined with accumulation of saccharose and starch during increased growth suggests that the nutrition of two-year-old cones ensures either excess of carbohydrates or absence of conditions for their realization in xylem tissues of growing shoot. In either of
51 these cases, it can be suggested that the nutrition of two-year-old cones promotes an increase of quantity or activity of starch- and saccharose-synthesizing enzymes.

A number of studies have shown that the accumulation of complex carbohydrates is an essential stage preceding lignin synthesis from low-molecular aromatic precursors. One of the main regulators of lignin formation rate in conifers is the activity of β-glucosidase. Its increased activity in the presence of two-year-old cones indirectly confirms increased synthesis of cell wall material.

Along with the change of carbohydrates content as well as the rate of their synthesis and hydrolysis, the nutrition of two-year-old cones influences also the form of auxin-type agents (ATA) in the xylem of the growing shoot. It is generally regarded that the hormone level in the cambial zone depends on their flow from the bud and leaves. Along with this process, the formation of growth-controlling agents is possible directly in the cambial cells as well as their supply from the growing cones.

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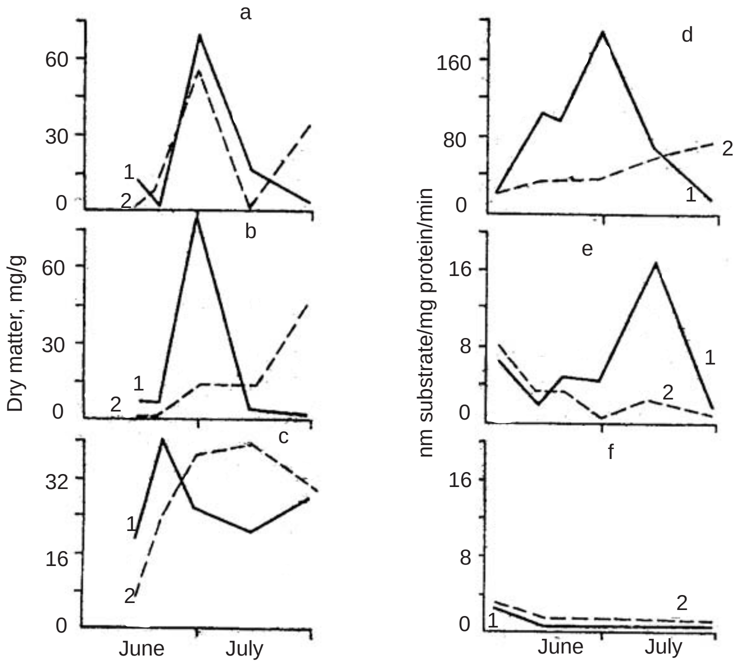

Fig. 16. Variations in the xylem of one-year-old female shoot in the presence of (1) and absence of (2) two-year-old cones.
Content of: a—monosaccharide, b—saccharoses, c—starch; activity of: d—β-glucosidase, e—invertase, and f—amylase.

According to the observations of N.A. Larionova, the composition and total activity of ATA in the xylem of the growing shoot at different stages of cone growth do not vary (Table 17). The variations of the biological activity of different ATA are, however, not at the same level. The change of direction of activity is also different. For example, during fertilization, the activity of ATA with R_f 0.2–0.3 (presumably indolyl acetic acid), 0.6–0.7, and 0.9–1.0 increases under the influence of nutrition of cones while the activity in other cases decreases (see Table 17). Variation of the activity of different ATA occurs, as shown before, in the period of reduced apical growth and transition from a more active xylem growth to its inhibition.

In pine, as also in angiosperms, the growth of vegetative organs, specially shoots, increases during auxin activation and slows down under the influence of inhibitors (Fransson 1959 and Kopcewiez 1966). Changes in the activity of growth regulators are related not only with the rate of linear growth of the shoot but also with the course of tissue differentiation in the shoot axis
52 (Wareing and Philips 1971, Wodzicki 1971, and Menyailo 1974). A mirror image of the variation direction of growth stimulators and inhibitors in the vegetative as well as regenerative organs has been noticed and it has been

51 Table 17. Biological activity of auxin-type agents (ATA) in xylem of one-year-old shoot in the presence of (1) and absence of (2) two-year-old cones, % of control

R_f	June 2 to fertilization		June 14 to fertilization	
	1	2	1	2
0.0–0.1	94	69	95	113
0.1–0.2	88	69	100	114
0.2–0.3	81	85	144	124
0.3–0.4	77	76	106	79
0.4–0.5	84	103	108	117
0.5–0.6	80	109	108	132
0.6–0.7	90	100	130	127
0.7–0.8	32	99	102	117
0.8–0.9	28	79	105	75
0.9–1.0	104	104	114	97

emphasized that the rate of growth processes depends not so much on the contents of auxins or growth inhibitors as on their ratio.

When interpreting in this background, the growth data and ATA content in the female growing pine shoot relative to the nutrition of two-year-old cones, it should be remembered that the content of gibberellins in its structures in the fertilization period (ovules and seed scale) is very high according to the data of E.G. Minina and N.A. Larionova (1979). It can therefore be assumed that the changes of ATA activity in axis xylem appear simultaneous with the accumulation or activation of gibberellins. Evidently, the totality of their variations determines the inhibition of apical and cambial growth which, at this stage is a consequence of the absence of conditions for the utilization of soluble carbohydrates and their increased utilization for forming temporary non-active metabolic reserves.

The nutrition of two-year-old cones in the next stage (July) coinciding with the commencement of growth of fertilized ovules reduces the starch content in the xylem of the growing shoot, increases the activity of invertase and β-glucosidase, and alters the predominance of saccharoses and monosaccharides. As in the earlier period, amylase activity was practically undetected. During this period, the growing shoot begins additional storage of photosynthetic products of needles which eliminates any possible deficiency of soluble carbohydrates to the growing shoot. Thus, the reduction of monosaccharides and saccharoses in the shoot xylem indicates their increased utilization. A simultaneous reduction of starch content and activation of β-glucosidase suggests the association of such a reduction not with the synthesis of polysaccharide but with increased lignification which is one of the elements of the growth process.

In the light of the foregoing, the initial predominance of monosaccharides and saccharoses may be regarded as a consequence of increased starch utilization and their later reduction as the result of utilization in the growth processes. The invertase activization shows that it is not the extent of the formation of enzymes but rather their activity that controls metabolic rate at this stage (Khavkin 1977).

The growth of female strobilus before flowering (June 1–20) does not modify the ratio of mono- and disaccharides in the xylem of one-year-old shoot but reduces their quantity and starch content (Fig. 17). In the absence of a current crop of cones, these changes arise simultaneous with the reduced activity of amylase and increased activity of β-glucosidase and invertase. The activation of the latter at reduced monosaccharide content and the contrary course of changes of their content with invertase activity may be judged as a sign of increased utilization of monosaccharides. The
53 simultaneous reduction of starch content and amylase activity as well as the activation of β-glucosidases suggests that the carbohydrates utilization is aimed at using them for the growth processes and not for starch formation. Evidently, the growth of a winter crop in the absence of a standing crop promotes greater availability and utilization of carbohydrates simultaneously. As a result, the growth of xylem in the axis, as demonstrated before, intensifies.

In the presence of two-year-old cones, the content of carbohydrates and invertase remaining unchanged in the xylem, amylase activity increases, i.e. the utilization of stored matter for sustaining growth shows further increase.

The shift in the excessive utilization of carbohydrates in growth processes or starch accumulation in some growth periods brought about by the nutrition of regenerative organs (female strobili or maturing cones) is

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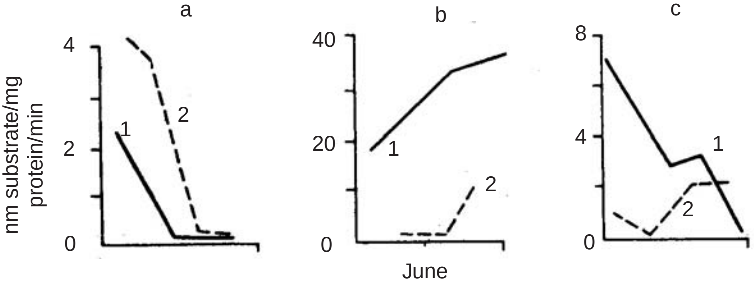

Fig. 17. Changes in the xylem of one-year-old female shoot in the presence of (1) and absence of (2) strobili.
Activity of: a—amylase, b—glucosidase, and c—invertase.

associated with a change of hydrolase activity in phloem and xylem of shoot axis in opposite directions: in the initial growth period, the nutrition of cones reduces hydrolase activity in the phloem and increases it in xylem. As a result, the utilization possibility of carbohydrates entering from phloem decreases in the xylem but the utilization of stored polysaccharides increases. In the next stage, the situation is reverse. A consequence of the varying activity of conversions of carbohydrates of different groups is their growing quantitative difference in altering the ratios between different groups. The direction of this shift runs counter to its course in the annual dynamics. Thus, as a result of the changing activity of carbohydrate utilization in the different processes, the growth (apical and cambial) intensity changes in one-year-old shoots and prolongs its course.

In spite of the change in the activity of carbohydrates utilization in the growth processes, the simultaneous growth of female strobili and two-year-old cones in the period of their growth before the fertilization of ovules causes starch accumulation in the xylem of one-year-old shoots. Evidently, the increased transport of carbohydrates under the influence of the reproductive organs of two generations is so strong that it exceeds their likely consumption for growth. It can therefore be assumed that the crop size influences the state
54 of physiological parameters of one-year-old shoots.

In order to test this assumption, carbohydrate metabolism was studied in the xylem of growing shoots with varying number of two-year-old cones. It was found that nutrition of a heavy crop in the absence of female strobili reduces the utilization possibility of carbohydrates in the xylem of axis as could be judged from the reduced activity of invertase (Fig. 18). At the same time, changes of starch content, its hydrolysis rate, β-glucosidase activity, as also the extent and activity of xylem growth are insignificant. Evidently, a heavy crop does not significantly influence the utilization of carbohydrate reserves. A possible reason for this is that the extent of invertase activation in the presence of a heavy crop is significantly less, as noticed during the nutrition of cones, compared to their absence, i.e. as the crop size increases, the range of changes caused by its requirement decreases. A somewhat reverse tendency is noticed in the direction of variations due to which these changes appear inadequate to shift the activity or the growth rate of shoot axis.

The foregoing discussion shows that the nutrition of regenerative organs does not prevent the availability of sugars to the tissues of the growing shoot but, at some stages of their growth, determines the shift in the utilization activity of stored and dissolved carbohydrates. Moreover, there is a change in the direction of their dominant utilization in the growth processes or accumulation of temporarily inactive carbohydrate reserves. The duration and extent of activity changes and the excessive utilization of

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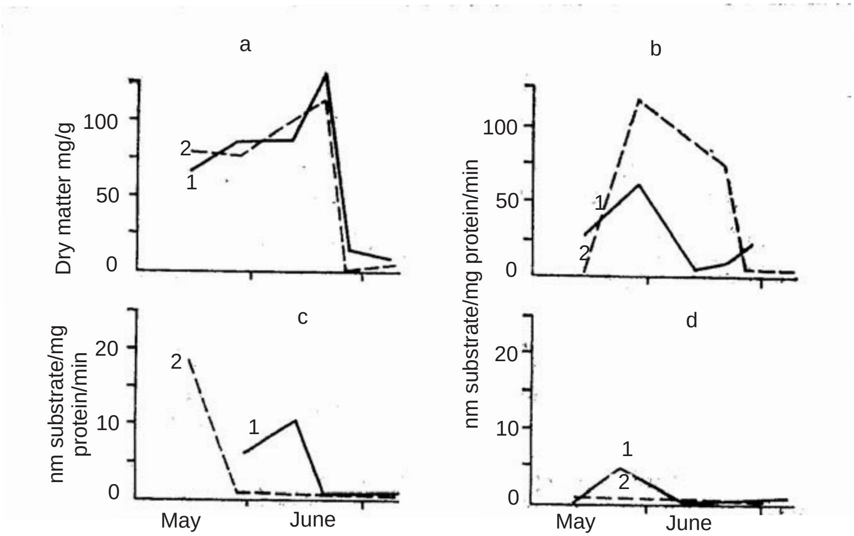

Fig. 18. Changes in the xylem of one-year-old female shoot with high (1) and moderate (2) cone crop:
a—starch content; activity of: b—invertase, c—amylase, and d—β-glucosidase.

carbohydrates are determined by the crop size and extent of winter crop. As a result, the direction of carbohydrate metabolism in the annual morphological cycle is maintained but its duration is prolonged and the intensity of shoot 55 growth modified. Consequently, the nutrition of cones displaces in time the morphogenesis of the growing shoot. According to E.G. Minina (1979), it is the asynchronism of the morphogenesis of male and female shoots that determines their physiological differentiation. In this case, the extent of displacement of the duration of morphophysiological cycle taking place in the growing shoot in the presence of a crop forms the basis of relations between cone production and growth processes as also the control of their proportions.

Cone Production and Growth of Trees

The preceding evidence predominantly dealt with an analysis of relations between growth and cone production at the level of tissues and shoots. The following discussion is mainly concerned with evaluating the state of trees at the commencement of the reproductive phase and a study of the corresponding indexes of growth and seed productivity. In this context, material on the variability and relation between growth parameters and yield of trees at different levels of their interrelations would be of interest. As in the first part of investigations, these observations have a bearing on different aspects of crop control.

Ontogenetic Characteristics of Process Relations

Among the ontogenetic characteristics of relations between growth and seed production in trees, a study of the commencement of reproductive phase in order to establish the conditions for increasing seed productivity of young plantations would be of particular interest. In our case, this aspect was studied on the example of the onset of cone production in forest plantations and young natural pine undergrowth.

The plantations are located around Yakhroma town in Dmitrov Forest Combine, Moscow district. At the time of their investigation carried out in 1977 in collaboration with M.V. Tvelenev, the plantations were 33 years old, their average height 9.2 m and diameter 15.7 cm, and number of trees per hectare 500 against 2500 when initially planted.

A study of cone production showed that trees with moderate and high mean diameter entered the reproductive phase. Of the total number of trees, a third did not bear cones while the bulk of them bore about 10 female shoots (Table 18).

The formation of female primordia began at the age of 25 years in some trees. Most, however, entered the reproductive phase at 29 years, nearly the same age as under the conditions of the European North (Krest'yashin 1972). The formation size was initially less than one cone per shoot but rose thereafter. The systematic fall of strobili (37 to 73%) can be regarded as the defining moment. When computing the seed productivity from the maximum possible level of cone production, it was found that such a plantation in some years could yield about 2500 mature cones or 30 kg seeds. However,

Table 18. Onset of cone production in forest plantations

Evaluation of female level of trees			No. of trees		Value of female level (number of female shoots/ha)
Ball	Number of shoots		No./ha	%	
	Range	Average			
0	0–6	2	160	32	320
1	6–10	9	160	32	1440
2	11–20	15	130	26	1950
3	Above 21	23	50	10	1150
		Total	500	100	4860

considering not only the fall of strobili but also cones and their heavy pilferage, such a plantation cannot yet be regarded as of practical importance for adequate seed collection. One of the causes of poor cone production is the high density of the planting. According to contemporary calculations, for maximum production the total number of trees should not exceed 200/ha (Alekseev 1979). An important factor responsible for low yield is also the small number of shoots suitable for producing cones, low level of formation, and high percentage of premature fall of strobili and cones. Without the active application of several measures for preparing the young trees for the forthcoming cone production and for creating conditions for its successful course, such plantations will not be of immediate practical importance (Vorob′ev 1973 and 1981).

The follow-up of the course of plant growth is an important aspect in their preparation to the reproductive phase. Observations showed that cone production commenced soon after the trees crossed the first peak of increased growth which occurred at the age of 15–20 years (Figs. 19 and 20). Available information suggests that the onset of cone production in pine is associated first of all with their attaining certain parameters of trunk and shoots, later with growth inhibition and the stabilization of its intensity in the optimum range (about 30 cm a year of trunk height, 4.5 mm in diameter, and an increment of about 20 cm of cone-bearing shoots).

Similar patterns were detected at the commencement of cone bearing in the natural pine plantations. The author studied the latter at the following stand values: age 60 years, average diameter 18.7 cm (sic!), height 12.1 m, number of trees/ha 342, cross section 10.4 m^2, and reserves 58 m^3/ha. For the

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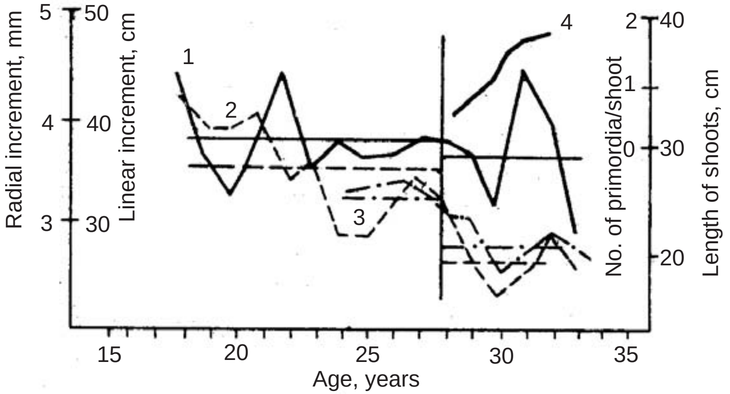

Fig. 19. Growth of trees in plantations:
1—radial, 2—linear, 3—linear growth of shoots, and 4—cone production of central shoots.

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Fig. 20. Cyclicity of tree growth:
d—radial, l—linear, 1—in forest plantations, 2—natural young plantations, and 3—specimens not yet cone bearing (+ denotes the commencement of cone bearing).

age of these trees, these indexes are not high since the plantation occurred at about 1000 m above sea level.

Seed production of pine under these conditions, as in the case of crops
examined, began after the lapse of a similar but more prolonged growth cycle
of 40 years. Significantly, the increment of diameter is of decisive importance
for the commencement of regenerative phase, i.e. the cambial activity of young
57 plants. In the case of barren trees, the rate of linear growth differs little from
the corresponding values that characterize the cone-bearing specimens based
on annual increment or the overall length of trunk (in the first case 10.6 m
and in the second 13.3 m). Based on radial growth, barren trees lag far behind
the cone-producing trees.

58 The proportion of barren unpromising trees among natural young trees is high as in forests. An assessment of this segment of the stand facilitated recovering 26% of timber resources or 46% of the number of trees during improvement felling, leaving the best of them to form the seed section (187/ha).

The reproductive characteristics showed that in good crop years, these trees begin to yield adequate quantities of seeds. Thus, during 1978 to 1980, 45 kg of seeds matured per hectare on an average or 20 cones per tree. This value cannot, however, be regarded as optimum for the given age of the trees since the number of cone-bearing shoots did not exceed 10 per tree, suggesting that the development of the female level was still poor.

Improvement felling and several other measures practised in forestry should change this situation. In the present case, it is important to emphasize their objectivity and not their details. This, as stated before, should primarily pertain to the preparation of trees for reproductive activity (Vorob'ev 1973). Its basic principle is to accelerate growth initially, predominantly cambial, later inhibit the radial growth to the average size and hold the linear growth to below the average. In other words, the task lies in promoting an accelerated course of well-known S-growth phase in the young plant. These efforts should be coupled with producing the maximum number of cone-bearing shoots which determine the bulk of yield; maximum diameter as the area of their transport system; and a good root system as the storage organ. Only thereafter is it possible to stimulate the regenerative processes by adopting direct as well as indirect measures through optimum growth inhibition.

Cyclic Characteristics of Process Relations

Cone production. Processes with intermittent dynamics have an important bearing on the study of the reproductive activity of woody plant. Their knowledge is important for treating prognostic problems as well as measures related to crop control.

The study of these aspects in woody plants has a long history. More or less regular attention began being paid in this direction only in the '70s of the last century. Based on an analysis of the available information and her own data, T.P. Nekrasova (1961, 1972, and 1974) categorically declared that cone production was not strictly cyclic and that it would be more correct to talk of an alternation of different cycles and not of seed-producing and barren years. The change of outlook on the nature of these processes led to an essentially new understanding of the principle of this process but some "remnants" of the prevailing concepts persisted. These concerned primarily the alternation of crop and non-crop years. The impression prevailed that the change was periodic although G.E. Komin (1973) demonstrated its 59 typically cyclic fluctuations. For example, in several deciduous and coniferous species, G.E. Komin detected cycle durations of 2 to 9 years. The lack of fairly long-term observations at that time did not help in developing these investigations to gain a relatively complete idea of the cyclicity of the reproductive activity of woody plants.

Such a possibility became available following the development of a method for prolonged retrospective analysis of traces of fallen cones of Siberian stone pine that provided data on the magnitude of formation of female primordia and the number of cones over 100 years or more (Vorob'ev 1979).

The retrospective study of seed production helps in understanding the influence of the reproductive activity of trees on the size and structure of annual rings, trace the crop cyclicity, develop methods for their long-term and super-long-term prognosis, and build an ontogenetic model of relations between growth and cone production of shoots.

Apart from these tasks, it is important to study the relation of the cyclicity of reproductive activity with the ambient conditions, specially astrophysical. Among the latter, solar activity is mainly studied at present (Sitnikov 1964, Nekrasova 1972 and 1974, Afanas'ev 1973, Khokhrin, Kirsanov, and Smolonogov 1977, and Rostovtsev 1978). Several factors are, however, known to influence the biological processes and their influence is much broader and nature more complex. N.V. Lovelius (1979), for example, included many of them under the index "bioeffective solar activity" (BSA) which most completely explains the cyclicity of the radial growth of trees. A.A. Maksimov, V.A. Pan'ko, and A.G. Sytin (1979) assign much importance to the ecliptic latitude of Jupiter and Saturn in the evolution of biospheric phenomena. In this context, the work of T.A. Uranova (1979) is of utmost interest.

Quite clearly, a multipronged approach to the solution of the problem would hold more promise than a one-sided attempt. Nevertheless, the role of constituent factors should also be ascertained. It is necessary to examine the influence of solar activity on the reproductive activity of woody plants since quite a few contradictory views on this subject have emerged by now.

T.P. Nekrasova (1972 and 1974) who devoted much attention to this theme categorically states that cone production of Siberian stone pine is subject to a 11-year cyclicity of solar activity. A.V. Khokhrin, V.A. Kirsanov, and E.P. Smolonogov (1977) confirm this hypothesis for the Urals pine forests. The favorable impact of solar activity on cone production of Scotch pine was reported by S.A. Rostovtsev (1978) who analyzed the distribution in the European USSR on a ball scale of crop evaluation.

60 In many other works, specially of V.A. Afanas'ev (1973), it has been shown on the example of Kurile Dahurian larch that increased yield was largely associated with a depressed solar activity.

These and other investigations while emphasizing their own conclusions explain the deviations as caused by local climatic variations influencing crop maturity, etc. In our view, no single factor can explain such deviations as clearly seen from the many theoretical concepts on various aspects as well as the data of our own investigations which are analyzed below.

The problem under consideration is closely related to the eco-geographic features of the cyclicity of reproductive activity in woody plants, specially in Siberian stone pine. Investigations have pointed to several common crop and barren years over much of the distribution range of Siberian stone pine. In western Siberia, this observation was made by T.P. Nekrasova (1974), in the Urals by A.V. Khokhrin, V.A. Kirsanov, and E.P. Smolonogov (1977), in Sayans and Altay by A.I. Iroshnikov (1963), and in the mountains of southern Siberia by V.N. Vorob′ev (1967).

All the same, the influence of local characteristics of cone production, extensively investigated by D.N. Danilov (1952) cannot be ignored. In the case of Siberian stone pine, it has been shown that crop frequency rose from west to east. The reasons for this phenomenon are associated with a change of cyclonic climate in the west to anticyclonic in the east, which is the optimum for pine yield (Vorob′ev 1967).

According to L.I. Krest′yashin (1966), non-crop years have not been reported in a large forest territory under conditions of eastern Sayans. From this, he concluded that cone production periodicity cannot be an impediment for organizing comprehensive economies. A similar conclusion cannot be applied to the regions of northern Altay since the dynamics there are more sharp and infrequent due to crop losses and the role of exposure is weakened due to the predominance of a wet climate.

A study of the cyclicity of reproductive activity and growth of pine shoots was carried out within altitudinal and latitudinal profiles of its distribution range.

The altitudinal profile lay in Altay State Forest Reserve in Kyga river region where we carried out investigations before on the cone production of Siberian stone pine under mountainous conditions (Vorob′ev 1967 and 1974). In this case, for recording long-term series of pine cone production, branch specimens were collected from three permanent test plots: black soil subzone—test plot 2^{a} (450 m above sea level), mountain-taiga subzone—8^{a} (1250 m above sea level), and subalpine subzone—13 (1850 m above sea level). The characteristics of the test plots were described in Chapter I. Cone production characteristics of pine in the upper mountain segment were studied also in Gornaya Shor′ya in Potyn-gor town region (1630 m above sea level).

The latitudinal profile in the plains of western Siberia comprised the following points: southern subzone—Baza village (55°), midzone—
61 Tundrino village (61°), northern subzone—Tarko-Sale village (65°), and polar limit of pine distribution—head of Yavoyakha river, tributary of Pur river (66°).

A time series of the reproductive activity of pine was constructed on the basis of long-term retrospective analysis of traces of fallen cones (Vorob′ev 1979). The fundamental principles of this method were laid independently by A. Renvall (1912) and N.S. Nesterov (1914) and were later detailed and extensively used by many investigators for studying the dynamics of seed production in coniferous plants (Sharnas and Dzhebeyan 1934, Gorchakovskii 1947, Nekrasova 1957, and others). The principle of the proposed method, most completely described by A.A. Korchagin (1960) involves the counting of year-wise traces of fallen cones on shoot bark. From such data, it is possible to reconstruct crop dynamics of pine for the past 20–30 years. Later, with the growing annual rings, cone-bearing branches thicken, bark on them stretches and external traces of cones turn indistinguishable.

In such cases, these traces can be found not on the bark but in the cross-sections of branches. Cuts at the base of whorls showed that cone traces remain inside the shoot and are well distinguishable. Based on them, crop dynamics can be reconstructed for practically the entire life of the tree. The site of the cut, the appearance of out-sized traces of cone stalks, and their differentiation from the remnants of lateral shoots are all considered.

Determining the site of cut and the nature of traces of out-sized cone stalks should commence from the whorls on which external traces are distinctly visible. This is particularly important for establishing the differences between the traces of mature, normally grown cones and those that fell during formation and maturity. Outer traces of mature cones are oval-shaped, quite 62 deep and visible on the bark of cuttings. In the cross-sections of branches, they correspond distinctly to well-defined contours of the heart-shaped part of stalk terminating in a distinct rounding of the resinous gash or a light-colored "ray". Such traces are often accompanied by specific deformations of annual rings.

The underdeveloped cones falling prematurely leave shallow traces on the bark in the form of small "triangles" or "rays". These usually persist after the fall of one-year-old cones before or after their pollination. Such traces correspond in the sections to less bright, nonresinous cone stalks terminating only in a small "ray".

Branches for analysis are selected in the female level of the crown with three samples in age groups of 30, 60, and 100 years. Trees of I and II classes of development aged 200–250 years with not less than 3–5 trees are selected in each test plot. When processing the data into a single series of productivity (number of cones per shoot), extreme values are discarded: on all branches, for the first 3–4 years (before the commencement of cone production) and on older trees for the last 10 years (after cessation of seed production). The basis for estimation in both the cases is the "clear" absence of cone traces. Such information is regarded as comprising a cyclic series since it reflects barren years in which the traces are poorly seen due to predominant fall of strobili.

The time series of productivity as also the linear growth of shoots are plotted as graphs. Some structures analysed by V.P. Cherkashin using a mathematical model based on the work of G. Jenkins and D. Watts (1972) as well as J. Bendat and A. Pirsole (1974). The interpretation of spectra and correlation functions took into consideration the studies of D. Merser (1964), J. Milsum (1968), and V.P. Cherkashin and V.V. Kuz′michev (1977). The analysis also kept in view the work of A.A. Maksimov, V.A. Pan′ko, and A.G. Sytin (1979) carried out using similar mathematical methods.

The generalized and processed series of primordia formation and the number of cones revealed cycles of 28–33 years with a weak attenuation of the correlation function (Fig. 21). Judging from it, it was felt that the spectra of these indexes would be of low quality and hence much information covering long periods is required and its study becomes cumbersome even on such relatively long series as in the present case.

In the background of above discussion, the low-frequency component of the series was filtered for primary differences. The autocorrelation function of the resultant series detected a similarity of their probability structure, specially in the range of a 3-year cycle (see Fig. 21). A comparison with the spectrum of the series revealed a predominance of the above cycle with respect
63 to primordia formation as well as cone yield (Fig. 22).

At frequencies typical of a near-11-year cycle, the peak value was insignificant. The comparison spectrum of the linear increment of shoots

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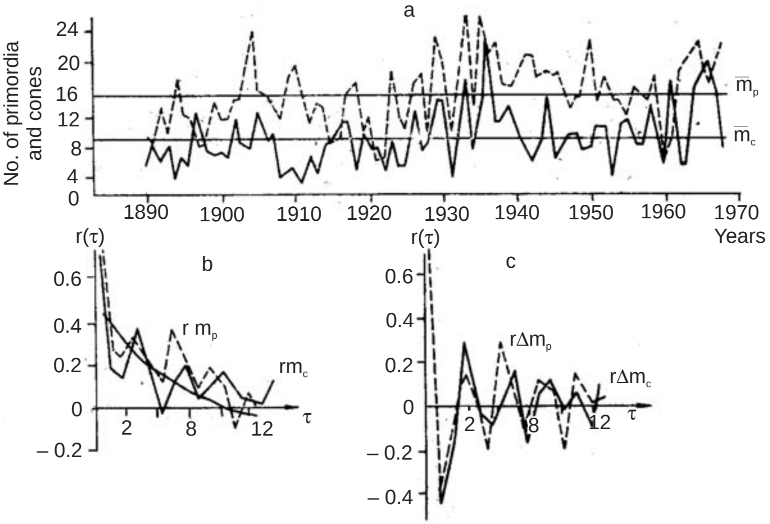

Fig. 21. Generalized and processed series of (a) primordia formation (m_p), number of cones (m_c) as well as the correlation function of initial (b) and autocorrelation function of filtered (c) series.

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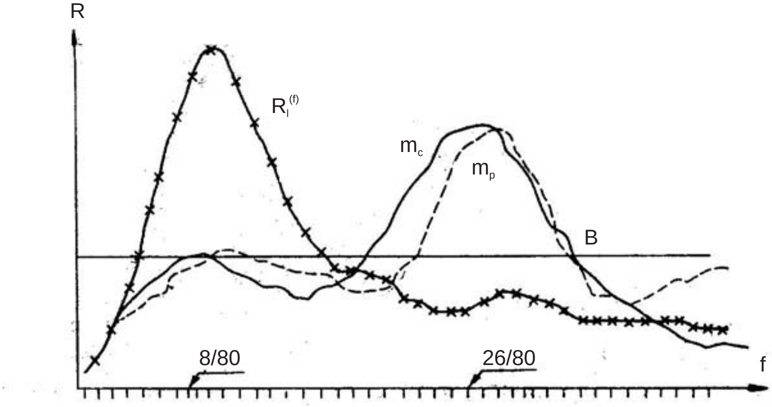

Fig. 22. Spectra of distribution series of female primordia (m_p), cones (m_c), and linear increment (l) of shoots.

showed an inverse ratio, i.e. the domination of a 10-year and not 3-year cycle. This comparison revealed the essential difference of the series compared which characterize on one hand growth and on the other regenerative
64 processes.

The above pattern of the cyclicity of reproductive activity is characteristic of pine as a species and prevails over much of its distribution range. Our analysis of eco-geographical data leads to the same conclusions. Of primary interest here is the material analyzed using modern mathematical methods. The reciprocal correlation function of the series of primordia formation and the number of cones for Gornaya Shor'ya is very close to that of Gornyi Altay. It is particularly significant for the structure of series, specially involving a 3-year cycle. The observed similarity of the series examined is largely because they describe the same high-altitude Altay-Kuznetsk system.

The characteristics of the reproductive activity of pine growing at high altitudes and latitudinal zones are of interest in this context.

The altitudinal differences of cyclicity and cone production of pine studied by us for the conditions of Gornyi Altay (Vorob'ev 1967 and 1974) showed that pine forests in black soils exhibit relatively smooth dynamics of primordia formation in the different years (Fig. 23). These data reveal a tendency for increased number of primordia in the years with a warmer climate. This relation was, however, not constant since increased formation of primordia occurs at a moderate temperature. This denotes that the temperature here is adequate and is not a limiting factor as noticed high in
65 the mountains.

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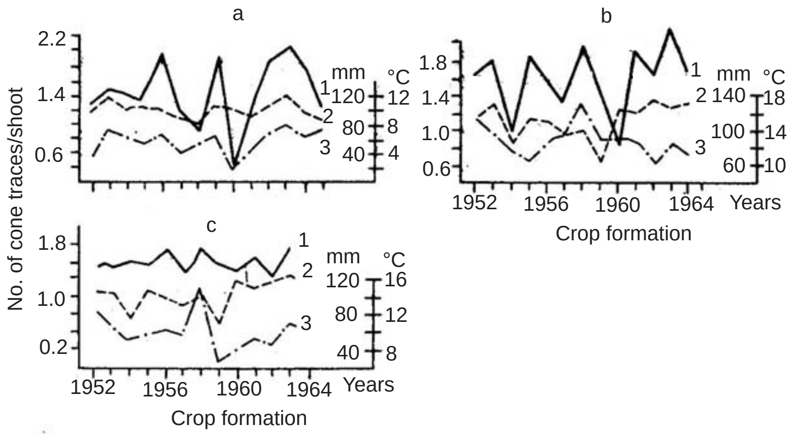

Fig. 23. Cyclicity and formation conditions of female primordia in shoots within the altitudinal profile (a—subalpine subzone, b—mountain-taiga, and c—black soil): 1—primordia formation, 2—moderate atmospheric temperature in the subalpine subzone in the middle 10 days of August, in the mountain-taiga subzone in the last 20 days of July, and in black soil in the middle 10 days of July, and 3—total of precipitation for the corresponding period (from the data at the base of the profile).

A weak correlation is also noticed with precipitation exhibiting a positive influence. This is perceived from the example of high cone yields in 1954, 1958, 1960, and 1965.

65 A change of cyclicity of cone production and the nature of influence of weather conditions on the formation of primordia is clearly evident in the midportion of the mountains. Here, the alternation of seed cycles maintains the same trend but amplitude broadens. While the former can be explained by the similar range of temperature conditions for the formation of primordia, the latter could be due to greater effect of heat and moisture. This role of temperature can be informed from the example of high yields in the period 1962 through 1966 (crop failure in 1962 was not due to lack of formation but the destruction of primordia in the following spring). Moderate precipitation plays a positive role. When the rains are abundant and heat adequate, they do not exert any adverse influence. Since the proportion of heavy downpours is more in the mountains, drainage is of importance. In some years, in spite of favorable conditions for primordia formation, the number of traces of normal cones is minimal or almost wholly absent. Observations showed that primordia on transition from the embryonic phase to the post-embryonic perish and leave behind only faintly visible traces. Such a situation prevailed in the spring of 1961 with respect to the 1962

crop. Similar losses, although to a smaller extent, were recorded in 1956, 1959, 1965, 1968, 1971, and 1972.

In the subalpine subzone, the range of crop fluctuations increases and close association is observed between the level of primordia formation and weather conditions. The influence of temperature is specially significant although the importance of precipitation also increases. On the whole, wet and cold weather make for an unfavorable combination of conditions while warm and dry weather promote a good crop. The crop in latter case is quite high and points to high potential possibilities for the autoregeneration of subalpine pine forests. For example, 1964 to 1966 represent such productive years.

The dynamics of primordia formation in the subalpine and mountain-taiga subzones are not the same but assume a transitional form at their boundary. This is because the female primordia of pine in the upper parts of mountains are formed in August under temperate conditions that are different than in July when they are formed in the mountain-taiga subzone. Moreover, as a result of lag in the growth periods, the extent of differentiation of primordia persisting into the spring of following year differs in the mountain-taiga, subalpine, and the intermediate zones. As a result, the formation conditions in the "intermediate" pine forests in some years coincide with the corresponding values in the mountain-taiga subzone and in some others agree with those in the subalpine zone. In several cases, the level of primordia formation is an average of mountain-taiga and subalpine subzones (Vorob'ev 1974).

More complete data on the cyclicity of cone production confirmed the earlier conclusions and demonstrated maximum proximity of the series for the different subzones over long periods (Fig. 24). The overall coefficient of crop convergence (C_x) between subalpine and mountain-taiga pine forests determined by the accepted dendroclimatic method (Bitvinskas 1974) was 49% (less than 50%) and between mountain-taiga and black soil forests 62%
66 (more than the above criterion). In the latter case, deviations were noticed in the development of some cycles.

The characteristics of cone production in pine in the high altitudes reveal an increased range of crop fluctuations (Iroshnikov 1963a and Vorob'ev 1974). In this case, the sensitivity index (Ch_k) of trees to the changing environmental conditions is interesting. In pine forests in black soils, it is 22% for primordia formation and 33% for crop size; in the subalpine subzone, these values are respectively 35% and 56%.

Within the latitudinal profile, a similar pattern of sensitivity index is noticed. With respect to the crop level, it is 68% for the northern subzone, 55% for the central subzone, and 61% for the southern subzone. The high sensitivity to climate and the high crop loss in the southern subzone is

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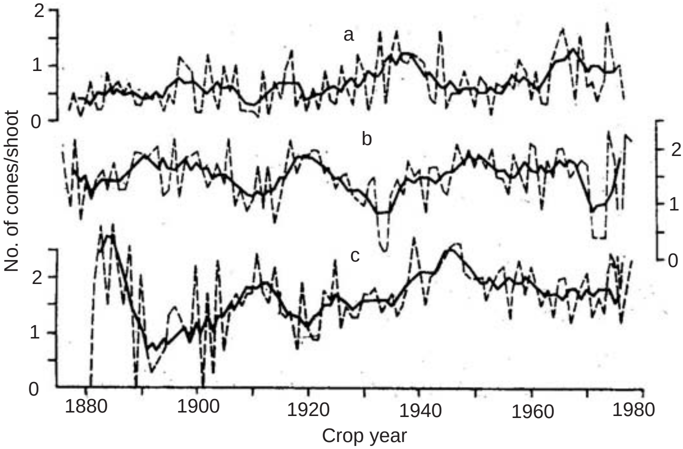


Fig. 24. Cyclicity of Siberian stone pine crop within the altitudinal profile in Gornyi Altay: a—subalpine, b—mountain-taiga, and c—black soil subzones.

explained by the proximity of selected observation points (Baza area) to the forest-steppe boundary of pine.

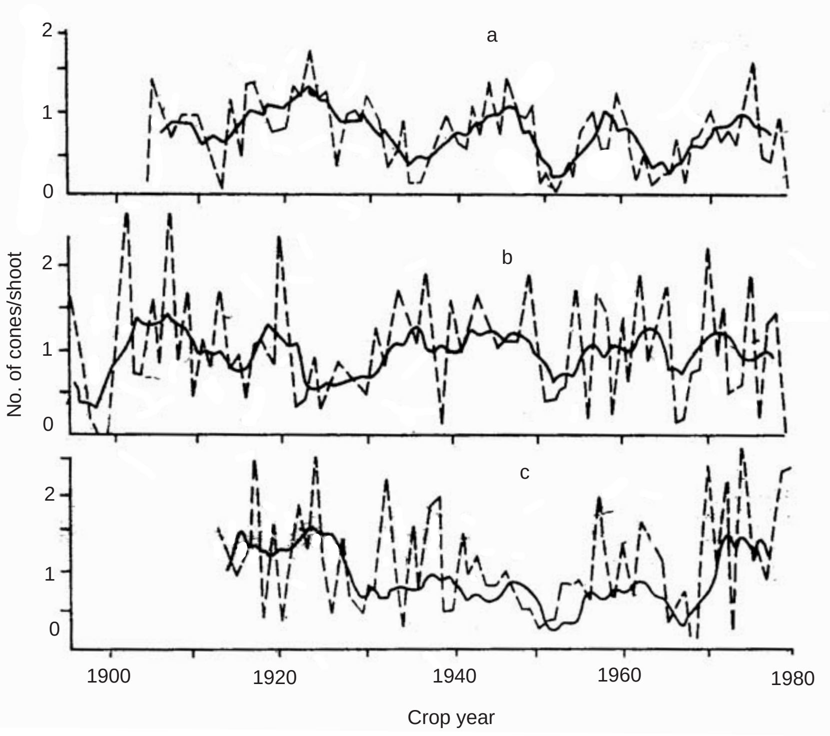
Another factor determining the pattern of cone production cyclicity in pine in the plains is the persistence of a high level of primordia formation at the northern boundary. According to the studies of N.P. Mishukov (1973) and our own, the average level of primordia formation in the northern subzone (Tarko-Sale region) is 1.7 cone traces per shoot. In the portion of subalpine pine forests under comparison, this value does not exceed 1.3. At the same time, a comparison of the level of mature cones reveals a reverse pattern suggesting that crop preservation at high altitudes is greater than in the high latitudes. It is also significant that, at the altitudinal limit of pine distribution, crop losses mainly arise at the commencement of the growth of strobili and during their transition from the embryonic to the post-embryonic
67 phase (Vorob'ev 1974); in the polar subzone, losses are mainly during spring frosts in the second year of cone growth.

The frequent and high pine crop failure in the northern forest subzone is explained not only by the relatively high and stable level of primordia formation but also by the reduced range of its fluctuations. The so-called uniform formation of primordia (Mishukov 1973) has in this case an anomalous character relative to their fairly constant value which is typical, for example, of black soil pine forests (Vorob'ev 1974 and 1978).

Differences in the nature of pine cone production at the boundaries of its distribution result from differing growth conditions, primarily light. The duration of solar radiation toward the polar boundary of forests is known to fall but rise in the mountains (at the same level).

The reproductive activity in northern pine forests generally exhibits all the features of cyclic variations (Fig. 25). Cycles of different durations are noticed here too in the course of primordia and crop formation. Most important among them are the long-duration cycles favoring long-term prospects for promoting the renewal of pine forests at the polar boundary.

68 The variation range of reproductive activity of pine in the central and southern subzones is more because of the upper limits. Insofar as cyclicity is concerned, it is generally uniform all over the extensive territory of western Siberian plains. This can well be perceived from the yield pattern, specially from the 5-year sliding curve (Fig. 26). T.P. Nekrasova (p. 72, 1974) pointed out that, in this territory, cycles of Siberian stone pine seeds essentially coincide all over the forest zone. This conclusion is confirmed



67 Fig. 25. Cyclicity of Siberian stone pine crops within the latitudinal profile of western Siberia: a—northern, b—central, and c—southern subzones.

68

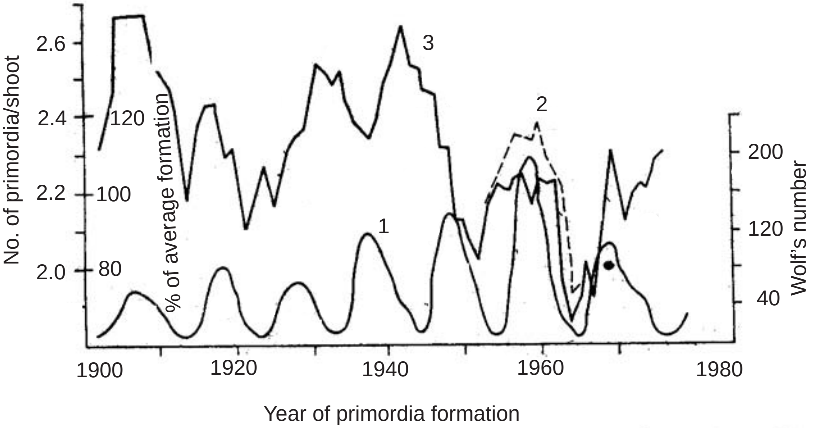


Fig. 26. Solar activity (1) and cyclicity of formation of female primordia in shoots in central and southern subzones of western Siberia:
2—according to the data of T.P. Nekrasova (1974), and 3—according to the author's data.

by the vast data which incidentally helped predict more positively the shifts of seed seasons.

T.P. Nekrasova (1974) divided the central and southern subzones of plains taiga into the following cycles according to the level and years of formation of primordia: 1947–1952 (non-seed), 1953–1959 (seed), 1960–1965 (non-seed), and 1967 (seed). However, the actual structure of cyclicity of cone bearing of pine for the above period was somewhat different. Figure 26 depicted the curve of primordia formation based on 5-year sliding data of T.P. Nekrasova. There was only one seed cycle (1952–1964) with ascending (1952–1954) and descending (1962–1964) non-seed years. This cycle stands out distinctly in our data too. In the above graph, many 10–14-year cycles are clearly perceived: 1902–1914, 1914–1925, 1925–1938, 1938–1952, 1952–1964, and 1964–1974. Judging from the data studied, these periods are somewhat differently related to the solar activity than was regarded before. It is understandable, for example, that the matching of seed and solar cycles over 60 years served as a basis for confirming a positive relation between the two (Nekrasova 1972 and 1974 and Khokhrin, Kirsanov, and Smolonogov 1977). At the same time, as can be seen from the above data, many seed cycles fall in
69 the period of minimum solar activity. This pattern of association of cone bearing with solar activity explains also the contradictory conclusions of V.A. Afanas'ev (1973).

Thus, as stated earlier too, it is not possible to provide a straight answer to this problem. A formal approach to analyzing the association between cone bearing and solar activity draws attention to the systematic alternation of pairs of seed cycles agreeing and disagreeing with it. Such an alternation is possibly associated with the more significant 22-year solar cycles. It is also likely that fluctuations of reproductive activity of pine depend on a shift of the sign of solar activity.

Geographic factors have a definite place in the cyclicity of cone bearing. The matching of not only many crop and barren years but also some cycles in a part of the distribution range of pine was demonstrated before. A particularly good agreement was noticed in these 60 years in the midportion of southern Siberian mountains (Fig. 27).

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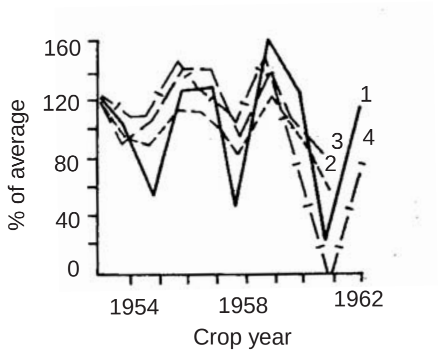

Fig. 27. Crop cyclicity of Siberian stone pine in the midportion of southern Siberian mountains:
1—north-eastern Altay (Vorob′ev 1965), 2—western Sayan, 3—eastern Sayan (Iroshnikov 1963), and 4—trans-Baikal (Sitnikov 1964).

The common cyclicity of crops over the vast territory confirms its dependence on cosmic conditions which exert great influence on the temperature regime. Considering that this is a major factor in the mountains and moisture is adequate, and formation of primordia in the midmountains proceeds at the same time (July), it is quite clear that the above assumption is well-founded.

It is presently difficult to state to what extent the cyclicity of reproductive activity of pine in the plains and mountain parts of its distribution range coincide although some comparisons go in favor of a commonality of the development of reproductive processes. Data on the structure of large cycles of primordia formation also point to a similar conclusion (Fig. 28). It is at least clear that the course of the 38-year cycles in pine forests on plains (1922–1959) and mountains (1926–1964) is identical. Some shifts of their variations are seen, age influences are not excluded, and deviations
70 are noticed in the background of smaller cycles and some years. Nevertheless, a characteristic feature is the common pattern of changes of

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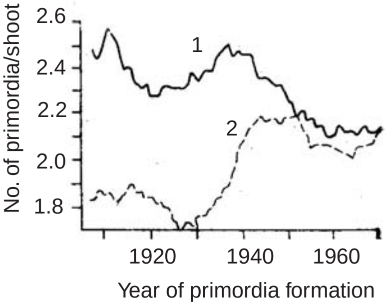

Fig. 28. Crop cyclicity of Siberian stone pine in the plain (1) and mountain (2) parts of western Siberia (on a 15-year sliding of the basic series).

reproductive activity in pine over a significant portion of its range. This pattern reveals the presence of micro (3-year) as well as macro (large) cycles of specific rhythms of regenerative processes in pine evolved in the course of interaction between internal and external factors of cone formation.

The aspects discussed above call for further study. The possible methods for collection and processing of available data at present open up an entirely new avenue in this field of studies, i.e. dendrochronology. It would be possible to resolve our present as well as a whole series of conventional dendrochronological problems like the structure of cyclicity, association with climatic factors, relation with growth, its role in regenerative processes, long-term forecasts, etc. One of the primary problems in this direction could be the development of a "reproscale", or reference data on crops of pine and other woody species in the different regions of their distribution range. With this objective, indexes of the reproductive activity of Siberian stone pine have been given in Table 19 for the altitudinal and latitudinal profiles of southern and western Siberia.

Indexes in Table 19 have been given as percentages relative to the standard mean calculated arithmetically and given in the note to the table. This has been prepared so as to eliminate subjectivity in processing the series by different methods of sliding and retain the original information. Such an objective was also expressed in the works of T.A. Uranova (1979) and N.V. Lovelius (1979). Later, after adopting an accepted method, the original data could be represented in a different form.

Growth. Cambial growth of trees is the most studied aspect in the cyclicity of growth processes. Studies related to dendrochronology and dendroclimatology have considerably broadened the views on the time frame of the radial growth of trees. The study of linear growth was complicated due to the availability of a large series of observations and hence investigations

71 Table 19. Indexes of the cyclicity of reproductive activity in Siberian stone pine

Year	0	1	2	3	4	5	6	7	8	9
Altitudinal Profile										
Subalpine subzone, Altay State Reserve, Kyga profile, test plot 13, 1876–1977, 102 years										
Formation of Female Primordia										
1970	99	107	231	165	132	148	—	—	—	—
1960	33	66	115	148	157	157	132	157	165	132
1950	124	60	115	82	82	90	132	148	90	140
1940	124	140	157	115	115	107	145	82	74	82
1930	148	140	41	157	173	99	173	181	173	124
1920	56	82	24	33	124	90	57	107	132	50
1910	124	124	107	57	90	82	50	66	99	107
1900	99	66	74	99	91	157	82	99	91	74
1890	41	57	49	90	49	124	90	82	57	49
1880	49	90	148	49	90	115	99	82	49	99
1870	—	—	—	—	99	16	49	82	57	57
Cone Crop										
1970	250	109	47	109	281	125	156	15	—	—
1960	47	203	31	46	172	218	265	172	62	234
1950	62	109	93	15	125	109	109	93	187	156
1940	140	125	62	15	234	31	94	94	140	98
1930	140	63	125	250	47	172	250	140	109	172
1920	15	94	15	140	47	31	156	93	62	172
1910	46	15	125	15	93	62	140	156	46	78
1900	46	31	187	78	31	156	78	156	31	31
1890	15	109	46	62	31	62	31	171	156	109
1880	31	109	31	31	140	78	93	62	125	15
1870	—	—	—	—	—	—	62	31	93	89
Mountain-taiga subzone, Altay State Reserve, Kyga profile, test plot 8[a], 1879–1979, 101 years										
Formation of Female Primordia										
1970	92	112	154	104	115	96	133	127	—	—
1960	65	107	89	128	109	111	102	105	99	89
1950	107	117	95	97	85	105	111	105	120	107
1940	116	109	89	107	97	130	107	125	110	111
1930	89	46	37	73	113	67	103	107	104	74
1920	106	109	97	84	85	96	92	85	77	93
1910	67	113	65	87	96	121	111	10	122	111
1900	84	86	91	101	112	80	91	46	81	96
1890	108	132	89	78	120	82	112	119	119	105
1880	96	89	111	89	124	106	115	123	128	102
1870	—	—	—	—	—	—	—	96	96	85
Cone Crop										
1970	107	24	11	12	174	50	121	7	158	144
1960	140	135	60	122	95	132	134	99	107	116
1950	108	127	109	132	103	97	79	126	107	81

(*Table 19 contd.*)

(*Table 19 contd.*)

Year	0	1	2	3	4	5	6	7	8	9
1940	111	62	116	111	85	81	107	139	107	136
1930	65	92	100	24	9	75	102	76	123	102
1920	131	132	130	104	110	101	101	107	83	73
1910	72	115	69	118	47	79	113	145	107	127
1900	128	115	86	98	118	94	142	68	92	58
1890	132	127	132	140	79	90	149	79	126	125
1880	96	66	103	111	83	116	88	83	111	132
1870	—	—	—	—	—	—	—	—	—	52
Black soil subzone, Altay State Reserve, Kyga profile, test plot 2[a], 1887–1979, 93 years Formation of Female Primordia										
1970	98	107	116	133	104	97	108	123	—	—
1960	101	96	78	113	117	95	98	105	113	92
1950	93	104	116	125	99	110	128	136	116	100
1940	114	111	134	136	105	137	122	128	109	114
1930	96	86	89	95	80	86	101	127	130	99
1920	45	105	101	132	87	92	84	91	109	90
1910	136	96	105	124	93	85	42	102	85	58
1900	102	26	128	38	102	102	102	89	89	119
1890	38	26	89	89	102	5	51	77	128	89
1880	—	—	—	—	—	77	128	5	102	102
Cone Crop										
1970	134	81	115	87	158	141	77	15	66	147
1960	130	113	91	115	87	135	131	75	106	120
1950	126	127	99	115	134	141	72	15	149	106
1940	141	92	129	134	153	159	101	167	133	127
1930	109	108	116	90	110	111	81	92	125	151
1920	70	54	56	115	104	149	72	97	78	78
1910	111	132	153	109	95	154	88	80	42	120
1900	142	6	111	16	142	47	95	111	95	111
1890	127	47	16	32	47	79	95	3	63	63
1880	—	—	—	—	—	—	—	95	158	3
Latitudinal profile Northern subzone, Tarko-Sale region, Yavoyakha river, 1840–1979, 140 years Formation of Female primordia										
1970	85	86	96	134	105	88	99	118	—	—
1960	69	73	86	86	96	72	92	114	117	86
1950	98	110	91	124	118	104	115	109	112	82
1940	110	113	113	104	109	107	105	106	91	83
1930	92	85	96	68	81	110	120	107	109	76
1920	106	107	127	96	105	138	112	122	124	108
1910	96	99	111	83	112	128	111	93	115	134
1900	110	101	62	114	95	118	114	99	104	99
1890	118	89	74	128	51	93	110	93	127	110

(*Table 19 contd.*)

(*Table 19 contd.*)

Year	0	1	2	3	4	5	6	7	8	9
1880	118	104	118	74	89	177	104	59	138	118
1870	89	89	89	118	89	104	149	89	104	104
1860	89	59	59	74	158	59	40	74	59	74
1850	118	104	89	74	74	104	104	74	44	74
1840	59	59	89	30	59	89	118	99	138	99

Cone Crop

Year	0	1	2	3	4	5	6	7	8	9
1970	165	83	106	118	118	201	95	95	142	83
1960	189	106	59	24	59	83	95	71	142	59
1950	47	95	59	106	35	83	142	83	83	130
1940	118	59	83	106	118	71	165	142	106	177
1930	130	95	83	71	130	71	35	95	118	95
1920	106	118	95	118	95	118	83	59	213	59
1910	106	59	71	24	118	71	106	201	118	118
1900	59	118	106	106	47	142	106	118	95	95
1890	236	236	59	154	35	201	71	83	83	118
1880	95	35	95	118	95	118	95	236	201	201
1870	35	59	59	35	59	95	154	154	213	35
1860	35	59	59	12	59	118	236	12	12	35
1850	236	35	201	177	12	59	35	95	95	59
1840	—	—	12	12	177	12	59	12	59	12

Central subzone, Tundrino region, 1890–1977, 89 years

Formation of Female Primordia

Year	0	1	2	3	4	5	6	7	8	9
1970	107	94	77	107	103	99	90	94	—	—
1960	112	69	107	116	86	112	82	103	133	69
1950	86	77	99	112	103	103	103	86	94	73
1940	103	124	116	129	112	73	99	103	120	77
1930	133	90	124	107	103	120	103	73	133	77
1920	86	56	107	64	107	103	94	86	103	99
1910	129	129	43	99	107	56	120	99	142	99
1900	129	107	43	86	129	129	129	107	107	107
1890	43	86	64	86	107	107	129	107	129	129

Cone Crop

Year	0	1	2	3	4	5	6	7	8	9
1970	221	87	150	63	71	181	24	126	142	8
1960	134	71	189	87	134	166	32	32	87	87
1950	103	47	55	71	95	166	8	166	142	32
1940	158	87	118	158	126	103	110	110	110	174
1930	55	126	71	103	166	110	87	181	110	24
1920	221	142	39	55	103	39	79	95	79	63
1910	39	118	79	158	79	103	39	103	118	79
1900	8	118	237	79	79	158	79	237	79	158
1890	—	—	8	8	118	8	158	79	39	8

(*Table 19 contd.*)

(*Table 19 contd.*)

Year	0	1	2	3	4	5	6	7	8	9
Southern subzone, Baza region, 1911–1979, 69 years Formation of Female Primordia										
1970	111	102	153	98	98	89	94	102	—	—
1960	115	98	89	68	102	77	47	111	111	51
1950	85	123	89	89	47	119	94	85	106	123
1940	115	119	94	106	115	94	145	85	111	89
1930	123	98	89	98	85	106	115	94	81	106
1920	102	89	123	111	47	132	89	89	89	98
1910	128	140	85	102	94	136	85	115	89	102
Cone Crop										
1970	196	71	180	39	267	86	125	71	165	173
1960	125	55	141	149	110	39	55	78	8	47
1950	39	47	47	86	78	86	47	173	71	63
1940	55	133	86	110	71	78	94	71	212	55
1930	78	71	188	78	31	133	71	149	165	55
1920	47	86	157	102	212	133	47	125	86	47
1910	—	55	24	133	141	94	125	204	39	141

74

Note. Average number of primordia and cones per shoot in subalpine subzone 1.21 and 0.64; in other subzones and sublevels 1.96 and 1.51; 1.96 and 1.58; 1.69 and 0.85; 2.33 and 1.27; and 2.35 and 1.27, respectively.

were clearly inadequate. In our case, the structure of linear growth has been studied on the example of the annual increment of skeletal cone-bearing branches which, judging from the available data, exhibit a high level of agreement with the linear growth process of trees.

The initial growth series of shoots is shown in Fig. 29. An ascending tendency of the growth curve can be seen. This fact together with adequate

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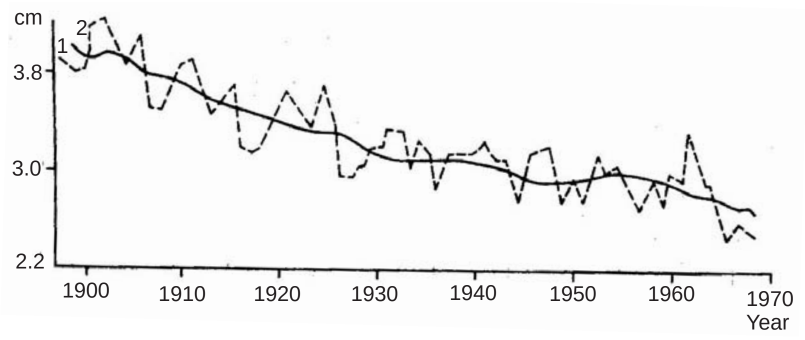

Fig. 29. Rising series of linear growth of female shoots:
1—initial and 2—sliding mean values.

number of observations help construct a non-stationary series for a stationary case by adopting appropriate methods (Cherkashin and Kuz'michev 1977 and Cherkashin, Vorob'ev, and Fattakhov 1981).

On the basis of a similar treatment of the series (see Fig. 21), a spectrum of aligned series of linear increment of shoots has been given before. It revealed a weak peak at a frequency of 26/80 and a strong one at 8/80 (years). The value of the latter is well marked on comparing the 10-year growth cycle of
74 shoots with the "white noise" level and the magnitude of the 3-year cycle of reproductive activity. The general variation of the main growth cycle falls within 7–17 years.

Structure of relations between growth and cone bearing of pine shoots is depicted in Fig. 30. The spectrum of coherence showing the relation between their length and the number of cones in all periods has a maximum at lower frequencies, i.e. at the level of the 10-year cycle. This has prompted the suggestion that the 3-year cycle of reproductive activity of shoots is poorly related to growth due to the dominant influence of current generations and also, as will be demonstrated later, due to a definite shift of relative cycles of growth and cone bearing. The area of maximum correlation between growth and cone bearing, however, falls in the low frequency range, specially within the 10-year cycle.

The nature of relations of these processes noticed at this level is quite complex due to apparent contradictions between growth and cone bearing. Nevertheless, many characteristic patterns are seen (Fig. 31). The most important among them shows that the cyclicity of cone bearing is shifted relative to growth in some time interval. The course of these processes reveals that shoot growth is induced initially under the influence of solar
75 activity and later, on this basis, the reproductive activity. Its peak activity corresponds to the downward branch of the solar cycle and the period of inhibition of shoot growth. The commencement of the next rise of harvest is associated with the preceding activation of solar activity and growth processes.

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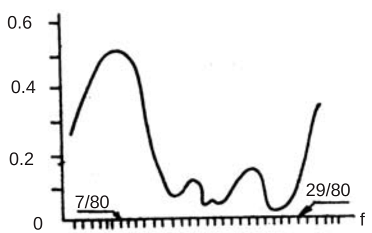

Fig. 30. Spectrum of coherence of relations between linear increment of female shoots and number of cones.

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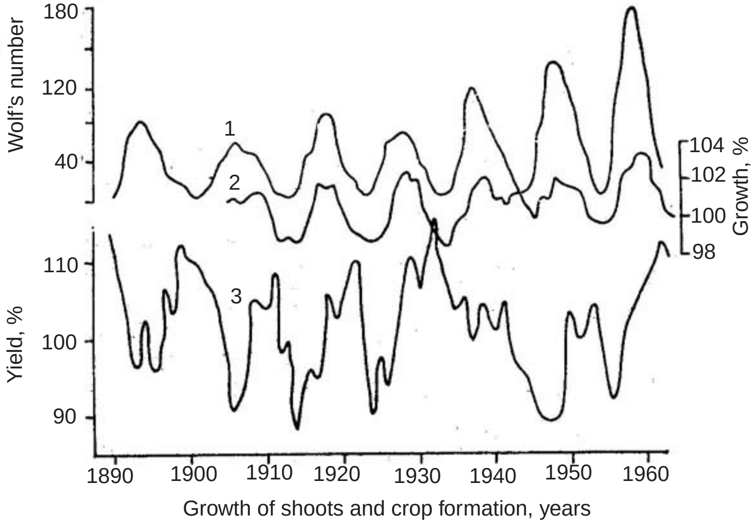

Fig. 31. Solar activity (1), cyclicity of growth (2), and crop size (3) of Siberian stone pine in the subalpine subzone of Gornyi Altay (on 15-year sliding of series converted to the average value).

On year-wise comparison of growth and cone bearing indexes of shoots, a contradictory relation between these processes is detected. This is clearly seen from the example of ontogenetic development of a single cone-bearing branch for which the measurements of linear growth of shoots, their diameter in the first year of growth, and the corresponding characteristics of reproductive activity were recorded (Table 20).

With the increase of shoot length beyond a certain optimum, not only the level of formation of female primordia falls, but also the subsequent retention of strobili and cones decreases. Examples of such relation between growth and cone bearing of shoots explains to some extent the reasons for "physiological" crop reduction (Nekrasova 1972) and our own assumptions

76 Table 20. Relation between growth and cone bearing of female shoots

Growth				Cone bearing (per shoot)					
Length		Thickness		Primordia		Strobili		Cones	
cm	%	cm	%	No.	%	No.	%	No.	%
7.6	100	0.7	100	4.0	100	3.8	100	3.8	100
13.8	189	0.7	100	3.4	85	3.3	86	2.9	76
22.3	293	0.8	114	2.8	70	2.3	60	2.0	52

that the program of shoot axis growth and the cyclic course of a single generation are determined in the period of bud formation (Vorob′eva and 76 Vorob′ev 1982). From the results presented, it is also important to emphasize the stability of the extent of cambial growth which has great importance, as stated at the beginning of this chapter, for sex development and reproductive activity of shoots.

The foregoing discussion shows that the variation of reproductive activity of Siberian stone pine in time bears a complex cyclic form which is typical of many biospheric and biological processes on the earth. This detected pattern of shifts of cycles of growth and cone bearing helps treat it as a basis for crop forecast and control. In the latter case, this should be included in computing the growth and cone bearing tendencies of trees before applying any measures for influencing them.

Intra- and Interpopulation Characteristics of Process Relations

A study of the variability of woody species is necessary not only for organizing the seed production in a forest but also for the management of the forest as a whole. One of the first stages in its study is to ascertain the potential possibilities of the species for breeding. This aspect is generally considered on its phytogeographic basis (Vavilov 1967). It is on these lines that L.F. Pravdin (1964) set out the problem of studying the intrapopulation and geographic variability of the major forest-forming species of Siberia. The observations recorded so far detected considerable variability of characteristics among coniferous species and predetermined the prospects of their breeding. Much attention was paid to the characteristics of productivity, growth, and resin yield of Siberian stone pine. A general botanical study helped in establishing the limits and level of variability in terms of space as well as time and arrive at fundamental concepts on the population structure of the Russian forests. The researches of S.A. Mamaev (1972) and A.I. Iroshnikov (1964 and 1972–1975) greatly contributed to the study of polymorphism in the coniferous species.

Contrary to the end of the ′70s with emphasis on intense practical selection of woody plants for studying their variability (specially of Siberian 77 stone pine), the study of correlations between economically valuable characteristics has now become important (Vorob′ev 1980–1982). These investigations are directly associated with developing specialized as well as optimal combinations of several characteristics of artificial plantations. The results of these observations have also an important bearing on the theoretical justification of comprehensive utilization of pine forests.

The study of relations of the indexes of productivity with growth and cone bearing of trees at intra- and interpopulation levels in these directions is called for.

Productivity of Siberian stone pine, understood as the seed output of trees in terms of ripe cones or weight of seeds, according to many investigators, is the most important factor in the context of comprehensive evaluation of its usefulness and breeding possibilities. A.S. Yablokov (1960) and L.F. Pravdin (1960 and 1964) paid special attention to this feature when setting out the problems for study and selection of productive forms. The suggestions available at present on their evaluation recommend consideration of the growth characteristics of trees (Vorob′ev 1974 and 1981). The basis for this should be the nature of relations between growth and reproductive processes with consideration of the above-cited aspects at the intra- and interpopulation levels.

This can be illustrated in the first case by the data on the structure of productivity of a single population of Siberian stone pine in Gornyi Altay (Table 21). These results were recorded on total felling of trees in a test plot falling in the lower part of the mountain-taiga subzone (900 m above sea level). The test plot was laid out when organizing the forest zone in which the author participated (Vorob′ev and Pertsev 1966).

The stand under consideration represents a plantation of different ages comprising I level of three basic generations of pine (257, 212, and 168 years) and II level predominantly of fir (128 years) and young barren pine trees (120 years). Trees of the second generation comprise the most in the I level (70%). As this generation is clearly dominating, the age composition of the plantation should be regarded, according to I.V. Semechkin (1971), as comprising nominally different-aged trees.

Value-wise, the stand should be regarded as of class II quality index with a high mean diameter of pine (55 cm) and average number of trees per unit area (pine 94 and fir 124/ha). These indexes characterize a developed, highly productive reed grass-green moss type forest.

For the purpose of studying the structure of productivity of the plantation, the trees of the leading generation were divided according to the number of cones into five categories of relative productivity. Their distribution according to categories did not reveal any age differences but showed significant deviations of productivity. In category I, for example, with 30% of the entire cone-bearing segment of the stand, the average number of cones per tree is just a quarter of that of the average tree. The proportion of
78 trees of this category in the overall crop does not theoretically exceed 8%, judging from the number of cones formed but is practically nil due to a large fall and the futility of tending to such trees when gathering nuts. Thus, from the breeding as well as forest management points of view, low-yielding trees are not of interest for being retained in the stand as they are very old with

78 Table 21. Intrapopulation structure of productivity of plantation (relative to an average tree in absolute terms—No. of cones/tree)

Statistical index	Diam., cm	Age years	No. per tree of			C_v of crop over 10 years	In 1 ha			
			cones	female shoots	cones/ shoot		trees		cones	
							No.	%	'000s	%
Category I, 0 – 0.50										
M	38.8	186.5	15.6	14.4	1.06	50.8	21	30	0.3	8
m	1.2	5.4	1.2	1.0	0.04	1.8				
C_v	22.7	20.3	54.6	49.0	27.80	25.8				
Category II, 0.51–1.00										
M	51.1	211.0	45.7	34.7	1.37	38.4	20	30	0.9	22
m	1.1	4.4	1.3	1.4	0.05	1.5				
C_v	15.8	14.7	19.3	28.3	18.90	27.0				
Category III, 1.01–1.50										
M	55.7	206.0	72.3	51.6	1.41	37.1	12	17	0.9	22
m	2.2	5.7	2.1	1.6	0.04	1.5				
C_v	21.2	14.8	15.6	16.3	15.30	21.6				
Category IV, 1.51–2.00										
M	69.9	223.7	99.2	74.4	1.36	38.6	9	13	0.9	22
m	3.9	7.0	1.8	2.6	0.04	1.7				
C_v	27.5	14.3	8.4	15.8	15.10	20.0				
Category V, above 2.01										
M	62.9	222.2	150.6	96.5	1.58	35.1	7	10	1.0	26
m	1.5	5.8	6.5	5.2	0.05	2.9				
C_v	10.1	10.8	17.9	22.3	14.70	34.4				
Average										
M	51.2	205.5	58.7	42.8	1.31	41.6	69	100	4.0	100
m	1.1	5.8	3.4	2.2	0.02	0.9				
C_v	27.8	17.1	73.8	67.0	23.40	29.7				

little prospect of a compensatory growth of the female level of crown by freeing it from under the forest canopy. Eliminating this segment of trees by selective felling would free the population from the "minus" specimens and 79 provide adequate quantum of timber without loss of overall nut yield from the plantation.

Trees of category II differ noticeably from the preceding ones in all the crop indexes: the number of cones on them is thrice more, number of traces on each shoot approaches the average level as also the variation coefficient of crops. With their numbers in the plantation almost the same as those of category I, this group provides 22% yield. At the same time, at least half of the trees in this group are of a relatively low rank with respect to productivity, and hence are also of little value like the trees of category I.

Trees of categories III and IV bear good indexes of cone yield. Forming 30% of the total number of trees, they account for 44% of the overall yield.

Trees of category V are of special interest. Their yield exceeds the average by more than 2.0–2.5 times; they also exhibit a high reproductive energy, better developed female level compared to even stout trees, and post steady yield dynamics. Representing only 7% of total in the stand, these trees give a quarter of the yield or almost 4 times more than the output of all the low-yielding trees. Trees with best yield are also characterized by good growth indexes—their diameter is 20% more than the average value.

The individual characteristics of such trees reveal significant variations with respect to many features (Table 22). This can be seen from the number of
80 cones per tree, reproductive energy of shoots, and crop dynamics.

79 Table 22. Characteristics of trees qualifying for plus category of yield

No. of trees	Diam., cm	Age, years	Number of cones per			Cone yielding shoots per tree, No.	C_v of crop over 10 years	Selection rank
			tree	cm diam.	shoot			
17	52	198	160	3.1	1.9	83	13.6	2.8
29	64	228	154	2.4	1.9	81	29.0	2.2
30	64	180	191	2.9	1.7	115	42.2	2.6
95	67	198	170	2.5	1.3	129	37.6	2.2
98	56	190	199	3.4	1.8	107	28.5	3.1
107	60	210	163	2.7	1.6	99	31.8	2.4
12	68	190	197	2.8	1.4	142	59.7	2.5
Group average	60	199	176	2.8	1.7	108	34.6	2.5
Generation average	51	205	58	1.1	1.3	43	41.6	1.0

Significant fluctuations are also characteristic of the diameter of trees. The differences noticed in this respect in the ratio of growth and cone yield of trees with excellent yield suggest the need to discuss thoroughly the principles of their evaluation and selection.

Several trees shown in Table 22 with a positive record were selected for their absolute yield using the binary square deviation. Further, a 3-fold increase of the main index has been achieved and several other characteristics of it were bettered. The evaluation of the growth of these trees showed that the yield of some of them is determined by their large diameters and the corresponding number of cone-bearing branches. However, trees with a similar yield but of a smaller diameter offer great interest since, on further growth, they yield more. Such trees can be selected by relating the value of yield to any one single index of productivity with respect to growth—diameter, cross-sectional area, or mass of timber (Vorob′ev 1974 and 1981). This approach has been sourced to the work of V.F. Ognevskii (1904) who studied the relation of tree dimensions with the extent of their yield for purposes of assessing the cone yield. According to L.F. Pravdin and A.I. Iroshnikov (1963), V.F. Ognevskii "came to a very important conclusion that the number of cones varies in direct proportion to the cross-sectional area of trunk at the chest height. He attempted to express this dependence mathematically as follows: $N : N_1 = G : G_1$, in which $N_1 = NG_1/G$, where N is the number of cones per tree and G the cross sectional area of the trunk". In this background, N.V. Tret′yakov in 1927 (cited by L.F. Pravdin and A.I. Iroshnikov 1963) suggested that "every morphological index should correspond to a physiological one" and that "the reproductive energy of a tree is a function of its rank in the plantation" (p. 135). Based on these theoretical premises, L.F. Pravdin (Pravdin 1932 and Pravdin and Iroshnikov 1963) and other investigators demonstrated the possibility of ascertaining the yield of a plantation from the characteristics of an average tree. The misgivings expressed in this context (Nekrasova 1960 and Zemlyanoi and Nekrasova 1981), because of the phenomenon of individual variability, do not have adequate justification since the application of the prevailing relation between growth and cone yield provides satisfactory results. However, its absolute reliance at the level of functional importance and general biological principles does not correspond to the actual structure of relations between the indexes and, at the theoretical level, is basically unreliable because of ignoring the phenotypic and genotypic variations. It is well known for example that a given diameter of the trees can correspond to several values of an associate index, in this case productivity. Hence, the ratios of the ranks of cone yield ($N : N_1$) and growth ($G : G_1$) of trees given above are not equilibria but represent microvariation series suggesting a statistical and not a functional relation between the above processes (Tkachenko 1952 and Vorob′ev 1974).

The positive nature of this relation renders it suitable for mean statistical determination of the value of one index through another as discussed above and also for fine-tuning their rank in the stand for selection purposes. In the latter case, the ratio of growth and cone yield on the example of diameter (d) and the number of cones (c) may be represented not as $c_x : c_{\bar{x}} = d_x : d_{\bar{x}}$ but as $c_x : c_{\bar{x}} / d_x : d_{\bar{x}}$ or later as $c_x \times d_{\bar{x}} / c_{\bar{x}} \times d_x$.

The rank of a tree based on its productivity can thus be calculated from the relative value of this index ($c_x / c_{\bar{x}}$) with correction for the inverse ratio of diameters ($d_{\bar{x}} / d_x$) or the coefficient of productivity of a given tree (c_x / d_x) with allowance for the regular as well as inverse value of this index for an average model ($d_{\bar{x}} / c_{\bar{x}}$).

The last equation is of interest for studying the ratio of the number of cones per unit diameter, which is regarded as a coefficient of productivity of the tree, by analogy and in principle, with the coefficient of productivity of the shoot (number of cones per shoot). A comparison thus of the energy of reproductive and growth processes permits differentiating the influence of genotypic basis of the characteristic from that of phenotypic conditions of its manifestation, thus determining the extent of shift of metabolic direction in the organism of the tree to one or the other side.

An appropriate analysis of the structure of the above segment of the population with respect to the ratio of growth and productivity of trees makes for their significant redistribution among categories of relative productivity. Table 23 shows that, compared to the original assessment of trees on the basis of absolute yield, a part of the trees with poor yield moved from the category I to II. The group of trees with poor yield was left with the least productive trees which should be eliminated in the first instance during selective felling. The group of positive category of trees became more prominent. It contained only those trees which possessed the maximum indexes of productivity by the preceding method of evaluation.

Based on the above discussion, the change of rank relations of the indexes can be studied within the distribution limits of one of them. It may be seen from Fig. 32 that a linear increase of productivity the leading index in this case, is accompanied initially by a similar course of an associated index (diameter of tree) and later its change from a positive to negative correlation. In the zone of intersection of rank evaluation, the correlation records maximum proximity, suggesting an adequate theoretical justification for the method of determining the productivity of plantations on the basis of trees of average stoutness. The positive correlation of indexes weakens in the highly productive section of the distribution series of the leading index. Extent of deviation of this index from the associated characteristic depends on the sign and number of trees bearing this index. In the case of a tree with excellent productivity

82 Table 23. Intrapopulation structure of productivity of the plantation (with respect to an average tree in relative indexes—number of cones per cm diameter)

Statistical index	Diam., cm	Age, years	Cones/cm diam., No.	No. per tree of			C_v of crop over 10 years	In 1 ha			
				cones	female shoots	cones/shoot		trees		cones	
								No.	%	'000s	%
				Category I, 0 – 0.50							
M	39.8	185.2	0.30	12.8	12.8	1.00	52.7	17	25	0.2	5
m	1.5	6.6	0.02	1.2	1.3	0.04	2.2				
C_v	23.4	22.2	47.10	57.2	55.0	28.50	25.7				
				Category II, 0.51–1.00							
M	53.3	212.2	0.80	45.5	34.8	1.34	38.9	26	38	1.1	30
m	2.0	4.1	0.02	2.2	1.7	0.03	1.3				
C_v	30.1	15.3	19.60	37.8	39.8	17.70	26.9				
				Category III, 1.01–1.50							
M	55.7	205.7	1.40	78.4	54.5	1.46	38.0	14	20	1.1	27
m	1.7	5.1	0.03	3.1	2.4	0.01	1.4				
C_v	17.4	14.5	11.80	23.0	25.9	14.60	21.3				
				Category IV, 1.51–2.00							
M	56.3	219.0	2.00	106.5	78.7	1.37	37.7	8	11	0.8	19
m	2.2	5.4	0.06	9.3	4.2	0.05	2.0				
C_v	17.2	11.1	13.70	22.4	23.8	18.30	23.7				
				Category V, above 2.00							
M	61.9	201.5	2.70	169.4	105.0	1.64	35.4	4	6	0.7	19
m	2.0	5.1	0.10	7.1	6.8	0.07	4.2				
C_v	9.6	7.5	14.60	12.5	19.5	13.50	35.8				
				Average							
M	51.2	205.5	1.10	58.7	42.8	1.31	41.6	69	100	4.0	100
m	1.1	5.8	0.05	3.5	2.2	0.02	0.9				
C_v	21.8	17.1	63.70	73.8	67.0	23.40	29.7				

(No. 98), for example, the rank of the leading index is 3.4 and the diameter corresponding to it 1.1.

Such relationship between indexes is characteristic of not only intra- but
also of interpopulation variability. The section of pine forest in Gornyi Altay
83 (area 3000 ha) selected in this manner, i.e. by taking into consideration the
productivity indexes relative to growth and cone production, showed that

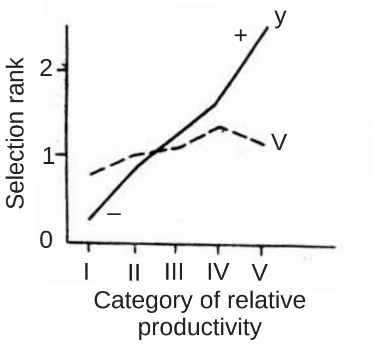

Fig. 32. Ratio of growth (V) to yield (y) of trees according to ranks (here and later, "+"
81 denotes plus and "–" minus).

highly productive plantations possess a moderate timber stock and, on the contrary, stands that hold promise for growth exhibit only poor productivity (see Table 89).

The heterogeneity of relations between indexes within a particular distribution series suggests genotypic isolation of a part of the trees under consideration and their freedom from the dominant form of relationship. The need for an independent study and the utilization of normal and plus portions of given series of indexes is apparent. In this context, attention should be drawn to the relation between the extent of growth and cone production of trees in the minus segment of the leading index. As shown in the given model of relations of indexes (see Fig. 32), manifest in the form of a "scissors" (Vorob'ev 1980 and 1982), a high value of the associated factor corresponds to the low value of the leading factor. This shows that when evaluating the trees with minus values of one of the characteristics, the value and state of the other index should also be considered. A multipronged approach to analyzing and selecting the indexes forms the foundation for raising plantations with an optimum genotypic composition.

The characteristics of trees in the plus zone show the possibility and usefulness of utilizing not only the evaluation of the indexes into ranks but also adopting fairly rigid selection criteria. The present practice is to raise the selected characteristic above its average value plus two sigma. Majority of specialists engaged in resin production from coniferous plants (see Chapter III) advocate the desirability of using a criterion of 2.6 sigma which distinguishes the normal series of distribution of the index from specimens belonging to a different biological entity. The high variability of pine yield and the frequent visibility of trees of such type fully justify relying on such a criterion. At an average variability level of 50%, the excess of the best trees with respect to yield at 2.6 sigma is 2.3 times and at 3.0 sigma 2.5 times. In such a selection system, specimens with maximum values of several indexes of productivity fall into the selected lot of plus category of trees. The number of cones per cm diameter approaches three units which, in our view, is an essential criterion, and to two units per shoot at crop variation coefficient below 20–30% (trees No. 17 and 98).

Such a combination of characteristics is not common and as such at a very high level of forest selection, trees should be selected not only for their seed productivity but also for their other indexes, specially the variability of crop dynamics. This is important when the available methods of stimulation (forest management practice, agricultural, and mechanical) cannot yet influence the natural course of crops and hence the optimization of 84 populations for their stable cone yield is of extreme interest (Vorob′ev and Vorob′eva 1980).

Based on the data available on the structure of this index, the trees of the above population can be distributed into the following groups:

I. Extremely irregular cone yield—C_v 77%, proportion of trees in the group 6.5%.
II. Irregular cone yield—C_v 51%, proportion of trees 37.9%.
III. Moderately irregular cone yield—C_v 41%, proportion of trees 50.9%.
IV. Regular cone yield C_v 18%, proportion of trees 4.7%.

It may be seen that a variability coefficient of 20% is an adequate criterion for the selection of trees by this characteristic. According to it, tree No. 17 in Table 22 forming 1.4% can be placed in the plus category.

Trees with regular cone yield are best identified in the barren years, as also suggested by A.I. Iroshnikov (1964). At this time, trees of this category or those which exhibit a crop cyclicity different from that of the bulk of the plantation can be detected. It would thus be interesting to search for trees with late phenological development that enables them to bypass the frosting season when the bulk of pine losses occur (Vorob′ev 1974).

The factor for selecting the plus category is lower for some trees because of the lower variability of the overall indexes. In the data given later (see Table 89), a factor of 1.5 sigma has been used although selection is quite possible with two sigma. These and other aspects related to the selective inclusion in pine forests and organization of their comprehensive management have been examined in Chapter V. It is important at present to emphasize the dependence of the selection factor on the level of variability of characteristics.

An analysis of the productivity of Siberian stone pine, taking into consideration the forest types, age, and quality classes within the altitudinal subzones, shows that the seed output of average trees in a plantation and the coefficient of their productivity vary greatly (Table 24).

85 Table 24. Indexes of interpopulation relations of productivity with the growth of trees

Quality index	Group of forest types	No. of cones in an average crop for different age groups of trees, years					
		121–160		161–200		201–240	
		per tree	per cm. diam.	per tree	per cm. diam.	per tree	per cm. diam.
		Black soil subzone					
II	Tall grass-fern	80	2.0	100	2.3	125	2.5
III	-do-	60	1.6	90	2.0	110	2.3
		Mountain-taiga subzone					
II–III	Green moss	75	1.8	110	2.3	135	2.6
II–III	Green moss-grass	95	2.7	115	2.8	175	3.8
		Subalpine subzone					
IV	Tall grass	50	1.5	70	1.6	80	1.7

The number of cones in years of average crop varies from 60 to 175 per tree or 1.6 to 3.8 per cm diameter. Plantations in black soil subzone, tall grass pine forests with quality index II in the age group 201–240 years, and those in mountain-taiga subzone, grass-green moss type with quality indexes II–III, also of 201–240 years age group, are most valuable for purposes of selection, retention and breeding productive forms.

Differences in the subzones are due to changes of relations between productivity and growth and regenerative processes, initially in favor of the latter. The shift of ecological optimum for cone production of plantations toward mountain-taiga subzone was demonstrated before on the example of
85 their seed productivity (Lebedinova 1952 and Vorob'ev 1967 and 1974a). This subzone was studied relative to the cyclicity and a distinct fall of reproductive organs due to the activity of growth processes in the lower part of black forests; in the present case, a shift of the optimum is noticed in the change of ratio between growth and productivity of trees.

The prevailing objections to this view are apparently associated with the one-sided evaluation of high ecological indexes of climate and soils of black forests (Talantsev, Pryazhnikov, and Mishukov 1979). However, the potential possibilities of these conditions are realized mainly in the activation of growth and formation of large trees possessing a low reproductive energy, compared to the mountain-taiga trees, not only in relative but also in absolute values, specially in terms of per unit area. When organizing seed plantations in the lower parts of mountains, the effect of some of the restraining factors, specially the domination of fir trees in the composition of the plantation which find here an optimum zone, can be weakened by controlled felling. However, the predominance of growth activity and corresponding crop loss at this level in the mountains call for much effort for their control. It would therefore be advantageous to distinguish optimum growth and cone yield of pine according to the management recommendations.

Beyond the optimum cone yield of pine in the mountains, the radial growth activity of trees decreases at a slower rate than their seed output. As a result, differences between timber reserves in black soil and subalpine pine forests are not so significant as the level of yields (Vorob'ev 1964 and
86 1974a). For example, three main test plots in the altitudinal section of Kyga profile (450, 1250, and 1850 m above sea level) show variation of timber reserves at 396, 470, and 340 m^3/ha while the average crop yield over 10 years was 164, 227, and 68 kg/ha, respectively. In this case, the ratio of seed output to timber yield in these plantations was respectively 0.4, 0.5, and 0.2 kg/m^3.

In the latitudinal ecological section, the ratio of growth to cone yield of pine trees is also characterized by many features. The four regions of Gornyi Altay described in Chapter I falling from the meeting point of pine with larch (500 mm precipitation/year) to the zone of predominance of fir forests (900 mm precipitation/year) were used for their study.

It is clear from Fig. 33 that, as humidity rises, the radial growth of trees increases and their seed output too rises but not proportionately. The reason for this is that the optimal reproductive activity of trees at these altitudes is in favor of lower humidity but growth in favor of higher humidity. As a result, the ratio of the yield of trees to their growth touches the maximum values in

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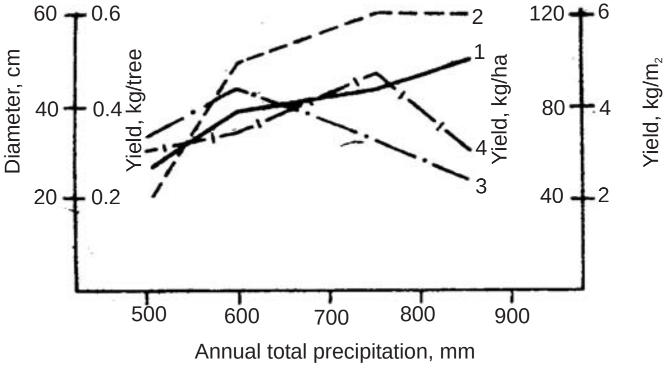

Fig. 33. Relation of growth and plant yield under conditions of subalpine subzone: 1—diameter of trees, 2—weight of seeds from an average tree, 3—per m^2 cross-section, and 4—per ha.

the zone of annual precipitation of 600 mm (at the base of the profile) and total productivity at precipitation of about 750 mm.

The foregoing discussion indicates the diverse relations between growth and cone yield of Siberian stone pine, their dependence on ontogenetic, ecogeographic, and other factors. It is necessary, and possible, to apply these relations between growth and reproductive processes when formulating the various measures, specially when raising plantations and controlling their activity. The essential basic approach to resolving these problems, on one hand, is to combine all aspects of the relations studied into a unified system of measures and, on the other, to differentiate their application not only in relation to growth and cone yield but also, in the first case, to control apical and cambial activity of shoots and the tree as a whole and, in the second case, the male and female reproductive processes.

Effectively influencing the relation between growth and cone yield at the ontogenetic level should lead at first to the activation of primary, later secondary processes while maintaining between them an optimal equilibrium in the later stages. From this standpoint, a scheme for experimental manipulation of the reproductive activity of Siberian stone pine has been incorporated in Chapter IV and Conclusion.

CHAPTER III

Cone Yield and Resin Productivity of Siberian Stone Pine

The study of cone yield and resin productivity of coniferous plants under conditions of undisturbed metabolism is of interest for taking advantage of their relations when selecting trees based on all the characteristics and for theoretical justification for combining tapping and nut production in an integrated economy.

The information available at present describes the relations between the above processes as positive (Prokazin 1959), opening up definite prospects in the breeding of coniferous plants (Efimov, Vysotskii, and Beloborodov 1981). Our data on this subject necessitates introducing some modifications in the prevailing concepts (Vorob′ev 1970, 1979, and 1981). They differ similarly from evaluating the relations between resin productivity and growth.

Among the problems concerning resin productivity of coniferous plants, the conditions and mechanism of biosynthesis of terpene compounds occupy an important position. Contemporary investigations in this direction have yet to attain the required level. Practically, from the time of G.V. Pigulevskii (1939) and L.A. Ivanov (1940), the most important area of dendrophysiology, according to B.P. Kolesnikov (1966), is not being advanced to meet the requirements of breeding operations with emphasis on resin productivity and find a theoretical justification for stimulating resin formation and its exudation.

In our country, N.A. Khlebnikova (1963) and Yu.E. Novitskaya (1967a, b) initiated original investigations which opened up a new phase in the field of physiology of resin-forming processes and identify their importance in the plant's life. Our data to some extent extend in the direction of these investigations but mainly on the influence of tapping on cone yield of pine

(Vorob'ev 1970, 1973, and 1974a, Vorob'ev and Pryazhnikov 1970, Vorob'ev Dubovenko, and Pentegova 1971 and 1977, Vorob'eva 1974, and Vorob'ev, Vorob'eva, Sviridenko, and Kolesov 1979). The recent monograph of A.E. Vasil'ev (1977) dealing with the functional morphology of secretory plant cells has made a significant contribution to the study of biosynthesis of terpenoids. The observations of E.E. Lazda (1975) are of interest in this context. Original concepts have been developed in the field of biochemical evaluation of the role of biosynthesis of terpenoids in the evolutionary advancement of species and forms in the pine family (Poltavchenko and 88 Rudakov 1973). Investigations on physiological-genetic conditions of resin productivity in many coniferous species (Avramenko and Vysotskii 1982) and also in general on aspects of the physiology of resin formation and exudation (Sobakinskii et al. 1978) hold promise. The above directions point to the growing interest on related studies in the recent years. The attention paid to these subjects even abroad is also evident. In the foreign literature, works have been published dealing particularly with an analysis of concepts on the biosynthesis of terpenoids (Dieter 1981).

Resin formation and exudation in conifers represent complex physiological-biochemical phenomena. Terpene synthesis completes the cycle of many chemical conversions and, in this sense, some investigators interpret it as a process of producing end products which play a dominant protective role in the body of the tree.

At the same time, a study of the biosynthesis of terpenes using isotopes (Sukhov 1956) and the isolation of growth inhibitors from pine galipot (Vorob'ev, Pentegova, and Raldugin 1979) at the Novosibirsk Institute of Organic Chemistry, Siberian Division, Academy of Sciences, USSR, point to their more complex importance in the metabolism of coniferous plants (Bernard-Dagan 1961) than was assumed so far. Several hypotheses exist at present to explain to some extent the resin formation and exudation processes.

According to Eiler (1905), terpene synthesis is associated with the fermentation of carbohydrates in an alcoholic medium as a result of which acetaldehyde and acetone are formed. The reactions between the latter results in β-methylprotonic aldehyde, the subsequent condensation of its two molecules yielding monoterpene (geraniol) and of more of these molecules forming polyterpenes.

O. Askan (cited after Kretovich 1956) developed his own carbohydrate hypothesis and proposed a different route of disintegration of precursors. He suggested that oxidation processes result in the production of acetaldehyde and acetone which yield isoprene on condensation. This isoprene cell represents a direct starting link in the formation of terpenes, resulting in polyisomerization. It is now established that the starting material is acetaldehyde (Bonner 1965). The formation of the latter in turn is associated with processes of anaerobic respiration.

The present understanding on the relation between resin formation processes and anaerobic respiration is fully reflected in the studies of Yu.E. Novitskaya (1967a, b) although it was proposed first by N.A. Khlebnikova and developed by her school (Khlebnikova 1963, Khlebnikova, Girs, and Kolovskii 1963, Khlebnikova, Mogileva, and Rastorgueva 1963, and Mogileva 1965 and 1970).

Terpene compounds represent reduction products (Kossovich 1948, Zubkova, Kolmazon, and Okuneva 1948, and Ivanov 1961) and hence their formation under natural conditions (or under the influence of artificial
89 conditions) should modify the state of redox processes. B.A. Rubin (1955) assigns exclusive importance to the latter as they unite into a single process the metabolism of proteins, carbohydrates, fats, and nucleic acids and other compounds of living cells. E.V. Artsikhovskaya and B.A. Rubin (1954) assign a leading role to respiration in the adaptation of plants to unfavorable environmental conditions and point out that the domination of aerobic or anaerobic phase of respiration depends on the aeration conditions in the cells. The investigations of F.V. Shatilov (1937) in particular and others showed that anaerobic respiration in trees is the main phase of survival in winter. Thus, resin formation under conditions of undisturbed metabolism should be associated with this type of respiration in some form. The observations of V.A. Petrova (1968) showed that, by December, the content of resinous matter in the needles of several coniferous species increases from 7% to 12%.

Respiration phases are controlled by a specific group of enzymes. The aerobic phase, for example, is associated with such oxidizing enzymes as catalase and anaerobic phase with peroxidase. The state of anaerobic respiration may also be characterized by the reducing ability of tissues. The available data show that, during winter, the catalase activity is characterized by insignificant fluctuations while the reducing capacity of tissues is high (Khlebnikova, Mogileva, and Rastorgueva 1963). Other investigators also cite similar data. L.F. Voroshil’skaya (1950), for example, in her dissertation on respiration and redox systems of coniferous species detected maximum intensity of respiration and peroxidase activity in the needles during winter and their reduction from the commencement of vegetation. L.I. Sergeev and K.A. Sergeeva (1964) as well as G.M. Kozubov (1974) came to similar conclusions. Kozubov in fact determined the activity of peroxidase in the reproductive organs which, in the concluding stages of their growth, represent abundant sources of resinous matter.

Thus, the energy required by the plant for physiological-biochemical processes in late autumn, winter, and early spring is formed, according to Yu.E. Novitskaya (1967), by anaerobic respiration. During this process, as stated before, intermediate products like acetaldehyde and acetone are formed and serve as the raw material for the synthesis of terpene compounds.

In spring, the anaerobic phase of respiration is replaced by aerobic in the light of overall activation of metabolism (Khlebnikova, Mogileva, and Rastorgueva 1963). Processes of resin formation are noticed only in the newly formed tissues (growing cells of phloem and xylem, needles, and reproductive organs) where appropriate conditions for anaerobic respiration arise as a result of increased inflow of plastic material and water.

N.A. Khlebnikova et al. (1963) reported the predominance of the
90 aerobic phase of respiration in summer and ascribed it to the temperature conditions. The activity of catalase, for example, is manifest in the temperature range +10 to +20°C. The daily and seasonal temperature changes during growing season create periodic hurdles in the course of respiration intensity and catalase activity. At this time, respiration proceeds under anaerobic conditions. Literature on the problems of tapping cite data of daily and seasonal dynamics of resin flow from the exposed gashes in the phloem and xylem tissues on the trunk. Thus, respiration during growing season evidently involves both the phases, aerobic and anaerobic, thus largely explaining the resin formation conditions when the entirety of tissues is disturbed.

In general, however, the characteristics of terpene synthesis under conditions of tapping are associated with the mechanism of resin exudation and the nature of damage of the transporting ducts in the tree. It is known that inflicting cuts on a tree results in intense clearing of resin ducts from galipot. Up to 80% of its seasonal yield flows out in the first few days (Kutuzov 1951, Kulakov 1971, and Mel'nikov 1975). Subsequent exudation proceeds for example at 0.02–0.04 g/cut/day (Kulakov 1971) suggesting, on one hand, the overwhelming importance of the initial energy of terpene synthesis in the resin-producing trees and, on the other, the low rate of their fresh formation under the prevailing conditions. Fresh formation depends on the reorganization of the metabolism of damaged cells around the cut, the regenerative capacity of tissues, and functional characteristics of resin ducts.

Several studies have shown that the nature of disturbance of transport ducts in the tree promotes the mechanism of resin formation through accumulation of carbohydrates above the cuts and adequate availability of water to this zone. One or the other of these conditions determines the shift of redox processes toward a predominance of anaerobic respiration (Sabinin 1927 and Kokin 1939).

Studies on the physiology of resin-forming processes are mainly associated with tapping and are examined below. In the present case, it would be advantageous to pay attention to the differences between normal and high resin-producing forms.

For high resin-producing trees, according to several investigators (Shul′gin 1973 and Sobakinskii, Kabanov, Bragova, and Sobakinskaya 1978), the characteristic features are a high content of carbohydrates in the needle as well as abundant water supply to the tissues and photosynthesis activity (Shul′gin 1973). The latter is increased as the exudation of galipot increases but not without a limit; our investigations (see Chapter IV) have shown that an exceptional disruption of root-leaf contacts suppresses photosynthesis. Resin exudation is positively associated with the osmotic pressure of cell sap. The rank of trees according to this index is uniform throughout the season and, as a physiological factor depending on the genotype of the tree, may be used for selecting resin-producing trees of plus category (Pardos Carrion, Solis Sanchez, and Moro Serrano 1976).

91 The high content of carbohydrates does not always make for high resin productivity of the trees and hence several suggestions have been made about the importance of overall resources of plastic substances in the crown (Shul′gin 1973). Their overall increase may explain the detection of highly resin producing forms among trees with broad and dense crown (Prokazin 1959 and Vasilevskaya 1960). Insofar as resin-producing forms of trees with a narrow and open crown are concerned, the energy of resin formation is evidently largely associated with the high rate of photosynthesis (Golomazova, Minina, and Shemberg 1978).

The assimilation system of high resin producing trees is characterized by a high content of green and small content of yellow pigments (Sobakinskii, Kabanov, Bragova, and Sobakinskaya 1978). In many cases, however, their differences are not significant (Shul′gin 1964).

For the above forms, a low activity of oxidizing enzymes (peroxidase and catalase) is typical. This suggests the shift of redox reactions toward reduction and increased formation of reduced products (Sobakinskii et al. 1978).

In the latter case, it would be interesting to compare the qualitative and quantitative compositions of monoterpenes and resin acids in the resin-producing forms. According to the data of E.P. Prokazin (1959), turpentine of highly resin producing pine trees has a low specific gravity and low refraction coefficient. It has accordingly been suggested that high resin-producing forms have a high content of α-pinene and low content of Δ^3-carene. This assumption has been justified for the composition of turpentine from galipot (Bardyshev, Zen′ko, Gorbacheva, Prokazin, Chudnyi, and Kulikov 1968), core wood of parent stock, and to a small extent in seedlings (Prokazin, Chudnyi, Bardyshev, Zen′ko, Gorbacheva, and Karachun 1976). This pattern of the composition of monoterpenes has been traced to the level of moderately and highly resin producing species of pine.

In Crimean pine differing from Scotch pine in high resin productivity, the turpentine of galipot essentially contains α-pinene (Bardyshev, Mal'tsev, Zen'ko, and Prokazin 1971). As a result, the ratio of α-pinene to Δ^3-carene in Scotch pine is <1 and in Crimean pine >1 (Akimov, Nilov, and Lishtvanova 1973).

These patterns reveal certain exceptions due to inadequate correlation of the index with terpene composition as well as possible deviations when selecting trees using indirect indexes (shape and color of cones). Significant variations are caused by different types and chemo-phenotypes of terpene biosynthesis (Chudnyi 1977). For some reason or the other, several investigators have not detected the relation between monoterpenes and resin productivity (Voronchikhin 1973 and Baumanis 1977).

On the whole, it has been argued that the type of biosynthesis of terpenes 92 is controlled at the gene level (Rudloff 1972) and is inherited during free pollination and grafting (Prokazin, Chudnyi, Bardyshev, Zen'ko, Gorbacheva, and Karachun 1975, and Baumanis 1977). In several cases, however, heredity is not guaranteed. Thus, when studying the composition of galipot in pine hybrids and grafts (*Pinus contortax* and *Pinus banksiana*), characterized in the first type of biosynthesis by a predominance of α- and β-pinenes and in the second by a predominance of β-phellandrene, Δ^3-carene, and partly pinenes, a satisfactory model of heredity could not be derived as terpenes of second type were not detected in the second and third generations (Zavarin, Critchfield, and Snajberk 1969). These investigators suggest that the participation of specific enzyme systems in the biosynthesis of terpenes facilitated independent production of a large quantity of compounds of the first type. The particular inheritance of terpene composition thus points, on one hand, to the complexity of these processes and, on the other, to the possible factors that disturb correlations with the level of resin productivity.

In Siberian stone pine as also in Scotch pine, the main components of monoterpenes are α-pinene and Δ^3-carene (Pentegova 1960 and Chudnyi, Mishukov, and Il'ichev 1980). A.V. Chudnyi et al. identified three types of biosynthesis of terpenes in pine. The ratio of α-pinene to Δ^3-carene in these three types differ, right up to the predominance of the latter. Our observations are on the type in which α-pinene has a significant participation.

The data given below were recorded at the Zh.V. Dubovenko Institute of Organic Chemistry, Siberian Division, Academy of Sciences, USSR. Samples were collected in 1975 from moderate and high resin producing trees. Galipot was processed by the well-known method (Shmidt, Lisina, and Pentegova 1964).

It has been established that, unlike in Scotch pine, high resin producing trees of Siberian stone pine have a low content of α-pinene and a high content of Δ^3-carene (Table 25). However, the observed differences are not as

92 Table 25. Composition of monoterpenes in galipot of resin-producing forms, % of total content

Monoterpene	Resin productivity	
	average	high
α-pinene	75.3 ± 0.7	67.8 ± 0.5*
Fenchene	+	+
Camphene	0.5 ± 0.1	0.6 ± 0.2
β-pinene	7.6 ± 0.5	8.8 ± 0.5
Δ^3-carene	10.2 ± 0.5	13.2 ± 0.4*
Myrcene	0.7 ± 0.1	0.8 ± 0.1
Limonene	0.7 ± 0.1	1.0 ± 0.1
β-phellandrene	4.1 ± 0.1	5.6 ± 0.1*
γ-terpinine	+	+
Terpinolene	0.7 ± 0.1	0.9 ± 0.1
η-cymene	+	+
% of turpentine	23.4	22.5

significant as under different tapping conditions (see Chapter IV) but are clearly conclusive and characterize an intense protective system in high resin producing trees. This feature is largely associated with the high content of Δ^3-carene in larch and pine (Isaev and Ryzhkova 1968 and Massel′ 93 1979).

More significant changes are noticed in the quantitative composition of resin acids (Table 26). While no deviations were detected in their content in the high resin producing forms of Scotch pine samples (Sobakinskii, Kabanov,

93 Table 26. Composition of resin acids in galipot of resin-producing forms, % of total content

Resin acid	Resin productivity	
	average	high
Δ^8-isopimirate	1.0 ± 0.1	1.7 ± 0.3
Pimirate	0.7 ± 0.3	1.9 ± 0.4*
Sandarac pimirate	1.1 ± 0.3	2.1 ± 0.3*
Palustrate + levopimirate	6.4 ± 0.3	+
Isopimirate	15.6 ± 1.2	28.7 ± 1.5*
Dehydroabietate	5.3 ± 0.2	20.0 ± 0.6*
Lambertionate		
Abietate	64.7 ± 1.9	45.1 ± 2.1*
Zeoabietate	5.7 ± 0.3	+*
% of resin acids	62.4	62.9

Bragova, and Sobakinskaya 1978 and Bardyshev, Bulgakov, Udarov, and Zimina 1979), in the galipot of Siberian stone pine, a distinct predominance has been noticed of isopimirate, dehydroabietate, and a low content of lambertionate, the latter the main constituent of resin acids. No differences in their total exudation as also in the amount of turpentine were detected between the different forms of pine. High resin-producing Scotch pine trees, compared to those with moderate, yield a higher quantity of turpentine (Sobakinskii, Kabanov, Bragova, and Sobakinskaya 1978).

Resin-producing forms also exhibit physiological differences in the composition of seeds—products of the reproductive system. These aspects are discussed below. It must, however, be emphasized here that the active synthesis of the toxic portion of monoterpenes and possibly the associated changes in the ratio of resin acids suggest a shift of redox processes of resin-producing forms towards corresponding reduced products, a very high level of protection of such trees, and prospects of using them for breeding.

Resin Productivity

Resin productivity of pine trees is understood as the metabolically facilitated capacity of plant cells to form terpene and similar chemical compounds and to exude some quantity in the form of galipot depending on the genotypic, phenotypic, and technological conditions.

94 The study of resin productivity is most important from the practical standpoint relative to intrapopulation variability. A study of the breeding structure of plantations, methods of assessment of characteristics, and criteria for selecting high resin producing forms are of interest. These aspects have special importance for Siberian stone pine in which these studies began quite recently (Mishukov and Kulakov 1970, Il′ichev and Kulakov 1977, Il′ichev 1979, Demidenko, Il′ichev, and Urusov 1979, and Chudnyi, Mishukov, and Il′ichev 1980).

Observations of the resin productivity of Siberian stone pine and its relation with growth and cone yield were recorded by us in Gornyi Altay in Kara-Su and Syulyuzen′ sections (1967), Bulandu-kol′ (1971–1974), and Samysh (1975).

The individual variability of pine with respect to resin productivity within a moderate degree of thickness and within a population was studied in the first two sections. In both the cases, correlations of resin productivity with the growth characteristics of trees were studied. The characteristics of plantations and average models of pine are given in Chapter IV.

In Samysh river basin, characteristics of growth and cone yield of 17 plus category of trees with respect to resin productivity selected by us and included in the genetic reserve of pine forests of Altay Board of Forest Management were studied. The high resin-producing trees were found in the single age group of 180-year-old plantations of class III of quality index after 3–5 years of tapping. Each of the plus category of trees was selected in sets of five similar trees of equal diameter and average resin productivity. The differences between moderate and high resin producing specimens were established as between two variation series.

Most of the investigations were carried out in Bulandu-kol′ section, targeted towards individual and annual variations of pine with respect to resin productivity, its relation to growth and cone yield, and characteristics of plus category of trees selected under conditions of undisturbed metabolism. The test section lay in the lower part of mountain-taiga subzone (900 m above sea level) on the gently inclined south-western slope along Bulandu-kol′ taiga lake (see Fig. 1). The plantation consisted of 9P1F (9 pine, 1 fir), tall grass type forest, class II of quality index, and stand of ages of trees: I generation 260–280 years, II 200–220 years, and III 160–180 years. The plantation as a whole is large-sized, with average diameter 58 cm, height 30.8 m, and fairly sparse, gently inclined crown, and trees standing apart. Their yield was established from traces of cones in each of 150 trees for 10 years. Resin productivity was determined by the method of triple tapping at 10-day intervals on both sides of the tree in the latter half of July. The resultant yield of galipot was calculated per dts (cm) of section (specific resin productivity). Resin productivity under tapping conditions was established by calculating per cm of fresh cut or per tree (for the resin producing forms in Samysh section).

The parameters of growth, cone yield, and resin productivity of trees
96 exhibit differences between generations (Table 27). With growing age, while indexes of overall productivity (diameter, number of cone-bearing shoots and number of cones, and anticipated yield of galipot) rose significantly, the "specific" characteristics (proportion of sapwood, its growth, number of cones per shoot and unit diameter, and yield of galipot per unit section) changed little. A fairly stable size of sapwood is noticed which generally suggests a weak variability of specific resin productivity relative to age and diameter of the tree.

Insofar as the annual variability of resin productivity is concerned, its range varies from 5 to 20 g/cm of section. Therefore, the resin productivity of plantations should be determined at least over three years or in one summer with average weather conditions. Otherwise, relying exclusively on the plus category stands (Il′ichev 1979), they may be classified as good in one case (1974) and as poor in another (1972) (see Table 27).

Rank-wise placement of trees is generally regarded as holding good for resin productivity (Mishukov and Kulakov 1970 and Baumanis 1977). According to the data of N.P. Mishukov and V.E. Kulakov collected in the

95 Table 27. Characteristics of growth, cone yield, and resin productivity of trees in Bulandu-kol′ experimental section

Index	M ± m	C_v	Generation-wise		
			I	II	III
Growth					
Tree					
diameter, cm	58.0 ± 1.4	26.8	69.0 ± 1.9	57.1 ± 1.4	35.8 ± 1.5
growth in 10 years, cm	4.0 ± 0.05	13.2	4.3 ± 0.1	4.0 ± 0.07	3.3 ± 0.08
Sapwood					
breadth, cm	2.2 ± 0.04	20.2	2.2 ± 0.06	2.2 ± 0.06	2.0 ± 0.1
area, m^2	0.03 ± 0.001	45.2	0.04 ± 0.002	0.03 ± 0.002	0.02 ± 0.002
%	16.4 ± 0.6	42.3	15.0 ± 0.9	16.3 ± 0.8	22.3 ± 1.5
growth in 10 years, cm	4.3 ± 0.06	18.0	4.3 ± 0.1	4.3 ± 0.1	4.3 ± 1.2
Cone yield					
No. of shoots/tree	65.5 ± 4.0	67.0	93.0 ± 6.3	60.2 ± 4.4	19.5 ± 6.7
No. of cones					
per tree	79.7 ± 5.2	72.0	113.4 ± 8.8	74.4 ± 5.9	19.5 ± 7.0
per cm diameter	1.4 ± 0.1	18.1	1.6 ± 0.2	1.3 ± 0.1	0.6 ± 0.1
per shoot	1.2 ± 0.02	20.3	1.2 ± 0.01	1.2 ± 0.01	1.0 ± 0.01
No. of cones/tree					
in 1971 and 1974 with average yield	24.4 ± 2.4	107.7	31.1 ± 4.5	24.9 ± 3.1	7.6 ± 3.8
in 1972 with poor yield	8.0 ± 0.9	119.2	9.3 ± 1.5	9.2 ± 1.3	1.4 ± 0.5
Resin productivity					
Specific, g/cm section					
for 3 years	10.1 ± 0.8	39.0	10.2 ± 0.8	10.4 ± 0.8	9.8 ± 0.9
in 1971	6.1 ± 0.3	41.9	6.2 ± 0.4	6.2 ± 0.4	5.6 ± 0.3
1972	4.7 ± 0.2	45.8	4.6 ± 0.3	5.2 ± 0.3	4.4 ± 0.4
1974	19.6 ± 0.3	35.6	19.8 ± 0.4	20.0 ± 0.3	19.0 ± 0.4

same Kara-Su section, the coefficient of correlation between resin productivity of generations in 1968 and 1969 was 0.7–0.9. These investigators point out that the relative position of trees with highly varying resin productivity is constant and the main year-wise fluctuations stand close to their ranks.

This view can be conceded in the case of trees falling in the minus and normal categories (Table 28). For them, the rank held good in 70% of cases while, in 20% of them, deviations were toward a reduced resin productivity, and in the rest 10% toward a higher value. These trees are evidently more constant in current characteristics of growth and cone yield, have a

Table 28. Ranks of trees according to resin productivity

No. of tree	Average rank	Year-wise rank		
		1971	1972	1974
		Minus category (< 0.6)		
56	0.37	0.86	0.90	0.40
74	0.40	0.42	0.40	0.88
60	0.45	0.52	0.10	0.57
72	0.59	0.68	0.54	0.62
77	0.53	0.96	0.49	0.45
101	0.52	0.57	0.21	0.62
111	0.56	0.42	0.58	0.65
112	0.37	0.50	0.63	0.28
144	0.50	0.67	0.69	0.49
Average	0.47	0.62	0.50	0.49
		Normal category (0.61–1.40)		
119	0.62	0.59	0.58	0.68
9	0.88	0.96	0.78	0.77
14	0.69	0.52	0.78	0.77
17	0.90	0.71	0.72	1.08
26	0.84	1.40	0.20	0.91
30	0.61	0.91	1.09	0.42
35	0.74	0.88	0.34	0.87
45	0.74	0.45	1.09	0.79
51	0.87	0.94	0.90	0.92
55	0.78	0.77	0.80	0.84
7	1.38	0.94	1.69	1.54
Average	0.82	0.82	0.81	0.87
		Good category (1.41–1.80)		
21	1.41	1.80	0.74	1.80
28	1.51	0.71	0.67	2.11
75	1.41	2.40	0.69	1.43
89	1.45	1.84	1.25	1.50
221	1.54	1.01	1.50	1.28
137	1.64	1.18	2.18	1.75
Average	1.49	1.49	1.17	1.64
		Plus category (> 1.81)		
6	2.30	1.96	1.50	2.80
31	1.82	2.05	1.63	1.77
136	1.84	1.18	3.13	1.30
Average	1.98	1.73	2.08	1.95

97 relatively stable type of metabolism, and show less adaptation to the ecological factors.

For the population as a whole, there is a fairly significant drift in the rank of trees. According to our data, the correlation coefficient between resin productivity of trees in 1971 and 1972 was 0.28. There was some unstable rank position in the group of good and plus category of trees (see Table 28). Thus, if the high resin producing trees are selected on the basis of the 1971 data, trees No. 6 and 31, on the basis of 1972 data, tree No. 136, and on the basis of 1974 data, trees No. 6 and 31 would fall in the plus category. Stable rank assessments of trees are possible only on the basis of three-year observations.

A study of resin productivity of pine showed that the main range of its fluctuations lay in the range 5–6 g/cm of section with variation coefficient of about 40% as in Scotch pine (Pilinovich 1975). The so-called coefficient of resin productivity (CR) for Siberian stone pine is 0.1 and for Scotch pine 0.3 (Gordeev 1966).

98 Interpopulation variability of pine with respect to resin productivity, apart from genotypic characteristics, is determined by the classes of quality index, age, and groups of forest density and type (Table 29). The patterns of this variability and its association with the above indexes are characterized by the following tendencies: as the forest density increased from 0.5–0.6 to 0.9–1.0, resin productivity dropped in reedgrass-green moss type of forests by 9% and as the age increased from 161–200 to 241–280 years, there was a drop of 10% in resin productivity. The fall per class of quality index in the green moss group reduced resin productivity by 8.5%. The overall range of its variability from class IV to I of quality index is 0.37–0.94 g/cm of section (Il'ichev 1979). Among the different forest types, the most resin productive are grass-green moss groups of plantations.

The positive relation of resin productivity with the overall productivity of the plantation can be used for zoning parts of pine forests so to organize tapping in them on an eco-geographic basis. Taking into consideration the forestry-based zonation of Siberian pine forests carried out by the Institute of Forests and Timber, Siberian Division, Academy of Sciences, USSR, which has data on the yield of galipot per unit area during tapping, and the conditions of tapping, i.e. climatic (vegetative period not less than 100 days), edaphic (outside permafrost and high swamped soils), phytocenotic (not below class IV of quality index), technical (tapping in the zone of summer fellings), and technological and economic conditions (galipot yield not less
98 than 25 kg/ha), northern (within 61° latitude) and altitudinal (1300 m above sea level) tapping boundaries, as also its northern, central, and southern zones have been established (Fig. 34).

The northern zone is treated as a reserve, the central zone as an occasional zone for galipot production at more than 30 kg/ha, while the southern zone

Table 29. Specific resin productivity (gm/cm of cut) of Siberian stone pine according to groups of forest types in Gornyi Altay (from the data of V.E. Kulakov)

Quality index	Age, years	Density		
		1.0 – 0.9	0.8 – 0.7	0.6 – 0.5
		Grass-green moss type		
II	161–200	6.2	6.4	6.8
	201–240	5.9	6.2	6.4
	241–280	5.6	5.8	6.2
		Grass-green moss type (sorrel-green moss)		
II	161–200	5.8	6.0	6.4
	201–240	5.6	5.8	6.0
	241–280	5.3	5.5	5.8
		Green moss type (bilberry-green moss)		
III	161–200	5.0	5.2	5.5
	201–240	4.7	4.9	5.2
	241–280	4.4	4.6	4.9
IV	161–200	4.2	4.4	4.6
	201–240	3.9	4.1	4.3
	241–280	3.6	3.8	4.0
		Tall grass-fern type (tall grass-sedge)		
III	161–200	5.4	5.6	5.9
	201–240	5.1	5.3	5.6
	241–280	4.8	5.0	5.3

falling mostly on the northern megaslope of southern Siberian mountains as the main zone which is being exploited at present and the most productive (more than 45 kg/ha in a season).

The data on interpopulation variability of specific resin productivity of Siberian stone pine within same zones of its distribution range agree to some extent with the above tapping zones (Chudnyi, Mishukov, and Il'ichev 1980).

The variability of pine with respect to resin productivity within the population is high. This is associated, on one hand, with the effect of age and, on the other, the structure of selection. The observations of N.P. Mishukov and V.E. Kulakov (1970), and our own data (see Table 29) showed that a much higher variability prevailed in the I and III generations (up to 65%). Taking this into consideration, the above investigators have recommended the study of resin productivity and selection of plus category of trees in mixed stands according to ages.

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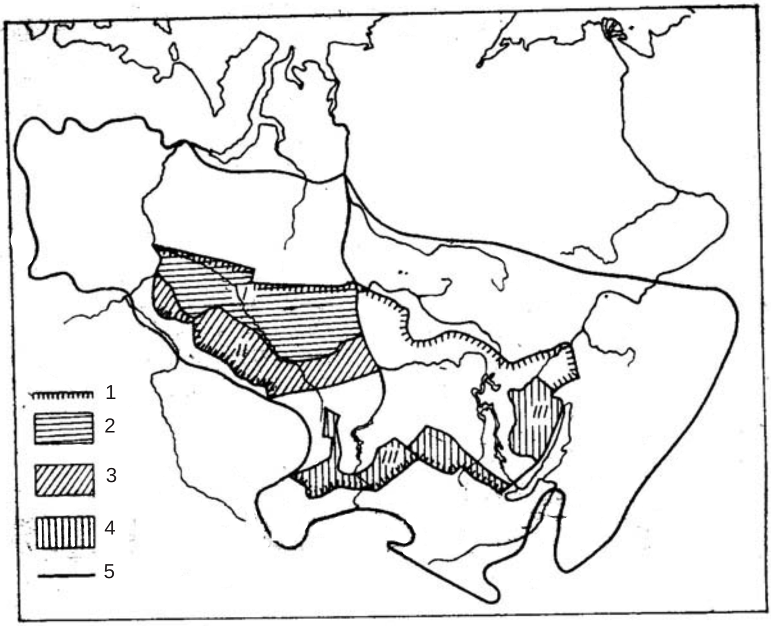

Fig. 34. Zonation of resin productivity and tapping of Siberian stone pine: 1—tapping boundary, 2—northern zone of tapping, 3—central zone, 4—southern zone, and 5—pine distribution range.

The distribution of trees according to ranks of relative resin productivity
in Siberian stone pine as well as in Scotch pine (Vasilevskaya 1960,
Khaziagaev 1965, Mishukov 1964, Shkapo 1966, Vink and Orlov 1970, Kirov
1971, Voronchikhin 1973, Tereshina 1973, and Pilinovich 1975) conforms to
99 the pattern of normal distribution. The noticed positive asymmetry of the
series and negative surplus in Siberian stone pine are expressed more sharply
than in Scotch pine (Fig. 35). This denotes that, in the case of Siberian stone
pine, more number of trees fall in the lower productivity ranges.

The proportion of trees which could be placed in the positive category in the case of Scotch pine and Siberian stone pine averages 4.0–4.5%. Apart from our own data, the above data for Siberian stone pine were obtained by N.P. Mishukov and V.E. Kulakov (1970), Yu.N. Il'ichev (1979), and A.V. Chudnyi, N.P. Mishukov, and Yu.N. Il'ichev (1980). A.V. Chudnyi et al. (1980) demonstrated that the variation of these investigated trees ranged from nil to 9.2% within the Siberian section of pine distribution range. In

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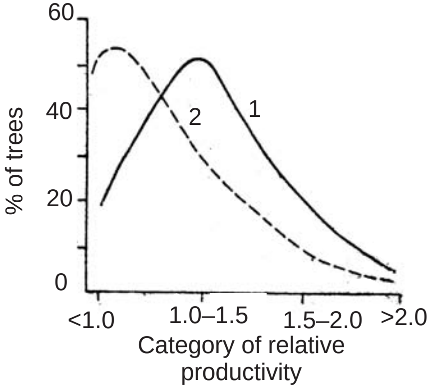

Fig. 35. Distribution of trees according to categories of their relative productivity: 1—Scotch pine and 2—Siberian stone pine.

the case of Scotch pine, judging from the generalizations of B.R. Vink and I.I. Orlov (1970) and V.F. Pilinovich (1975), the variations range from nil to
100 11.4%. It has been further reported that, in the strip forests of Siberian pine, there are more high resin producing trees than in the European part of the USSR. In Pavlodar and Kokchetav districts, their proportion is 6.5% (Vink and Orlov 1970) but goes up to 9.7% in Novosibirsk district (Mishukov 1964). A high proportion of resin-producing forms (11.4%) has been reported from the southern Chelyabin province (Orlov 1962). Such a pattern does indeed prevail since the total resin productivity of Scotch pine from the central latitudes toward south increases and it is for this reason that the central and southern belts have been marked out in the tapping maps.

In several cases, the proportion of high resin producing trees is evidently exaggerated. This is because some investigators place trees producing 1.5–2.0 times more than the average in the plus category of plantation while others use a figure of three times. In these cases, however, the adoption of different criteria of selection point out that the variability of the index which influences the thoroughness of division of highly producing portion of trees has not yet been taken into consideration. For example, it was pointed out above that the average variability coefficient of Scotch pine for this index is 40%. However, in several populations (Central Ob pine forests of western Siberia), it goes up to 57.3–75.8% (Mishukov 1964). The application under these conditions of a criterion of two times undoubtedly raises the proportion of investigated resin producing forms.

Spreading out trees according to breeding categories with consideration of mean square deviation has been suggested (Gordeev 1964, Mel'nikov 1971, Voronchikhin 1973, Tereshina 1973, Pilinovich 1975, and Vysotskii 1978). A selection criterion of 2.6 σ has been recommended as stated in Chapter II based on the suggestion that trees at this threshold value have a different set of biological characteristics than those conforming to the law of normal distribution. One way or the other, stray specimens above 3 σ are regarded as artefacts and have not been included in the analysis of variation statistics. These deviations are, however, of particular interest to biologists.

In each plantation, the selection criterion should be determined by the mean square deviation and should not be a constant either in relative or absolute values of the index. Recently, Yu.N. Il'ichev (1979) has recommended that Siberian stone pine trees with average resin yield less than 0.40 g/cm of section should be relegated to the minus category, 0.41–0.60 g/cm to normal, 0.61–0.80 g/cm to good, and 0.81 and above to the plus category. Based on these indexes, he placed stands of class I quality index in plus category, II and III in normal, and IV in minus category of trees.

Keeping in view the positive association of the index with the overall productivity of plantations, it would be more advantageous to combine with it the selection process in the plantation and not substitute it by forestry evaluation. Moreover, selection of plantations of different quality indexes may give different results when it is considered along with the coefficient of resin yield (CR) which describes the ratio of the index to
101 the diameter of trees. The variation in the evaluation of plantations and trees by using CR may be illustrated from the example of age-wise generations of pine. It may be seen from Table 25 that the specific resin productivity of trees of III to I generations show values of 9.8, 10.4, and 10.2 g/cm section while the CR for the corresponding diameters is equal to 0.27, 0.18, and 0.14.

Some investigators (Dyskin 1973) do not favor such a variation in evaluating resin productivity of plantations or trees and CR is not used in many cases to study the individual variability and for selecting the plus category of trees. Nevertheless, this aspect is important for studying the relation between resin productivity and growth and adopt a unified criterion for selecting high resin-producing trees in plantations.

The coefficient CR was proposed in 1940 by F.I. Terekhov (cited after V.F. Pilinovich 1975) and later supported by several scientists (Gordeev 1966, Chudnyi 1966, Pilinovich 1975, and Vysotskii 1978). The introduction of CR was necessitated by the fact that the prevailing units of measuring resin productivity, i.e. yield of galipot from existing or renewed holes, reflected the effect of technological elements of tapping and provided an idea of only the overall yield of trees largely depending on their diameter. Such units helped establish at one time, the positive relation between resin productivity and diameter of trees (Voronenko 1961 and Petrov 1968) although it was not confirmed in many cases (Orlov 1963 and Shkapo 1966).

In fact, as in the case of yield (see Chapter II), a positive relation between resin productivity and diameter of trees was regarded as absolute due to which the results obtained for untapped plantations by making microcuts did not agree with the former and contradicted each other. Nevertheless, the above method led to an altogether different evaluation of resin productivity, biological or specific, reflecting no longer the phenotype but the genotype of the tree. A study of resin productivity per cm^3 (Mishukov 1964), cm^2 (Voronchikhin 1973), and cm of section (Mishukov and Kulakov 1970) showed its weak correlation with the diameter of the tree or there was no correlation at all with this growth factor.

When using the indexes of specific resin productivity for studying its variability and for selecting good forms, growth characteristics have not been considered. It was thought that this index fully reflected the genotypic conditions of the characteristic as also the effect of its phenotypic development. Quite evidently, however, it is essential to know which of two trees should be preferred for selection if both of them exhibit an identical resin yield but are of different diameters. This cannot be determined using the specific resin productivity and hence not only in terms of the units of measuring the resin productivity by tapping but also in terms of growth indexes, the CR best distinguishes the genetic conditions of the index. The dominant freedom of
102 specific resin productivity from the diameter of trees forms the basis of the CR but there is no positive correlation with it as pointed out by B.F. Pilinovich (1975) and A.A. Vysotskii (1978) who supported the concept of CR. With such a correlation, the CR would, for all values of thickness, have a proximate value and would not help in detecting the resin productivity of trees with a smaller diameter, which after breeding under favorable phenotypic conditions could offer maximum benefit.

Based predominantly on the index of specific resin productivity, Yu.N. Il'ichev (1979) remarks that, from among trees with identical relative resin productivity values, those with more absolute yield of galipot and less diameter should be placed in the plus category. This suggests that, in such trees, resin productivity is largely caused by genetic factors. In fact, this is a recognition of the CR as no other method can identify such trees.

In our studies, high resin-producing forms were selected by both the methods (Table 30). The application of specific resin productivity showed that, in spite of the lower selection criteria, stout trees of I generation predominantly fell in the plus category of trees. According to the data of Yu.N. Il'ichev (1979), the plus category of trees were mainly detected in the stage of thickness that precedes the average diameter. Taking this observation into consideration, he recommended that the plus category of trees may be looked for in the second half of the distribution series of

102 Table 30. Structure of resin productivity of plus category of trees

No. of tree	Diameter		Specific resin productivity		CR, g/cm of diameter	Selection rank (relative CR)
	cm	relative	g/cm of cut	relative		
			Selection based on relative specific resin productivity			
5	53	0.85	9.9	1.84	1.87	2.16
6	80	1.30	9.9	1.84	1.24	1.42
31	64	1.06	10.6	1.97	1.66	1.92
67	70	1.13	11.0	2.05	1.57	1.81
Average	67	1.08	10.3	1.92	1.58	1.85
			Selection according to rank			
5	53	0.85	9.9	1.84	1.87	2.16
31	64	1.06	10.6	1.97	1.66	1.92
67	70	1.13	11.0	2.05	1.57	1.81
3	54	0.87	8.7	1.62	1.61	1.86
89	46	0.74	8.9	1.66	1.93	2.23
Average	57	0.93	9.8	1.83	1.75	2.00

trees according to their diameter. Judging from our data, such a method
102 would narrow the range of utilization of the valuable genetic stock and does not entirely insulate it from the growth characteristics. The energy of resin-producing capacity of stout trees, according to the CR, was detected in one (No. 6) out of the four trees found unsuitable for breeding. When using the CR, such trees are excluded and new ones (No. 3 and 89) found with diameter less than that of an average tree. Selection taking into consideration all the trees optimizes the range of search for resin-producing forms and counters the warning of B.M. Dyskin (1973) that, in such an evaluation, trees with least trunk diameter tended to be selected. This evidently does not occur since the specific resin productivity reflects not only the genotype of the tree but also indirectly its phenotypic development, i.e. the general growth parameters of trees and the structure of the resin-bearing system.

Selection based on the CR also showed that its application should be combined with the relative index, i.e. deriving the selection rank which reflects the ratio of resin productivity to diameter of test and average tree. On analogy with the corresponding rank of yield (see Chapter II), a similar index with respect to the resin productivity of trees can be calculated by correcting its relative value ($c_x / c_{\bar{x}}$) using the inverse ratio of diameters ($d_{\bar{x}} / d_x$). This mode of expressing the selection rank overcomes the unfavorable attitude of many investigators for dividing the galipot yield (especially from microcuts) by the diameter of trees.

Plantations are evaluated similarly by using only wood stock per hectare instead of the diameter and the total biological resin productivity of the stand (kg/ha) instead of the specific resin productivity of trees. The sequence and method of evaluation of plantations and trees based on resin productivity are studied in Chapter V.

Resin Productivity and Growth

The relation between growth and resin productivity was studied earlier mainly to identify the diagnostic characteristics of resin-producing forms of trees. Preliminary results of investigations were promising as they described the relation between growth characteristics and the total yield of galipot by tapping. The isolation of the characteristics of resin productivity from technological and phenotypic phenomena revealed its weak link not only with the diameter of trees as demonstrated before but also with many other growth characteristics.

The complex nature of relations between resin productivity and growth was pointed out by E.P. Prokazin (1959). N.P. Mishukov (1964), for example, pointed out a correlation coefficient of +0.5 with diameter, +0.3 with height, 0.5 with crown diameter, and +0.2 with its height. Resin productivity depends 104 little on the spread and form of crown, angle of branching, thickness and needle formation on branches, color of bark, and color of needles (Khaziagaev 1965 and Khirov and Nevzorov 1965).

Some investigators detected a positive correlation between resin productivity and needle characteristics and consider its application possible for selecting trees that are valuable for breeding (Prokazin 1959, Vasilevskaya 1960, Chudnyi 1966, and Shul'gin 1973). As this relation is statistical in nature, the degree of difference between the poor and high resin-producing trees is not always significant. I.I. Baumanis (1977) for Scotch pine and Yu.N. Il'ichev (1980) for Siberian stone pine demonstrated that the possibility of applying anatomical-morphological features of needles for assessing the resin-producing forms is limited. From several needle characteristics, Yu.N. Il'ichev established relatively positive relations with its length and thickness of surface tissues. Our observations revealed similar trends but they were insignificant. Similarly, no reliable differences could be detected in the external characteristics of trees and shoots (Table 31).

A weak correlation between resin productivity and growth is also manifest at the intrapopulation level (Table 32). From among the parameters

104 Table 31. Growth of resin-producing forms of trees

Index	Resin productivity	
	average	high
Diameter, cm	53.2 ± 0.7	52.7 ± 0.5
Height, m	27.5 ± 0.6	25.7 ± 0.7
Length of crown, m	15.0 ± 0.8	17.0 ± 0.8
that of cone-bearing section	5.0 ± 0.9	5.5 ± 0.9
Annual growth of axis of female shoots, cm	6.9 ± 0.3	6.4 ± 0.1
Length of needles, cm	11.2 ± 0.1	11.9 ± 0.4
Number of needle clusters on shoot	27.7 ± 0.8	23.7 ± 0.9*

104 Table 32. Growth and resin productivity of trees

Growth index	Relation with resin productivity	
	r	η
Trunk		
diameter	0.36	0.48
radial growth over 10 years	0.31	0.32
breadth of sapwood	0.44	0.54
growth of sapwood	0.38	0.42
Crown		
breadth	0.07 – 0.28	0.35
length	0.15 – 0.31	0.38
growth of axis of female shoots	0.05	0.26

Note: r—correlation coefficient and η—correlation ratio.

of the trunk, breadth of sapwood which largely determines the resin productivity of trees, calls for attention.

An analysis of relations between specific resin productivity of Scotch pine and the broad range of growth characteristics of trees showed that the
105 correlation coefficient reflecting the extent of variability of resin productivity caused by unknown factors was 2.5–2.8 times more than the coefficient of multiple correlation (Vysotskii, Mezin, and Ryzhkova 1977). On this basis, A.A. Vysotskii et al. (1977), as also many of their predecessors, beginning from E.P. Prokazin (1959) concluded that it was impossible to select pine on the basis of phenotypic characteristics of growth. The main route is the selection of trees based on direct characteristics, i.e. from the yield of galipot. In trees marked for felling, attention to specific differences of cones and seeds has been recommended (Prokazin 1959) but, in our view, these too do not provide a reliable guarantee of correct selection (see below).

Such results of many years of numerous investigations are largely a consequence of inadequate understanding of the basic theoretical premises. Foremost, a functional correlation has been assumed between resin productivity and growth. The reverse application of this correlation was assumed to give the unknown value from the associate index. The statistical nature of the relation neither permits, nor useful for, such an application from the properties of not only individual characteristics but also those of the entire complex.

In other words, the effect of phenotypic and genotypic factors on the structure of relations was not adequately studied. While in the lower and middle parts of the series of normal distribution of resin productivity, its relation with the associate growth indexes is usually positive and quite close, in the upper part of this series, it is weak or negative (Fig. 36). The growing antagonism between the leading and associate characteristics plays a decisive role in this regard. The breakdown of relations in this part of the series confirms the genotypic freedom of the leading index and the failure to detect it from the associate index, at least from the external growth parameters.

In several investigations, the problem of selecting breeds for a high yield of galipot and timber has been put forward in spite of the fact that no relation was detected between them either in mature plantations or in
106 clones of raised plantations or in natural communities (Baumanis 1977).
Bearing in mind the freedom of succession of growth characteristics and resin productivity, this author advocates solving the problem by greater care in selection as well. In our view, selection should be based on the leading index for its optimum combination with the associate index. Intensifying the latter to an equal extent is not theoretically possible because of the statistical relation discussed above as also the mechanism of its manifestation at the anatomical-morphological level. A.V. Chudnyi (1975) who compared earlier studies and also using his own data on the

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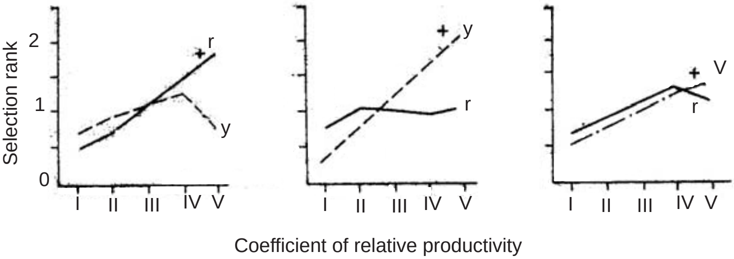

Fig. 36. Ratio of growth (V), yield (y), and resin productivity (r) of trees for different combinations of leading and associate indexes.

morphological structure of resin ducts in the wood of Scotch pine, pointed to the positive relation between resin productivity and the number of resin ducts and their diameter. He, however, pointed out that the number of resin ducts increased linearly with the growing thickness of the annual layer only up to 0.1 mm but their number decreased on further build-up of this layer.

On the whole, the selection of trees for resin yield is highly promising because of the high index of succession of the characteristic (Prokazin and Chudnyi 1968, Peters William 1971, and Baumanis 1977). Unlike many other characteristics, for example timber output or disease resistance which require testing for genotype, the breeding of resin-producing forms, according to I.I. Baumanis, is possible on the basis of phenotype.

The optimum combination of high resin productivity with growth parameters opens up real possibilities of organizing valuable plantations.

Resin Productivity and Cone Yield

The study of relations between resin productivity and cone yield in coniferous plants began with the classic work of E.P. Prokazin (1959). He and his successors (Khirov and Nevzorov 1965, Khaziagaev 1965, Mochalov 1972, and Shul’gin 1973) noticed a positive correlation between these processes and focussed on such distinctive properties of resin-producing forms of Scotch pine like the black color of seeds, flat apophysis, and greenish color of cones. The recent studies of these investigators were extended to the plantations raised from seeds to study the intensity of resin formation and cone yield with the application of mineral fertilizers (Efimov, Vysotskii, and Beloborodov 1981).

The overall result of these studies was the detection of a fairly close positive correlation between the indexes under study and the prospects of simultaneous selection for breeding.

Several investigators, however, contradict such a relationship (Tereshina 1973). Our observations show that the ratio of indexes of resin formation to cone yield is not infallible and several features in the concepts under consideration require appropriate corrections (Vorob’ev 1970, 1974, and 107 1981).

Firstly, intrapopulation analysis showed that, like the relationship with growth, there is a positive correlation of moderate significance between resin productivity and crop size. A comparison of total resin productivity and yield of trees for several years showed a variation coefficient in the range +0.2 to 0.4. In barren years, when one of the indexes under comparison bears a “random” character due to massive and indiscriminate fall of cones or when comparing yield with specific resin productivity which reflects predominantly the genotype of the tree, the relation between them turns weak or negative.

A study of the structure of correlations between the indexes at the level of rank reveals close positive relation only in the poorly and moderately producing sections of the distribution series of leading index (see Fig. 36). With its intensification and the increasing presence of genetically isolated specimens, this relation weakens. The rank of the associated characteristic decreases to the average level of relative productivity (1.0–1.5) and, in some cases, may reach the category of good trees (1.5–2.0). Insofar as the combination of characteristics at the level of plus category is concerned, such cases are rare and have not been detected under our conditions either among trees or among populations. They were also not detected in the data of Yu.P. Efimov et al. (1981). Nevertheless, it has recently been concluded that trees should preferably be selected using both the characteristics.

In our view, as in the case of growth, trees are best selected for the leading characteristic at its optimum combination with the associate index for maximum yield of one of them while maintaining a normal level of sexual reproduction or protection of plantation for the other feature. The objective, for example, should not be to organize high crop yielding and resin-producing plantations simultaneously, all the more so since the response of the indexes to the variable levels of mineral fertilizers keeps changing (Efimov, Vysotskii, and Beloborodov 1981). The conditions of formation of specialized plantations also differ: for high-yielding forms, thin spread of trees with well-developed and abundant cone-bearing crowns is needed but a more compact canopy with a predominance of trunks free of branches is required for resin-producing forms.

Resin-producing forms in nature are characterized by fewer reproductive shoots and, as a result, a lesser number of cones (Table 33). The differences on the whole are not significant since the rank of trees with respect to yield in both the cases shows average value. In such a situation, it is important that these trends are differentiated from those noticed under tapping conditions where the yield of resin-producing trees is more than that of average trees due to a large number of cone-bearing shoots (Vorob'ev 1973 and 1974c, see
108 Chapter IV). Thus, the positive relationship between the total resin output and crop yield identified by E.P. Prokazin (1959) and later investigators is evidently a consequence of the shift of root-leaf systems toward greater stimulation of reproductive processes. This response among resin-producing trees is more positive than in the average trees. At least, when comparing high and moderate resin producing forms of Scotch pine, significant differences of crop yield were detected only in good cone-bearing trees (Prokazin 1959). No differences were noticed in the reproductive energy of

108 Table 33. Cone yield of resin-producing forms under standard and tapping conditions

Index	Resin productivity	
	average	high
No. of cone-bearing shoots		
standard	64.8 ± 1.5	57.7 ± 4.1
tapping	52.6 ± 1.2	72.5 ± 5.1*
No. of cones		
standard	79.7 ± 2.5	62.7 ± 5.5*
tapping	68.2 ± 2.1	90.6 ± 8.0*
Reproductive energy of shoots (No. of cones/shoot)		
standard	1.23 ± 0.08	1.26 ± 0.06
tapping	1.29 ± 0.16	1.25 ± 0.10
Reproductive energy of trees (No. of cones/cm diam.)		
standard	1.3 ± 0.05	1.2 ± 0.06
tapping	1.3 ± 0.06	1.7 ± 0.07*

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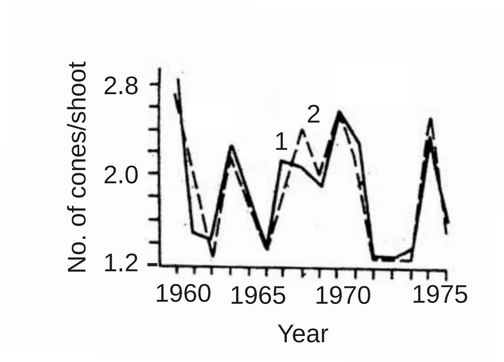

Fig. 37. Crop dynamics of moderate (1) and high (2) resin-producing trees.

shoots in either of the cases. Similarly, there are no variations in the nature or extent of cone fall as well as in the crop dynamics (Fig. 37).

Insofar as cones and seeds are concerned, specific relations of their parameters with resin productivity are poor as with the growth of trees but the following features may be noticed (Table 34). The color characteristics of cones, expressed in balls, shows that the resin-producing forms tend more to a glaucous violet coloration while the bulk of trees tend to be yellowish cream. A comparison of these variations with the greenish color of resin-
109 producing pines (Prokazin 1959, Khirov and Nevzorov 1965, and Khaziagaev 1965) exhibits some analogy. It is, however, absolutely possible, at least in the case of Siberian stone pine, that these differences are largely associated with the varying intensity of cone ripening. The evaluation of their

109 Table 34. Characteristics of cones and seeds of resin-producing forms

Index	Resin productivity	
	average	high
	Cones	
Length, cm	5.9 ± 0.5	6.5 ± 0.2
Breadth, cm	4.4 ± 0.2	4.7 ± 0.2
Color of scales, balls	4.2 ± 0.9	3.3 ± 0.2
Form of apophysis, balls	1.7 ± 0.4	1.5 ± 0.1
	Seeds	
No. of full-bodied seeds in average		
cone	64.5 ± 13.7	65.5 ± 3.3
barren	4.9 ± 2.5	3.5 ± 0.5
underdeveloped	1.3 ± 1.2	2.8 ± 0.4
total	70.7 ± 12.2	71.8 ± 3.5
Weight of full-bodied seeds, g	19.2 ± 3.6	22.1 ± 1.0
Color of seeds, balls	3.1 ± 1.1	3.3 ± 0.1
Viability, %	95.7	93.2
Absolute weight of seeds, g	234 ± 4	244 ± 7

apophysis reveals some pre-dominance of flat corymbs in resin-producing forms of Siberian stone pine as also in Scotch pine (Prokazin 1959). Their find is around 60% but the differences on the whole are not reliable and this characteristic of cones, like the color of seeds, cannot be used as a diagnostic feature.

Cones of resin-producing forms of Siberian stone pine contain a somewhat smaller number of barren seeds but many underdeveloped ones. In the first case, the increased resin productivity evidently improves or at least does not worsen the conditions of seed nutrition. In the second case, as under conditions of tapping (Vorob'ev 1974c), there is some adverse influence on the course of fertilization which occurs in June, in the period of intense resin formation in the growing tissues of trunk and leaf system. Positive trends are also observed in the weight of seeds but their vitality is not particularly affected; in the years of good yield, seeds of moderate and high resin producing trees fall in Class I.

110 Qualitatively, seeds of resin-producing forms exhibit more reliable differences (Table 35). Foremost, they have a higher content of nitrogenous matter, protein as well as non-protein matter. This pattern correlates positively with a high content of free amino acids (Vorob'ev, Vorob'eva, Sviridenko, and Kolesov 1979). Changes are most significant in the contents of cystine, tryrosine, and specially glutamic acid which, under the influence of resin-producing processes, increases three-fold (Table 36). In the background of

110 Table 35. Physiological characteristics of seeds of resin-producing forms, % of dry matter

Constituent	Resin productivity	
	average	high
Nitrogenous matter		
total nitrogen	2.08 ± 0.05	2.52 ± 0.07*
protein	1.93 ± 0.04	2.30 ± 0.06*
non-protein	0.15 ± 0.01	0.22 ± 0.01*
Fat	65.3 ± 0.3	64.4 ± 0.4
Carbohydrates		
starch	2.4 ± 0.1	1.0 ± 0.2*
readily-soluble carbohydrates	10.1 ± 0.4	14.3 ± 0.7*
oligosaccharides	8.7 ± 0.4	12.5 ± 1.1*
monosaccharides	1.4 ± 0.1	1.6 ± 0.1

111 Table 36. Content of free amino acids in seeds of high resin-producing forms (mg% of fat-free dry matter)

Amino acid	Resin productivity			
	Average No. 129	high No. 137	average No. 127	high No. 135
Cystine	2.8	18.0	19.5	34.5
Lysine	35.7	39.0	27.5	32.8
Histidine	8.3	8.3	21.0	46.1
Arginine	3.8	9.7	11.1	11.1
Aspartic acid	26.1	27.8	30.2	46.1
Serine	3.3	5.6	12.5	44.4
Glycine	+	+	+	+
Glutamic acid	36.0	107.0	13.2	48.1
Threonine	17.8	9.3	–	–
Alanine	19.1	37.2	20.0	22.2
Proline	35.7	37.6	–	–
Tyrosine	32.1	50.2	24.0	63.0
Methionine	9.5	3.6	42.9	21.5
Valine	6.5	4.6	13.0	48.2
Phenylalanine	34.0	10.3	–	–
Leucine + isoleucine	10.4	8.3	25.6	24.7
Total	283.1	376.5	260.5	442.7

Note. No. 129, etc. denote the number of tree, "+" qualitative identification of amino acids, and "–" amino acids not detected.

poor external differences of seeds, such changes open up some possibility of their analysis for study and early selection of resin-producing forms. In this respect, data on the presence of specific readily soluble proteins in the resin-producing Scotch pine trees are of interest (Avramenko and Vysotskii 1982).

The high content of nitrogenous matter evidently restrains the accumulation of fat in the seeds. Breeding investigations on sunflower showed that, in oil-bearing forms, the proportion of protein in the seeds decreases and, on the contrary, at high protein accumulation, the quantum of fat diminishes (D'yakov 1975). The same tendencies are observed in resin-producing forms of Siberian stone pine as well although not as significantly as the reduction of starch content. The observed shift in its utilization is accompanied by a high content of readily soluble carbohydrates, mainly through an increased quantity of oligosaccharides.

The above features only vaguely describe the physiological characteristics of resin-producing forms of trees, in turn emphasizing the obvious need for their objective study, mainly at the cell level.

111 The identified characteristics of relations of resin-producing trees with their growth and cone yield may be used for purposes of selection and for organizing an integrated economy in pine forests. The relevant aspects of these problems are discussed in the concluding chapter.

CHAPTER IV

Cone Yield, Growth, and Resin Productivity of Siberian Stone Pine under Experimentally Modified Root-Leaf Relations

Among the problems facing forest seed studies, the most important are the aspects of increasing the reproductive activity of conifers. For practical application, they are closely associated with the problem of enhancing the productivity of forests and, theoretically, with studies to control biological processes in the biocenoses.

Quite a large number of studies in the USSR and abroad (Pharis 1970, Ebell 1971, Enessen, Cogocarn, Popesen, and Ciocnetu 1973, Velkov and Kaludin 1970, Shol'ts 1973, Prokazin 1973, Kozubov 1971, and Iroshnikov 1973) have dealt with the subject of boosting cone yield. The results of these studies reflect some success in stimulating cone production. A significant rise of yield of Scotch pine has been reported with the application of mineral fertilizers (Breusova 1970, Kozubov 1971, Danusyavichus 1978, and Nekrasova 1982), Schrenk spruce (Pal'gov 1978), and Norway spruce (Kozubov et al. 1981). Data for plantations raised from seeds speak of higher yields in some years (Ronis 1978).

All the same, in many cases, stimulation tests are known to have failed or their results proved insignificant or temporary. The reasons could be many. One of them, evidently the most important, is the lack of a general theory of control of the reproductive activity in conifers.

The development of such a theory is a complex but important task. Its urgency is associated with the need to analyze the available data and

extend the investigations. The absence of a universal approach for resolving various aspects of this problem reflects on the state of modern concepts and investigations. In the forest seed studies, stimulating cone yield has been understood so far as mainly the activation of reproductive processes. Less attention is usually paid to the growth condition or it is treated as an independent topic. The physiological-biochemical processes accompanying the growth and cone yield variations have not been adequately studied. Experiments were mostly confined to establishing direct correlations between the stimulating factor and the end result of the experiment. It is also significant that most investigations are confined to the female reproductive processes; not much is known about the state of the male aspect although, quite
113 evidently, an adequate and full-value yield is possible only at optimum intrapopulation equilibrium of both the sexes. The underestimation of this aspect of the problem has necessitated seeking solution by an improved pollination regime, especially in seed plantations, by adopting artificial supplementary pollination (Nekrasova 1981).

The available data do not provide a general concept of methods for experimental control of reproductive activity in conifers and thus the results achieved are often of regional or partial relevance. The ongoing detailed studies on various aspects of the mechanism of the inducing effect of one or the other factors also do not provide a solution for this situation. The absence of a common approach will result in advancing field investigations on stimulation without adequate theoretical foundation and pursuing essentially applied aspects. Their advance ultimately turns out into a temporary phenomenon or does not provide the anticipated results which require theoretical substantiation.

A characteristic example of such a situation is met with grafts. At one time, it was thought that cone yield of coniferous plants could be significantly boosted through grafts. Later, it was found (Prokazin 1973 and Kolegova 1973) that information was lacking on the type of grafts used and could not be relied upon to provide faster and increased yields. Similar was the situation with the crown formation of conifers by decapitation of the tops of young trees (Beloborodov 1978 and Alekseev 1979).

All of this points to the need for intensifying the general theoretical studies in the field of crop control of conifers. The biological principles of seed formation and stimulation worked out in Norway spruce by Soviet and Swedish scientists (Kozubov, Ronis, Ivonis, Kondrat′eva, Samuelson, Eriksson, and Dunberg) are important. Significant results were reported in the field of eco-biological aspects of the reproductive activity of pine and spruce in the north-eastern European part of the USSR (Veretennikov, Artemov, Bobkova, Galenko, and Skupchenko 1981). There are even more problems for study. The present task, along with further detailed investigations of some aspects is, therefore, one of the most urgent problems in the forest seed science and seed culture. Its solution should be closely related to the study of the morphological characteristics of sexual reproduction of conifers under natural as well as experimental conditions. The latter route holds great promise as it helps in influencing the plant metabolism in specific direction and work out techniques for controlling it.

The study of woody plants under conditions of controlled metabolism encounters severe difficulties. Investigators are, therefore, drawn to the various changes of normal life processes in the tree arising in the natural environment as well as resulting from anthropogenic activity. One of the methods of modifying metabolism is by physiologically damaging the trunk (singeing
114 during low fires, damage of bark during landslides or floods, cleaving of pine trees during seed collection, and tapping). The physiological effect of these factors on the body of the tree generally leads to a shift of root-leaf relations which are important for the course of reproductive phase as well as for the ontogenetic development of the plant (Kazaryan 1969).

Out of the damaging factors listed above, tapping is an economically important activity of the forest industry and hence investigations involving it are of additional practical interest. A study of the condition of tapped plantations is important for determining the potential possibilities of galipot recovery as also for preserving the entomo-physiological stability of the affected stands and maintaining the optimum level of their seed output. The latter is particularly essential for pine forests because of the value of their seeds and the importance of the study of biological aspects of organizing integrated economies facilitating in particular a prolonged combination of tapping and nut collection in the stands under exploitation.

Various aspects of life processes in tapped trees were studied earlier to understand the applicability of different methods of tapping. The available data on its influence on growth and cone yield were found to be contradictory and could not be generalized without knowledge of the corresponding original state. Special investigations aimed mainly at studying the activation conditions and possibilities of controlling the growth and regenerative processes were called for. A disturbance of root-leaf relations was considered in this case as a model and as a method for objective redistribution of metabolites in the tree as a whole.

The following problems were investigated:

1. Study of the characteristics of relations between growth and cone yield under conditions of shift of root-leaf relations according to the type "root-crown".
2. Study of the physiological processes accompanying the optimum changes of growth and cone yield.
3. Establishing the permissible limits of the shift of root-leaf relations and characteristics of patho-physiological state of trees.

4. Evaluation and determination of the point of mechanical damage in the system of measures for crop control. Testing the actual technological methods for promoting the reproductive activity of full-grown trees and establishing the optimal combination of tapping and nut output in integrated economies.
5. Study of the general approaches to crop control in conifers.

Materials and methods of study. The material for investigations should be closely related to the method of recording observations. This aspect, in our view, has not been adequately taken care of in the preceding investigations. Studies are usually carried out without choosing uniform objects, their initial condition, and dynamics of subsequent changes in the life processes of 115 damaged trees. The results recorded, although true in each individual case, do not permit drawing generalized conclusions. This phenomenon could explain the divergent opinions on the influence of tapping on growth and cone yield of trees.

To avoid a similar situation, attention was specially devoted to the method of selection of material for study. The general premises of the method involved fulfilling the following conditions:

— formation of test sections in regions that hold promise for tapping and nut collection,
— recording observations in pine forests on mountains and plains, in the most prevalent types of forests,
— combining investigations under experimental and field tapping conditions,
— combining observations on model trees with inspections of plantations,
— carrying out integrated investigations including the application of physiological methods,
— carrying out observations on different varieties of trees (Siberian stone pine and Scotch pine),
— Adopting different methods of mechanical damage of trunks for modifying the normal activity of trees (tapping, cleaving, and notching),
— selecting material with uniform general characteristics,
— allowance for the original condition of the material for study with respect to the various characteristics, and
— studying the annual dynamics of the state of experimental trees.

By satisfying these conditions, it has been possible to formulate a fairly broad network of material and organize long-term integrated investigations. Observations commenced in 1966 in Teletsk taiga region of Gornyi Altay. The basic data on the morphological characteristics of trees subjected to tapping were drawn from the pine forests of this region. Information on the state of Scotch pine after notching was also gathered in this area. The effect of tapping on it was studied in the upper Ob pine forests. In the southern subzone of forests in the western Siberian plains, tapping of pine (Shegarsk Forest Combine of Tomsk district) and its cleaving (Tomsk Forest Combine) were studied. In all, 10 experimental sections were laid in these regions.

The first of these designed for the basic observations was located in Bulandu-kol′ area, 6 km from Teletsk lake. The section named BIN (Biological Institute), in which the investigations commenced, has two levels of plantations of class II quality index, comprising three generations of Siberian stone pine, with a small admixture of fir (Table 37).

116 Table 37. General characteristics of the stand in BIN section (850–900 m above sea level)

Level	Quality index, forest type	Composition	Density	Age, years	Height, m	Diameter, cm	No. of trees/ha	Reserves, m^3/ha
I	II, green	6 P_{I}	0.26	280	33.0	90.4	23	166
	moss-wood fern	$6P_{II}$	0.17	240	31.0	61.0	32	118
II	-do-	6F	0.12	120	21.0	22.0	77	45
		$4P_{III}$	0.13	160	27.5	35.4	30	33

Note. P—Siberian stone pine; F—fir.

The general characteristics of pine trees have very high values. The stand as a whole adequately represents the zone of pine forests in the upper part of black soil and lower mountain-taiga subzone. In the mountains, this strip of forest (700–1300 m above sea level) represents the most promising base for
116 developing tapping and nut collection.

In the experimental section, initially about a hundred trees of average cone-bearing model were selected. During visual inspection, some of them were removed from further study for various technical reasons. In the rest of trees, the main characteristics of vegetative and reproductive development were studied. Based on statistical analysis of the resultant characteristics, a group of most identical trees was selected for subsequent observations and these were further divided into five test variants (Table 38). This method helped select fairly uniform trees suitable for collecting reliable data for physiological analysis (Sudachkova, Osetrova, and Varaksina 1971). Significant deviations of some characteristics were identified and later considered when comparing with the control values.

The second section, located 2 km away from the first, was laid in 1962 by V. Berezhnyi, M. Tvelenev, and V. Zubarev, a group of workers at the Project-Research Bureau (PIB). For various reasons, observations ceased in the same

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Table 38. Initial characteristics of pine trees in the BIN section

Index	Average of values of 70 model trees	Test variant				
		I (control)	II	III	IV	V
Diameter, cm/height, m	65.1/31.1	65.2/32.8	64.0/31.0	65.0/32.4	63.0/32.3	63.6/31.2
No. of female shoots	88	89	91	86	88	88
Growth of female shoots over 10 years (1958–1967), cm	58.0 ± 0.4	65.6 ± 2.0	70.7 ± 2.2	58.8 ± 1.3	59.8 ± 1.0	60.9 ± 1.8
Breadth of sapwood, mm	27.6 ± 0.5	29.9 ± 1.4	26.2 ± 2.0	27.6 ± 1.1	29.1 ± 1.8	29.0 ± 1.8
Resin output/renewed cut, g	69	75	75	67	68	71
Average number of cones/tree over 10 years (1959–1968)	133.0 ± 3.1	127.0 ± 9.2	132.0 ± 9.2	156.1 ± 5.2	134.3 ± 5.0	126.6 ± 5.1
Reproductive energy of shoots over 10 years (1959 – 1968), number of cones/shoot	1.51 ± 0.03	1.43 ± 0.10	1.45 ± 0.10	1.80 ± 0.12*	1.41 ± 0.06	1.44 ± 0.06
Absolute weight of seed yield in 1966, g	246 ± 3.2	253 ± 5.2	227 ± 6.7	257 ± 6.7	261 ± 7.6	252 ± 8.1
Oil content of seed yield in 1966, g	64.5	64.2	64.0	64.0	65.0	65.1

year and the section was reorganized by the author in collaboration with V. Kulakov in 1967 for carrying out the same types of tapping as in the BIN section, but in the entire stand.

When resuming the tests in the PIB section the test plots were rearranged into relatively homogeneous groups (Vorob'ev 1974a).

For evaluating the original cone yield, cones and seeds collected in 1967 were analyzed (Table 39). Clearly, the sizes of cones as well as the yield of developed seeds were similar in the different groups of test plots. However, the absolute weight and oil content of seeds in the variants where tapping commenced early (in 1962) were more than in the control. That this occurred as a result of modified root-leaf relations was convincingly demonstrated by the data from the BIN section in which a corresponding rise of these indexes was detected in the very first year of tests (see below).

120 Table 39. Initial characteristics of pine cones and seeds in the test plots of the PIB section

Index	Test variant			
	I (control)	II	III	IV
Length of cones, mm	53.7 ± 0.6	53.1 ± 0.6	47.9 ± 0.5	54.2 ± 0.7
Shape of cones (l:d)	1.3 ± 0.1	1.3 ± 0.1	1.1 ± 0.1	1.2 ± 0.1
Yield of full-grained seeds from average cone, No.	51.3 ± 0.8	49.8 ± 0.7	45.4 ± 0.7	49.9 ± 0.8
Full-grained seeds, %	83.3	82.2	85.4	83.6
-do- % of control	100	98.8	102.4	100.6
Absolute weight of seeds, g	180.0	202.0	199.0	212.0
-do- % of control	100	112.2	110.5	117.7
Oil content of seeds, %	61.3	61.5	62.2	62.6
-do- % of control	100	100.4	101.4	101.5

The third section located on the bank of Teletsk lake (Ydyp area) contained
118 trees with their trunks damaged by cuts and notches, usually inflicted by tourists for gaining resinous wood shavings for camp fires. Trees damaged in this manner served as an example of the variety with severely disturbed root-leaf relations. Trees covered in the experiment had one-sided continuous cut from the root neck to a height of 1.5 m, up to 70% of the trunk's circumference was damaged, and cuts inflicted continuously for almost 10 years.

A similar Scotch pine section (No. 4) was selected in 1967. The trees were of 40 cm diameter on average, height 12–14 m, and age 60–80 years. Depending on the extent of damage caused by notches, pines with
119 moderately (50%) and intensely (80%) disturbed root-leaf relations were covered by inspections. As in Siberian stone pine, the duration of damages extended for almost 10 years.

Along with the above section, section No. 5 lay roughly 200 m from the bank. It was laid in the '30s by P.K. Kutuzov, the well-known specialist on tapping of coniferous species of Siberia (Kulakov 1971). At present, the smooth holes that were used formerly turned into cavities surrounded by highly enlarged "nutrient belts". Depending on the original condition and the tapping load, some trees are in the stage of dying while others continue to be normal. Model trees were selected from both the groups and studied by the author in 1970 and 1971. The
120 average age of the trees studied was 220–240 years, diameter 54 cm, and height 28–30 m; the composition of the plantation, located in a *Bergenia*-type forest, was 7P2F1B (7 pine, 2 fir, 1 birch).

The sixth and seventh sections fall in plantations in which tapping gashes were made continuously during 1961–1970. At the beginning of investigations, it was the only 10-year tapping experiment on Siberian stone pine in Siberia. In Gornyi Altay, such a section (No. 6) lay 30 km from the central farm of Gornyi Altay Experimental Combine on Iogach-Obogo road in Ozup area. The section is located in the upper half of mountain-taiga subzone (1200–1300 m above sea level) and represents more completely a body in which tapping is done at present. The stand in the section is assumed to be homogeneous (180 years) and of class II quality index. It is a green moss-bilberry type pine forest which is most widely spread and productive in this subzone. In the recent years, the section is being used for ground and remote control of the condition of plantations after terminating tapping.

The next section (No. 7) in Tomsk district is located in swamps on "Yarinsk islands" and is a low-yielding stand (class IV quality index) and advanced age (260 years).

One more 10-year tapping section has been studied by the author in the pine forests of upper Ob. Formerly, observations were made here to study the influence of tapping on reproduction and cone yield of Scotch pine (Paramonov 1973). Our investigations dealing more with the morpho-physiological aspects of cone yield supplemented these observations. The basic data were collected in 1971 in Borovlyan Forest Combine in sections that were tapped for 8 years using single (load 60%) and double (80%) holes.
121 The test plots lay in stands aged 100–110 years, with average trunk diameter 31 cm, height 23 m, density 0.8, reserves 300 m^3/ha, and number of trees 450/ha.

Investigations covering much of the above sections are examples of short-term use of cleared holes, a technique practiced for long. Experiments with sealing cuts designed for producing galipot for many decades have much less life. Section No. 9 using this method was designed by V.E. Kulakov in Gornyi Altay in the waterdivide of Kochesh river basin. The stand is located on the south-western slope and thus is of good general characteristics:

composition 8P2F (8 pine, 2 fir), diameter 52 cm, age 190 years, class II quality index, and density 0.7. Tapping was carried out during 1970–1975 by the technology described below.

The last section (No. 10) is located in the pine forest near the settlement in Tomsk Forest Combine (Aksenov forest resort). For 35–40 years, this plantation underwent cleaving which exerted an effect similar to tapping on the vitality of the trees. A distinctive feature of cleaving is that the utilization
122 of assimilation products for the synthesis of terpene compounds here is less since resin exudation around the sealing cuts ceases gradually. More favorable conditions prevailed in the trees for restoration of root-leaf relations by intense activity of cambium in the undamaged section of the trunk. The plantation in this section consists wholly of Siberian stone pine of average diameter 42 cm, height 25 m, age 135 years, and density 0.8. The section was inspected in 1971 and 1973. The above data for the different sections will be supplemented in due course for a more complete picture of each of the sections.

Resin Productivity

Resin production processes under conditions of tapping reflect the level of individual variability of trees with respect to this property, the parameters of their phenotypic development, and the technological shift of root-leaf relations.

Among the technological factors, important ones are the load along the diameter (% of trunk damage along the circumference) and extent of interval (number of days between making fresh openings of number of channels made in a season). The first of these determines the degree of disturbance to transport of metabolites between the roots and the crown while the second signifies their utilization for resin formation. Tapping duration is an important technological factor.

The development of tapping technology and observations of the resin productivity of trees were designed by V.E. Kulakov in collaboration with this author (Kulakov and Vorob′ev 1971, and Kulakov 1974).

In the BIN (No. 1) and PIB (No. 2) sections in which the most complete observations of the state of growth and regenerating processes were recorded, the following variants were pursued (Table 40):

I—control,

II—making a cut of sealing type (technology was designed to maintain the normal vitality of trees and yield galipot for some decades),

III—making usual renewals of existing cuts designed for load of moderate interruption on transport ducts in the tree for 10 –15 years,

IV—the same cuts but with a high trunk load that is optimal for short-term tapping, and

123 Table 40. Technology of experimental tapping in BIN and PIB sections

Process details	Tapping			
	poor, II	moderate, III	intense, IV	very intense, V
Duration, years	25	10	5	3
Extent of trunk damage (load), %	40	60	70	90
Number of cuts/season	6–8	12–14	14–17	14–17
Depth of cut, mm	2–3	2–3	2–3	2–3
Vertical distance between cuts, cm	7	2	2	2

V—special tests with the same cuts but with maximum disruption of root-leaf relations.

Relative to the technology used, the IV variant corresponded to a 5-year tapping used before the author's investigations in Altay and also now in use in Tomsk district and Krasnoyarsk region; the III variant was a 10-year tapping developed in the course of investigations and extensively used at present in Gornyi Altay; the II variant was prolonged tapping, also tested and recommended by the author for integrated organizations. The 123 technology of this tapping method has been studied in detail below. The author wishes to emphasize here that it was based on utilizing the high regenerative capacity of pine (Kutuzov 1955, Znosko 1960, Petrov 1968, and Kulakov 1976).

From the viewpoint of the physiology of affected tree, the tapping variations described correspond to four stages of disruption of root-leaf relations: II variant—weak disturbance with periodic restoration of transport network in the tree due to sealing of the cuts, III—moderate, IV—intense, and V—very intense, quite close in its effect to ringing but differing from the latter in regular resin exudation.

The resin productivity of trees in the BIN section in the first year of tapping per cut was: II variant 38, III 43, IV 53, and V 75 g. In the second and third years, the same level was maintained in all the variants. In the fourth year, resin output dropped in the fifth variant. A significant reduction of the resin output of trees occurred in the sixth year of test.

In the 10-year tapping sections in Gornyi Altay and in Tomsk district, the load along the trunk diameter was 65% in the first case with 11 renewals and 50% in the second with 14 renewals of cuts. On increasing the number of channels in the Tomsk section, the yield of galipot remained practically the same for the two stands that differed in the original condition of the stand (Table 41). As it turned out subsequently, this was the optimal intensity of resin exudation for the Altay section and extreme for the Tomsk section causing, as will be seen later, a significant adverse change of growth and cone yield of tapped trees.

124 Table 41. Dynamics of resin output of Siberian stone pine (Kulakov and Vorob'ev 1971)

Year of tapping	Gornyi Altay			Tomsk district		
	per hole, g	per renewal		per hole, g	per renewal	
		g	%		g	%
1961	336	24.0	100	279	20.0	100
1962	300	27.1	113	335	22.3	111
1963	394	24.6	103	327	21.8	109
1964	328	27.3	114	284	21.0	105
1965	297	27.0	112	365	22.8	114
1966	256	28.4	119	324	23.1	116
1967	285	28.5	119	355	22.2	111
1968	242	30.2	126	255	28.3	141
1969	324	27.0	112	300	21.4	107
Average	309	27.1	113	318	22.5	113

The data shown in Table 41, however, do not reveal this feature. All the same, it has been regarded so far that the vitality of damaged trees can be ascertained from the dynamics of resin productivity (Kutuzov 1952, Gavrilov 1953, and Kulakov 1972). The author's observations show that the fall of the vitality of the affected trees begins with the growth and regenerative processes 124 and only thereafter the resin productivity and its exudation are affected (Vorob'ev 1974b). Resin formation as a process resulting from several metabolic transformations in the body of the tree and performing the protective functions is the last faculty to weaken and thus its reduced activity is detected when the other processes have weakened significantly or have assumed an irreversible form. The observations of D.A. Bogdanova and N.G. Kolomiets (1972) on the state of Siberian stone pine in the cell of the Siberian silkworm showed that the method of turpentine indicator used for this purpose by P.A. Polozhentsev (1961) was unsuitable. The trees desiccated from the top and a thorough felling of the section for sanitary purposes was indicated. No differences were detected in the level of resin productivity of tapped Scotch pines between healthy trees and those infected with pine fungus (Mel'nikov 1970).

This situation necessitates the study of not only the growth and cone yield of trees, which will be discussed later, but also the composition of terpene compounds which are known to play a significant role in the protective system of coniferous plants.

Such investigations were undertaken by E.F. Votchal (1926), P.A. Polozhentsev (1951), Polozhentsev, Chudnyi, and Zolotov (1969), Polozhentsev, Zolotov, and Latysh (1970), Rudnev and Tsiopkalo (1927), and Rudnev, Smelyanets, Akimov, and Lishtvanova (1969). More complete and detailed observations in this direction were made under the guidance and participation of A.S. Isaev (Isaev and Ryzhkova 1968, and Isaev and Girs 1975) and A.S. Rozhkov (Rozhkov and Massel′ 1972, Massel′ 1979, and Rozhkov 1981). Among the investigations of foreign scientists relating the stability of woody plants with terpene composition, the following publications merit mention: Perttynen 1957, Gibbs 1968, Hanover 1975, and Hart, Wardell, and Hemingway 1975.

The change of composition of monoterpenes in Siberian stone pine under 125 the influence of various types of damages (Massel′, Rozhkov, Vol′skii, and Pentegova 1975), also under tapping conditions (Vorob′ev, Dubovenko, and Pentegova 1977), is characterized by a reduction of α-pinene and increase of Δ^3-carene contents (Table 42). Under conditions of tapping, this variation is associated with the intensity of tapping and corresponding level of resin exudation. According to the data for the first year of observations, the content of α-pinene dropped from poor to very intense tapping conditions from 81.6 to 54.3% and of Δ^3-carene rose correspondingly from 9.7 to 16.2%; further, the content of β-pinene rose from 5 to 22%.

125 Table 42. Composition of monoterpenes in galipot under different tapping conditions, %

Monoterpene	Tapping			
	poor, II	moderate, III	intense, IV	very intense, V
α-pinene	81.6/66.4	70.8/49.9	67.3/48.8	54.3/48.5
β-phenchene	1.0/-	1.5/-	–	–
Camphene	2.7/1.1	2.2/0.8	1.7/1.9	2.5/0.7
β-pinene	5.0/10.9	6.9/22.8	10.7/23.5	22.0/19.3
Δ^3-carene	9.7/11.8	11.7/10.6	15.4/14.8	16.2/15.9
Sabinene	trace/-	trace/-	1.3/-	1.4/-
Myrcene	trace/0.8	trace/1.0	2.6/1.3	trace/0.8
Limonene	trace/1.5	trace/1.5	0.7/1.7	trace/0.6
β-phellandrene	-/7.3	7.9/14.3	-/7.9	trace/14.1

Note. Numerator, 1967 data; denominator, 1968 data.

No definite patterns were detected with respect to the rest of monoterpenes. It is significant that, in the variants with poor and moderate intensity of tapping, there were only traces of sabinene, myrcene, and limonene, while their presence was fixed in the range 0.7–2.6% in experiments with intense tapping.

In the second year of tapping, the variation trends of the main monterpenes remained as before but differences were detected between these trends and the tapping methods: in the usual technology, the contents of α-pinene, β-pinene, and Δ^3-carene in all the experiments (III–V variants) stabilized at the same level but were significantly different in the experiment with sealing-type cuts (II). The content of rest of 126 monoterpenes changed to some extent. Thus, while β-phellandrene was detected in the first year only in the variant with moderate tapping, it was detected and, that too, in significant amounts in all variants in the second year. The contents of myrcene and limonene stabilized more in the second year and at the same time camphene content fell while β-phenchene and sabinene were not detected.

Changes in the composition of monoterpenes during moderate tapping extend for a long period. This was seen from the data of experimental section (No. 6) in Gornyi Altay where tapping was practiced by the III variant for nine years. In the galipot collected at the end of August, the content of α-pinene was 37.4%, camphene 1.6, β-pinene 21.3, Δ^3- carene 30.1, myrcene 0.9, limonene 12, and β-phellandrene 7.6%. This composition proximated that established by the intense tapping variant after a two-year test. Thus, prolonged tapping at moderate load and short-term intense tapping produce the same result.

Season-wise, the quantitative composition of main monoterpenes similarly undergoes certain variations. The content of α-pinene decreases by autumn and of Δ^3-carene increases in the same manner as seen in the Siberian stone pine ascending into the mountains (Vorob′ev, Dubovenko, and Pentegova 1971) and its tapping (Vorob′ev, Dubovenko, and Pentegova 1977).

A similar strengthening of the protective system of trees has been noticed in Siberian larch affected by xylophages (Isaev and Ryzhkova 1968, and Massel′, Rozhkov, Vol′skii, and Pentegova 1975). According to these investigators, the reorganization of the main constituents in the composition of monoterpene carbohydrates proceeds toward an increase of toxic compounds. Their effect on various entomotoxins or stimulants is not the same. On the whole, as pointed out by G.I. Massel′ (1972), Δ^3-carene and α-pinene exhibited maximum toxicity to larvae and imago of bark beetles while resin acids and their oxygen-bearing fraction were effective against large larch bark beetle. Resin acids detected in high quantities in highly resin-producing trees (see Chapter II) in fact promote increased stability of xylem tissues of spruce against fungal infection (Hart, Wardell, and Hemingway 1975). Among terpenes, Δ^3-carene stands foremost in the toxicity to trunk pests (Isaev and Rhyzhkova 1968, and Massel′ 1972, and 1979). A similar effect of Δ^3-carene is noticed toward root fungus (Chudnyi, Krangauz, and Gundaeva 1972). At a combination of traces of Δ^3-carene and high level of α-pinene (70–80%), the growth of colonies in tests approached that of control. Field observations of the state of Scotch pine trees affected by root fungus revealed the presence of Δ^3-carene and increase of α-pinene and β-pinene (Polozhentsev, Chudnyi, and Zolotov 1969, and Fedorov and Manukov 1972). These changes related to the stage of infection coincide with reduced Δ^3-carene in Siberian larch trees colonized by xylophages (Isaev and Girs 1975 and Massel′ 1979).

Thus, the condition of affected trees can be classified into stages of active adaptation and subsequent weakening of their vitality in the case of 127 unusual influence of the attacking factor. A.S. Isaev and G.I. Girs (1975) in this context have distinguished the periods of "active" and "passive" antibiosis of trees.

The nature of variations of monoterpene composition is associated with the species variation. While the damage of pine and larch causes increased content of Δ^3-carene and reduced presence of α-pinene, on the other hand, a reduction of the former and increase of the latter occur in the case of pine and spruce (Massel′, Rozhkov, Vol′skii, and Pentegova 1975). Available evidence demonstrates the association between the resistance of Scotch pine and α-pinene level. According to A.V. Chudnyi (1981) who studied these aspects, to enhance resistance, pine varieties with high resin productivity, galipot containing more of α-pinene and less of Δ^3-carene should be selected. In all probability, such a recommendation may be relevant only to certain types of damages since it was demonstrated before that the higher content of Δ^3-carene in Scotch pine makes for its stability against root fungus (Chudnyi, Krangauz, and Gundaeva 1972).

Insofar as Siberian stone pine is concerned, the selection of such varieties should be evidently associated with identifying trees containing a high amount of Δ^3-carene in galipot. This view is supported not only by the nature of strengthening of the protective system of damaged trees but also the higher content of Δ^3-carene in galipot of pine as it ascends into the mountains (Vorob′ev, Dubovenko, and Pentegova 1971). Moreover, as already pointed out (see Chapter III), resin-producing varieties of Siberian stone pine possess a high content of Δ^3-carene.

The above discussion does not signify that this index is an absolute value for the stability of the trees. Suffice to say that A.S. Isaev and G.I. Girs (1975) noticed in many cases the colonization of Siberian larch with xylophages in spite of high content of Δ^3-carene in the terpene composition. It is therefore evidently useful to study the phytoncide activity of affected trees keeping in view the fact that the action of volatile compounds forms the first line of defense against entomotoxins and phytopathogenic microorganisms (Vorob′ev and Pryazhnikov 1970).

Observations showed that the phytoncide activity of severely tapped trees decreases in the fourth year of experiment (Table 43). The most perceptible differences are noticed in the overall phytoncide activity of shoots

128 Table 43. Variation of phytoncide activity of trees under the influence of tapping

Organ	Phytoncide activity in relative units	
	control	experimental
	Female shoots	
One-year-old, needles	7	5
Two-year-old, needles	6	5
One-year-old, axis	1	1
Two-year-old, axis	1	0
Buds	1	0
One-year-old, cones	0	1
Two-year-old, cones	1	1
Seeds	2	0
	Male shoots	
One-year-old, needles	8	5
Two-year-old, needles	8	7
One-year-old, axis	0	0
Two-year-old, axis	2	1
Buds	2	1
	Growth shoots	
One-year-old, needles	6	5
Two-year-old, needles	11	8
One-year-old, axis	1	1
Two-year-old, axis	1	1
Buds	2	1
Total phytoncide activity	60	43

which incidentally exhibit some tendency to rise from the apex of the tree to the base of crown. The noticed reduction of phytoncide activity of pine needles is maintained within the indicated range for up to 10 years of tapping (Talantsev, Pryazhnikov, and Mishukov 1978).

Phytoncide activity is largely associated with transpiration. According to Yu.E. Novitskaya (1967a, b), transpiration is a complex physiological-biochemical process of liberation of solutions of various organic and mineral matter as well as volatile compounds by the tree. If the formation and accumulation of phytoncide agents occur as a result of photosynthesis, which decreases (as will be demonstrated later) under the present experimental conditions, the intensity of their liberation should be determined by transpiration.

128 Under conditions of moderate tapping, transpiration in Scotch pine remains at the initial level for five years (Mogileva and Rastorgueva 1963). Transpiration of the needles falls at a much deeper disturbance of root-leaf relations (ringing). According to G.A. Mogileva (1965) and P.A. Kolomiets (1966) on ringing of plants and also the results of tapping Siberian stone pine (Vorob′eva 1974), this is due to the accumulation of carbohydrates in the needles which facilitate a higher concentration of cell sap and water retention of tissues. According to the observations of B.F. Pilipenko (1967) and our own investigations given below, an increase of bound water during tapping is noticed not only in the needle but also in the bast under the cuts. Evidently, under these conditions, as also in highly resin producing varieties (Khirov and Nevzorov 1965 and Chudnyi 1966) and also beetle-resistant trees (Perttynen 1957), water consumption and material transpiration become more economical, pointing to the relation of these processes with resin formation and its exudation.

In this case, the reduction of phytoncide activity of tapped trees, on one hand, serves as an index of activation of resin-producing processes and, on the other, of the commencement of weakening of the protective system and impairment of sanitary and hygienic properties. When evaluating these aspects, it should be borne in mind that under discussion is an extreme instance, i.e. an experiment with ringing-type tapping. Under lesser damages, as can be judged from an analysis of resin output and quantitative composition of terpene compounds, the protective system of the tree remains active for a long period and can cope with trunk damages by itself.

128 Growth

The phenomenon of growth processes under conditions of tapping was studied before mainly in the trunk portion of trees so to determine the qualitative and quantitative losses of timber (Kutuzov 1951, Gavrilov 1953, Shaternikova 1960, Voronenko 1961, and Kulakov 1972). Without going into the importance of the results obtained—the effect of tapping on the growth of trees will be examined directly under experimental conditions—it may be pointed out that the study of this factor relative to the growth of crown metameres has not been adequate. Nevertheless, in the case of Scotch pine, it is known that the growth of terminal shoots in well-maintained plantations under the influence of tapping decreases by 20–24% (Paramonov 1973) and in poor plantations by 50% (Shaternikova 1960).

The improvement of the linear growth of shoots is first noticed in Siberian stone pine (Fig. 38). The maximum effect is recorded in those variants with poor tapping and correspondingly a low intensity of resin formation and its exudation. The activation of growth processes depends on the gender of the

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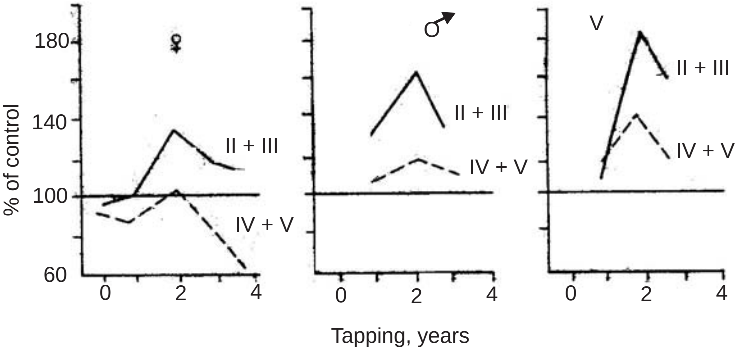

Fig. 38. Length of female shoots under different tapping conditions: variants II+III—poor and moderate, and IV+V—intense and very intense.

shoots. Figure 38 shows that the growth of male shoots is more than that of female shoots and that of vegetative shoots more pronounced than male shoots.

The positive effect of tapping begins to decline in the third year of the experiment. It has also been found that the weakening of growth is also associated with the sex of shoots, intensity and duration of the disturbance of root-leaf relations. Thus, in female shoots, where the least activation of growth has been noticed, there was also a very sharp fall of growth under the influence of severe tapping. Parallel observations in 10-year continuous tapping sections confirmed these trends and revealed their simultaneous dependence on the initial conditions of the stand (Table 44). While a positive effect of tapping has been noticed in a plantation of class II quality index (Altay section) in the first five years, it was not so in plantations of class IV
130 quality index (Tomsk section). Moreover, in the latter case, the adverse consequences of tapping were greater than in the former.

Insofar as less severe disturbance of root-leaf relations than under 10-year conditions is concerned, more so in five-year tapping, the growth of female shoots is maintained at the control level over a long period. Results of the study of consequences of 40-year cleaving of Siberian stone pine plantations in Tomsk province were most convincing (Table 45). Not only the linear but also the cambial growth of shoots was maintained at the normal level which is very important (as shown in Chapter II) for their stable cone yield.

In male and vegetative shoots, the adverse consequences of tapping were less perceptible than in the female shoots (Table 46). At least toward the end of the 10-year tapping period, differences in the growth of shoots between
131 control and test were insignificant while the growth trends in them continued to depend on the original condition of the stand.

130 Table 44. Variation of the annual growth of female shoots during 10-year tapping, cm

Period of observations, years	Control M ± m	Tapping M ± m	Variation allowing for initial condition, %
	Altay section		
1956–1960 (before experiment)	4.48 ± 0.10	4.78 ± 0.18	0
1961–1965 (first half of experiment)	4.53 ± 0.09	5.11 ± 0.20*	+6.0
1966–1969 (second half of experiment)	4.08 ± 0.11	3.69 ± 0.21*	−16.3
	Tomsk section		
1956–1960 (before experiment)	4.65 ± 0.04	5.25 ± 0.03	0
1961–1965 (first half of experiment)	4.19 ± 0.03	4.47 ± 0.03	−5.9
1966–1969 (second half of experiment)	4.26 ± 0.03	3.88 ± 0.03*	−22.5

130 Table 45. State of growth processes in the female shoots of crown in cleaved trees (three-year data for needles and 10-year data for shoot axis)

Test variant	Shoot axis		Needles	
	length, cm	diameter, cm	number of fascicles growing/year	length, cm
Control	5.6 ± 0.1	1.23 ± 0.03	28.6 ± 0.2	9.9 ± 0.1
Cleaving				
moderate	5.0 ± 0.2	1.28 ± 0.03	29.3 ± 1.8	9.7 ± 0.2
severe	5.7 ± 0.3	1.25 ± 0.05	27.0 ± 1.2	10.7 ± 0.2

Simultaneous with the study of shoot growth, observations were made on needle length (Vorob′ev 1974b). Its variation in the early years of 10-year tapping showed that their original growth parameters were maintained as in tests using chemical methods of resin exudation (Khlebodarov, Maksimchuk, and Manakov 1979).

Later, the response of needle growth began to differ: in vegetative and female shoots, its length began to decrease and, in male shoots it showed an increase. Under cleaving conditions, needle length in female shoots remained the same as in control (see Table 45).

From the growth indexes studied, it may be seen that, toward the end of the 10-year test period, in female shoots the length of needles and shoots in Siberian stone pine decreased while, in the male shoots, it exceeded the initial level or reverted to the original state and, in the vegetative shoots, occupied an intermediate position relative to the first two.

46 Table 46. Annual growth of male and vegetative shoots under tapping conditions, cm

Test variant, years	Male	Vegetative
	M ± m	M ± m
	Altay section	
Control	0.83 ± 0.03	1.13 ± 0.05
Experimental, 7–9	0.93 ± 0.04	1.19 ± 0.04
	Tomsk section	
Control	1.51 ± 0.01	1.43 ± 0.08
Experimental, 7–9	1.43 ± 0.01	1.67 ± 0.09

A similar situation was also noticed in the state of the dry mass of needles. Thus, in the ninth year of tapping, while the dry weight of 100 needle fascicles in the female (12–17 g) and vegetative (7–8 g) shoots was 68–81% of control depending on the condition of the stand, it was 6–7 g or 117% in the male shoots.

Calculations for an average tree and for unit area reveal significant variations of photosynthesizing mass of the female shoots of crown (Table 47). At optimum shift of root-leaf relations (moderate tapping and cleaving), the number of needles increased and on their excessive disturbance by these same methods, it dropped. The needle content of shoots (Fig. 39) and

47 Table 47. Weight of one-year-old needles in the female shoots of crown

Test variant, extent of damage, period of inspection	For average tree		Weight/ fascicle, g	Dry weight of needles		
	shoots, No.	needle fascicles, ’000s		per tree, g	kg/ha	%
		Tomsk section, cleaving				
Control	100	2.8	0.09	280	28	100
Moderate, 38th–40th year	122	3.5	0.11	420	42	150
		Altay section, tapping				
Control	32	0.9	0.12	109	15	100
Moderate, 7th–9th year	38	0.9	0.09	88	12	80
		Tomsk section, tapping				
Control	58	1.0	0.17	175	36	100
Moderate, 7th–9th year	49	0.9	0.11	108	22	61
		Tomsk section, cleaving				
Control	100	2.8	0.09	280	28	100
Intense, 38th–40th year	54	1.4	0.11	160	16	57

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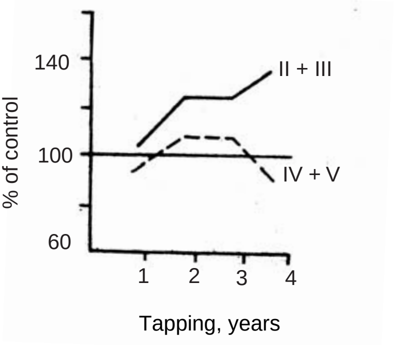

Fig. 39. Needle content of female shoots under different types of tapping conditions (variants as in Fig. 38).

the weight of needle fascicles changed correspondingly (see Tables 45 and 47).

Different opinions have been expressed on the question of growth variations of the trunk. Some point to the stimulating role of the tapping cut 132 (Yakhontov 1931) while others do not find significant deviations from the control (Vink and Gurskii 1969, Kraevskii 1955, and Kulakov 1972), and yet others (Vysotskii 1970, Gavrilov 1953, Shaternikova 1960, and Paramonov 1973) noticed impaired growth processes. These contradictory results can be explained in that the observations describe the state of growth at different stages of the effect of experimental conditions and under different technological test regimes.

Ten-year tapping of Siberian stone pine established that the radial growth of class I trees varied in the same manner as the length of shoots in the portion of crown, i.e. initially, the growth of trunk rose, later reverted gradually to the initial state and, in the 8th–9th years of test was 14–17% less than in the control (Kulakov 1972). In class II trees, there was practically no growth activation, its deterioration commenced earlier, and dropped latter by 40%. In class III trees, deterioration of growth processes commenced right from the time of making the cuts. These observations demonstrate the significance of the dependence of variations on the rank of trees in the stand, the original condition of the stand, and importance of these in the studies. The overall losses of timber growth in the case of Siberian stone pine are insignificant. In Altay section, these were 0.3 m^3/ha at the end of the 10-year period and 0.5 m^3/ha in the Tomsk section. In the case of Scotch pine, losses over the same duration exceeded 0.7–1.0 m^3/ha (Vysotskii 1970).

Growth recovery after cessation of damages proceeds slowly. As could be seen from the data for P.K. Kutuzov experimental section (No. 4), radial growth decreased distinctly even one year after making the cuts (Fig. 40).

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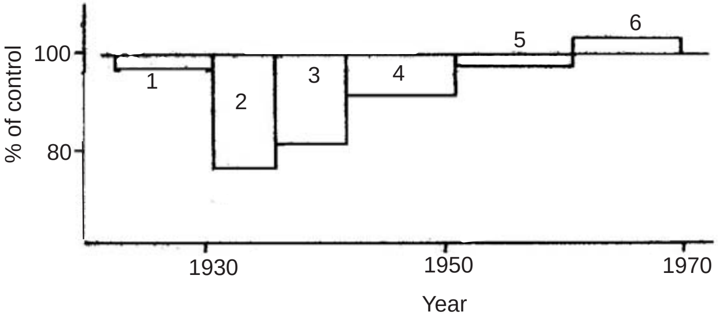

Fig. 40. Variation of the radial growth of trees under the influence of intense tapping in P.K. Kutuzov section:
1—before tapping, 2—after first tapping, 3—after second, and 4, 5, 6—after cessation of tapping.

133 Tapping carried out in the '30s through smooth holes caused deep cuts and thus this experiment should be regarded as the result of growth variation under conditions of a significant shift of root-leaf relations.

Restoration to the normal state occurs through the increased activity of cambium in the unaffected portion of the trunk. The mechanism of this process can be clearly perceived from the state of growth under conditions of cleaving (Table 48). At the base of the cut (section 1), the breadth of annual layers, sapwood, and its diameter decrease, suggesting the

133 Table 48. Growth of trees during cleaving

Test variant	Opposite side of cut			Back of cut			Sapwood area, cm^2/ cm of diameter
	sapwood breadth, mm	breadth of annual layer, mm	radius, cm	sapwood breadth, mm	breadth, of annual layer, mm	radius, cm	
			Section above cut				
Control	22	1.0	19.5	22	0.9	17.7	8.9
Cleaving	16	0.9	16.5	24	1.0	19.0	9.1
			Section across cut				
Control	20	1.2	20.3	21	1.3	20.0	8.1
Cleaving	—	—	11.7	26	1.9	23.1	9.4
			Section under cut				
Control	22	1.4	21.3	22	1.0	22.1	8.0
Cleaving	10	0.6	17.5	23	1.4	22.0	8.6

Note. Dash (–) signifies the absence of sapwood (crushed).

cessation of the flow of initial biosynthesis products of wood. On the opposite and lateral portions, the sapwood breadth and radius are the same as in control but the annual growth is more. The cross-section at the level of the cut 134 (section 2) represents the original form, characterizing on one hand the flat sapwood-free portion and, on the other, the broad, oval, intensely active, unaffected portion of the trunk. Here, the superior growth characteristics make for a larger area of active wood (sapwood) than in the control. A similar picture is noticed above the cut as well (section 3). The restoration thus of the zone of active wood in the trunk guarantees, as shown above, normal growth conditions of needles and shoots.

In the case of fairly severe but wholly permissible tapping cuts, the reduced flow of assimilates from the crown similarly supports the normal growth conditions of shoots. This can be seen from the example of Altay 10-year tapping section.

The restoration of the growth of trees thus proceeds with moderate resin exudation or its cessation. The relation between resin-forming and growth processes is traced in trees of different levels of resin output. It has been established that in the case of high resin producing Scotch pine trees, the reduction of growth proceeds more strongly (Vysotskii 1970). A similar phenomenon has been detected in Siberian stone pine (Kulakov 1971). Based on these studies, it may be suggested that the growth and resin formation processes in the trunk are interrelated as in the crown such that when one of them increases—in this case, resin exudation—the other process—growth—is suppressed.

On the whole, observations showed the presence of some stages of behavior in the variation of growth processes under conditions of this type of shift of root-leaf relations. Their initial activation is followed by a reduction of growth energy to the original level, and finally its suppression.

The extents of these stages vary depending on how intense and prolonged is the shift of root-leaf relations, activity of resin exudation, gender of shoots, and original condition of the tree. The greater the resin exudation and the more significant the shift of root-leaf relations, the less favorable are the conditions for the growth processes. On a sharp variation of root-leaf relations, the period of active growth is insignificant and brief or altogether absent. A similar growth in characteristic of high resin-producing trees compared to the poor resin-producing trees and for Scotch pine compared to Siberian stone pine.

The activation of growth processes is least noticed in those sections and organs of trees which are most associated with the utilization of nutrients for resin formation or for the formation of regenerative organs. These are female shoots and needles as well as the annual sapwood rings in the trunk portion of tree. Here, during tapping, assimilates accumulate

rapidly (Vorob'eva 1974), they make for increased cone yield in the crown, and are utilized for the synthesis of terpene compounds in the trunk. Growth increase in these sections of the tree is rather short-lived. The response of trees to tapping or similar natural damages thus leads to the inhibition of growth processes and generation of predominant conditions
135 for protection and reproduction. Such a response behavior is evidently evolutionary.

Growth is activated over a much longer period in trees which are less involved in energy-consuming processes like cone yield and resin formation and the adverse consequences of metabolic shift are manifest later. In the male and vegetative shoots of the crown in which such changes are noticed, shoots fall close to the so-called "centers of resin formation" (part of trunk above cuts) which receive nutrients from the upper part of the crown. Utilization of nutrients and consumption of lesser energy in the reproductive processes than shoots of female type (feeding cones of two generations), male and vegetative shoots are ensured of adequate nutrition for a long period.

These explanations only partly reveal the characteristics of growth conditions in the damaged trees. These aspects can be more fully judged with the help of physiological-biochemical evidence.

The differences noticed in the response of different levels in the crown to the shift of root-leaf relations may be used for evaluating plantations affected by tapping or similar processes. Thus, when there is a weakened development of vegetative and male shoots, significant changes in the female shoots can be anticipated. Since the female shoots are important for cone yield and resin formation, significant deviations from the normal levels should not be permitted. A reduction in the needle formation of shoots also may serve as a characteristic of the weakened vitality of trees consequent on tapping or other damages.

As pointed out above the change of growth processes under conditions of controlled metabolism depends on the initial condition of trees. On the example of Altay and Tomsk 10-year tapping sections, it was shown that growth deterioration commenced right in the first year of tapping in oppressed and deteriorated plantations. The absence of the growth activation stage here points to the low potential possibilities of such plantations and their unsuitability for prolonged tapping. The same applies to trees of low classes of growth.

Cone Production

While studying cone production in tapped trees, earlier investigators were essentially concerned with crop size, i.e. the ultimate index of the regenerative process. The reasons for the changes taking place and duration of their occurrence have been ignored.

The author's observations dealt with resolving the question of the influence of tapping and cleaving on cone yield as also with the study of the characteristics of the progress of different phases of the regenerative process under conditions of controlled changes of root-leaf relations.

136 The regenerative cycle of woody plants commences with the initiation of cone formation. Their number in the test objects was determined from the total number of cone traces per shoot (Nekrasova 1961). This index reflects the formation conditions of female strobili in the embryonic period and indicates their formation energy, i.e. the level of the reproductive activity of shoots.

The effect of the shift of root-leaf relations on the extent of initiation was fixed in the third year of the test since the number of primordia in the first two years were already predetermined by the conditions preceding the commencement of the test. Many investigators have ignored this factor associated with the course of regenerative cycle in pines and began determining the effect of tapping on the number of cones in the first year of test (Kutuzov 1949).

The change of initiation under the experimental shift of root-left relations proceeds differently (Table 49). On a fairly significant reduction of the flow of assimilates from the crown, the energy of primordia formation under tapping conditions rises initially but falls toward the end of the 10-year cycle. During cleaving, it remains high after almost 40 years. In the latter case, a slightly better initiation does not offer any significant independent effect but promotes the growth and overall yield of female shoots; its extent, as will be shown later, increases perceptibly.

136 Table 49. Formation energy of female primordia, numbers/shoot

Test variant, extent of disturbance, period of observations	Control	Test	
		M ± m	% with allowance for original condition
Tapping cuts of non-sealing type:			
Moderate, years			
3–5	1.71 ± 0.10	2.00 ± 0.10*	112.0
7–10	1.59 ± 0.05	1.27 ± 0.09*	80.0
Cleaving cuts:			
Moderate, 30–40	1.51 ± 0.11	1.56 ± 0.11	103.0
Intense, 30–40	1.51 ± 0.11	1.65 ± 0.10	109.3

On the whole, initiation is intensified in the course of a short spell and is noticed mainly in years with favorable weather conditions when optimal possibilities for the formation of female primordia also arise in the unaffected trees. Under unfavorable conditions, their number is the same in the control as well as in the experimental trees. Quite clearly, the ecological, more than the trophic, factor in this case plays a significant role. Such a situation is well exemplified by cleaved Siberian stone pine trees which exhibit the same cone yield dynamics as unaffected trees (Fig. 41). A similar freedom of cone production dynamics from the variations of trophic factors is noticed when using mineral fertilizers (Breusova 1970, Kozubov 1971, Iroshnikov
137 1973, and Ronis 1978) and thinning of stands (Alekseev 1979). The characteristics of the effect of this shift of root-leaf relations on primordia initiation show that reproductive energy can thus be intensified but its dynamics cannot be altered.

Cone production increased in some years not only due to a rise of formation energy but also as a result of the involvement of shoots, primarily lateral, which were vegetative before. The significance of this factor has been discussed in Chapter II. Such trends were detected when using tapping cuts as well as under moderate cleaving (Vorob′ev 1974a). On severe cleaving, the number of cone producing shoots falls appreciably.

The change in the number of cone producing shoots exerts a more significant influence on the yield of trees than the intensification of the energy of initiation. This is particularly evident on the example of Scotch pine which responds more clearly than Siberian stone pine to the shift of root-leaf relations (Table 50).

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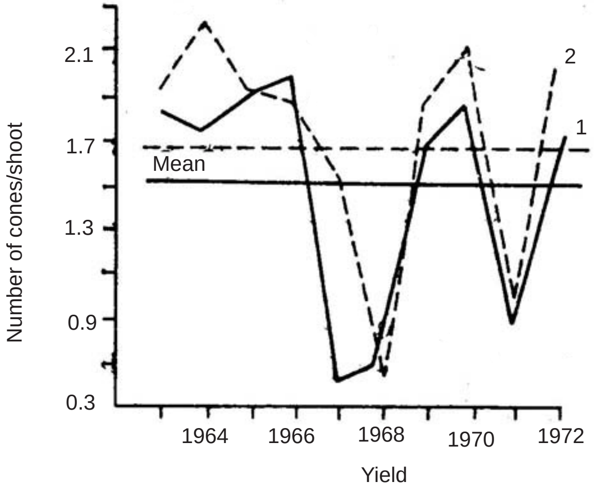

Fig. 41. Cone production dynamics of cleaved Siberian stone pine trees: 1—control; 2—cleaving.

137 Table 50. Cone production in Scotch pine under conditions of optimal tapping, numbers

Test variant	Cones/shoot	On average tree	
		cone-bearing shoots	cones
Control	0.73 ± 0.11	125.2 ± 11.3	92.3 ± 7.3
Tapping cuts, after 7–8 years	0.72 ± 0.12	295.3 ± 17.6*	211.7 ± 19.3*
%	98	235	269

A significant rise in cone production in the case of Siberian stone pine trees is noticed mainly under conditions of moderate cleaving (Table 51). When using tapping cuts in a well-developed stand (Altay section), the total number of primordia rises at first due to increased energy of initiation. Toward the end of test, this rise becomes insignificant and the rise is maintained as a result of the large number of cone-bearing shoots. A similar situation may prevail in a less productive stand as well (Tomsk section) but by the end of the 10-year cycle, the formation of primordia per shoot here fell so much that the total number of cones per tree lay below the level of the control in spite of a larger number of shoots.

During the post-embryonic development of primordia, the retention of 138 cones rises initially but falls later (Vorob'ev 1974b). In either case, deviations from the normal are insignificant since evidently the change of root-leaf

138 Table 51. Number of female primordia on an average tree in the plantation

Test variant, duration	Control	Test	
		M ± m	% with allowance for original condition
	Altay section		
Initial stage	30.3 ± 2.7	23.1 ± 2.1	
Tapping cuts, after 10 years	61.3 ± 5.5	57.3 ± 4.2	+13.8
	Tomsk section		
Initial state	52.0 ± 4.6	52.0 ± 5.1	
Tapping cuts, after 10 years	71.2 ± 6.8	51.7 ± 6.3	–28.2
	Cleaving section		
Average interference, after 30–40 years	150.8 ± 18.2	190.4 ± 21.6	+36.0
Intense interference, after 30–40 years	150.8 ± 18.2	89.1 ± 12.1	–59.0

relations does not influence the post-embryonic development of primordia to the same extent as during their formation. If the extent of the drop of laying energy and the fall of cones under conditions of abnormal shift of root-leaf relations are compared, it becomes quite clear that the attenuation of the regenerative process proceeds not because of a greater loss of the formed organs but due to a sharp reduction of the number of primordia. These processes evidently outstrip the reduction in the total number of cone-bearing shoots as can be seen from the results of severe cleaving in which a high level of energy of primordia formation is maintained for long and an insignificant increase of cone fall is noticed but the volume of the female regenerative regions shrinks appreciably.

The disturbance of root-leaf relations influences positively the growth of reproductive organs. Unlike the vegetative organs, the growth intensity of cones is well marked and proceeds more rapidly in the variants in which the shift of root-leaf relations is more (Fig. 42). On a minor disturbance of these relations, the increase of cone length is insignificant and short-lived. Toward the end of the fourth year of test period, the cone sizes begin to decrease in 139 both the cases. In tests with prolonged tapping, this is evidently associated with the sealing of cuts and restoration of assimilates flow from the crown; when making a large number of non-sealing type cuts, it is associated with the significant interruption of flow and accumulation of assimilation products in the crown. At an intermediate level of disturbance of root-leaf relations which prevails under the technological parameters of 5- to 10-year tapping, the cone length diminishes insignificantly only toward the end of the tapping cycle (Table 52). Under cleaving conditions, cone length

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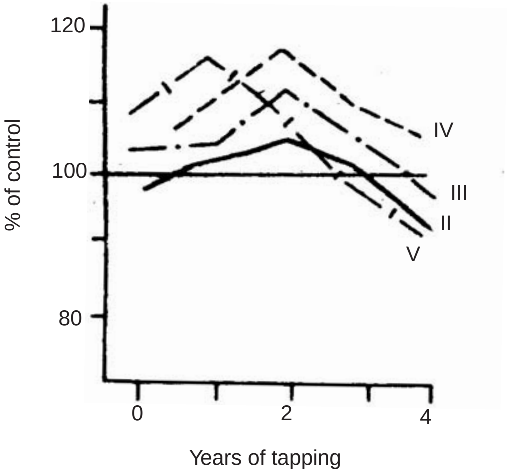

Fig. 42. Cone length under different tapping conditions (variants as in Fig. 38).

139 Table 52. Characteristics of cones and seeds

Test variant	Cone length, cm	Total number of seeds	Seed type, % of total			
			normal	full-grained	hollow	under-developed
		Intense tapping, sixth year, section 1				
Control	6.2 ± 0.1	80.5 ± 3.2	98.7	97.4	2.6	1.3
Test	6.8 ± 0.1	88.5 ± 3.1	99.3	95.5	4.5	0.7
		Moderate tapping, ninth year, section 6				
Control	6.1 ± 0.1	83.5 ± 1.4	98.7	96.3	3.7	1.3
Test	6.0 ± 0.1	80.5 ± 1.8	96.3	98.7	1.3	3.7
		Moderate tapping, ninth year, section 7				
Control	5.5 ± 0.1	38.1 ± 0.6	97.3	78.3	21.7	2.7
Test	5.5 ± 0.1	37.1 ± 0.4	97.2	86.1	13.9	2.8
		Moderate cleaving, 40th year, section 10				
Control	5.3 ± 0.1	45.7 ± 1.1	71.1	81.3	18.7	8.9
Test	5.4 ± 0.1	45.2 ± 1.2	75.5	82.3	17.7	4.5
		Intense cleaving, 40th year, section 10				
Control	5.3 ± 0.1	45.7 ± 1.1	71.1	81.3	18.7	8.9
Test	6.3 ± 0.1*	57.2 ± 1.4*	73.6	83.3	16.7	6.4
		Intense tapping, 39th year, section 5				
Control	7.2 ± 0.1	83.5 ± 3.2	98.7	97.5	2.5	1.3
Test	5.6 ± 0.2	65.9 ± 3.4*	98.4	89.2	10.8	1.6

maintains the same value as that of control or even a higher value. A distinct fall of cone growth is noticed only in severely tapped trees (P.K. Kutuzov section).

The growth variation of cones in Scotch pine essentially follows a similar pattern. In the first few years of test, their length too increases (Paramonov 1973), thereafter remaining at the same level as control toward the end of the 10-year period (Korobchenko 1975 and Paramonov 1973), and decreases significantly only on unusual or prolonged interruption of root-leaf relations (Besser 1941).

The breadth of cones in Scotch pine as well as in Siberian stone pine remains unchanged throughout the long duration of tapping. Since the length of cones increases in the early years, their form becomes somewhat elongated. 140 In the tapped Siberian stone pine trees, the original length to breadth ratio of cones is 1.30 ± 0.2 and in control 1.20 ± 0.01. The form is restored later but, if the linear growth of cones is affected, it becomes oval.

The number of seeds is closely related to the cone length. This is clear from the investigations reported earlier (Iroshnikov 1963) as well as clearly from the data given in Table 52 in which the changes of the total yield of seeds from cones follow the fluctuations of their length. A very similar relation holds good for the normally developed and full-grained seeds. No definite conclusions are possible regarding the content of hollow and underdeveloped seeds. It can only be pointed out that, on moderate tapping, the amount of hollow seeds decreases; on cleaving, these remain the same as in control but increase on intense tapping. The level of hollow seeds remaining unchanged under conditions of optimum shift of root-leaf relations suggests the absence of interference in the embryonic development of seeds. Information on the content of underdeveloped seeds suggests some deviations of fecundity. The proportion of underdeveloped seeds in the total number of seeds on cleaving and short-term tapping is less and on prolonged tapping more than in the control. These differences are, however, not significant nor are they of any practical importance for the qualitative yield of seeds since the natural content of hollow and full-grained seeds exerts a more important influence on their vitality.

These correlations are supported by the author's data (Vorob'ev 1974a) in which increased vitality of seeds has been demonstrated in the first few years of tapping. On moderate disturbance of root-leaf relations, the improvement of seed vitality is not significant but improves by one class on moderate and severe interference. This is promoted by the improved qualitative structure of seeds as well as the greater vitality of embryos. The latter, as already shown, is associated with the improved biochemical composition of seeds (Vorob'ev and Rush 1974).

A better vitality of seeds under conditions of moderate interruption of root-leaf relations is noticed for a fairly long duration. At the end of the 10-year period, their vitality remains higher than in the control by one class even under the conditions of Tomsk section (Table 53). During cleaving, it remains the same as in unaffected trees after 40 years. Two years after the same period but on very severe tapping (Kutuzov section) the vitality of seeds falls. This fall is associated to a significant extent with the impaired growth of embryos (Table 54). Data on their length show corresponding changes of this parameter on improved or impaired seed vitality.

Under conditions of tapping cuts, the vitality of Scotch pine seeds also changes in a similar manner. Toward the end of the 10-year period, their quality was better than in the control in tests in Kharkov district (Korobchenko 1965) as well as in Altay region (Paramonov 1973). In the Belorussian pine forests, seven years after tapping, some deterioration,
141 although insignificant, of the planting quality of seeds was detected (Gunyazhenko and Tolkachev 1965). Similar results were recorded on prolonged tapping of Scotch pine with stimulators (Drochnev, Vishnevskaya, and Khuden'kikh 1978). A significant reduction of the vitality of pine seeds

141 Table 53. Vitality of seeds at the end of tapping, %

Test variant	Live	Hollow	Dead	Absolute vitality	Class of vitality
		Altay section			
Control	83	15	2	97	2
Tapping cuts, ninth year	94	4	2	97	1
		Tomsk section			
Control	52	22	26	66	3
Tapping cuts, ninth year	66	16	18	78	2
		Kutuzov section			
Control	85	3	12	88	2
Annual tapping cuts, 39th year	66	11	23	75	3

141 Table 54. Length of seed embryos, mm

Test variant, degree of disturbance	Statistical indexes		
	M ± m	σ	C_V
	BIN section		
Control	6.71 ± 0.08	0.8	11.7
Tapping			
poor, II	6.68 ± 0.09	0.9	14.3
moderate, III	7.68 ± 0.12	1.2	16.0
intense, IV + V	7.43 ± 0.08	0.8	11.3
	PIB section		
Control	6.84 ± 0.08	0.8	12.1
Tapping			
poor, II	6.93 ± 0.10	1.0	15.1
moderate, III	7.30 ± 0.09	0.9	13.5
intense, IV	7.23 ± 0.10	1.0	14.3
	Kutuzov section		
Control	7.74 ± 0.08	0.8	10.5
Intense tapping, IV	7.09 ± 0.08	0.8	11.7

was noticed only on very intense and prolonged use of tapped plants (Besser 1941).

The absolute weight of seeds which reflects the intensity of accumulation of dry matter plays a definite role in altering the planting qualities of seeds.

Observations of this index revealed its variation conforming to the magnitude of interruptions of root-leaf relations (Table 55). The maximum weight gain of seeds was noticed in the third year of tapping and, from the fourth year, it began to revert to the original level.

On moderate interruption of root-leaf relations, this process proceeds over a long period. Toward the end of the 10th year of tapping and 40 years of cleaving, the absolute weight of seeds remained higher than in the control (Table 56). The weight of seeds fell significantly only under conditions of Kutuzov section.

142 Table 55. Absolute weight of seeds at the commencement of tapping (BIN section), g

Year	M ± m	%
	I variant (control)	
1966	253.0 ± 5.2	100
1967	224.0 ± 6.5	100
1968	243.0 ± 2.4	100
1969	252.0 ± 4.5	100
1970	242.3 ± 3.8	100
1974	244.6 ± 4.6	100
	II variant (weak tapping)	
1966	227.0 ± 3.6	89.7
1967	202.0 ± 8.0	90.1
1968	231.0 ± 2.3	95.0
1969	245.8 ± 3.7	97.9
1970	208.5 ± 4.0	96.0
1974	238.3 ± 5.1	97.0
	IV variant (intense tapping)	
1966	261.0 ± 7.6	103.1
1967	233.0 ± 4.9	104.0
1968	270.0 ± 3.1	111.1
1969	265.4 ± 6.3	105.7
1970	255.0 ± 4.3	104.9
1974	238.3 ± 5.1	97.0
	V variant (very intense tapping)	
1966	252.0 ± 8.1	99.6
1967	228.0 ± 8.0	101.7
1968	262.0 ± 3.5	107.8
1969	257.7 ± 6.7	102.6
1970	245.8 ± 6.0	101.4
1974	162.6 ± 3.0	66.3

Note. Seeds were not collected for III variant.

142 Table 56. Absolute weight of seeds at the end of tapping and cleaving, g

Section, year of test	Control	Test
Altay, ninth	241 ± 4.3	268 ± 3.5*
Tomsk section, ninth	217 ± 4.0	241 ± 5.1*
Kutuzov, 39th	278 ± 3.8	200 ± 4.6*
Cleaving, 40th	238 ± 3.0	275 ± 6.0*

The increase of the absolute weight of seeds not only improves their planting qualities but significantly influences the crop size. Thus, in Altay section, toward the end of the 10-year period, the yield was 11.8% more than the control in the number of cones but by 51.9% in terms of seed weight (Vorob'ev 1974b). The increase of the absolute weight of seeds similarly balances crop losses in stands as in Tomsk section. Toward the end of the test period, the number of cones on the tapped trees here was 36.6% less
143 than on untapped trees but the weight of seeds was 30.7% less. The increase of seed weight exerted positive influence on the yield of cleaved trees as well.

Mechanical damages of trunk in some manner influence the reproductive activity of the male organs of trees. On a weak disturbance of root-leaf relations, the productivity of male shoots, expressed as the number of microsporophylls per shoot, increases but decreases on intense disturbance (Table 57).

Table 57. Number of microsporophylls/shoot

Section, year of test		Control	Test (disturbance)	
			weak	intense
BIN, on test,	second	13.4 ± 0.6	13.3 ± 0.4	13.8 ± 0.7
-do-	fourth	7.3 ± 0.4	10.3 ± 0.3*	5.8 ± 0.4*
BIN, after test,	second	14.0 ± 0.7	11.7 ± 0.4*	8.9 ± 0.5*
-do-	fourth	9.9 ± 0.4	8.2 ± 0.4	10.5 ± 0.6
143 Kutuzov, 39th		13.0 ± 0.7	12.3 ± 0.3	9.3 ± 0.4*
Ydyp, notching, 7th–10th		9.6 ± 0.4	10.7 ± 0.6	8.4 ± 0.5*
Scotch pine, notching, 7th–10th		33.1 ± 1.2	30.5 ± 0.9	28.7 ± 0.8*

The cessation of tapping influences differently the number of microsporophylls. In the experiment with sealing-type cuts, they are fewer evidently due to the restoration of the transport system in the tree and reduced supply of assimilation products to the crown. On tapping with maximum damages, they are more probably because of significant isolation of the root system and, as a result, spurts are seen in the productivity of the male shoots before the death of the tree. The gradual weakening of the vitality of trees noticed in long-term tests with intense tapping or notching of trunks essentially suggests a reduction of the productivity of male shoots.

The vitality of pollen in this background changes in a characteristic manner (Table 58). At the beginning of the test, its quality improves, more significantly under conditions of greater interruption of root-leaf relations and fewer microsporophylls. If the latter are associated with the reduced growth of male shoots, the improvement of the quality of pollen, as well as seeds, is evidently determined by the activation of
144 biochemical processes. The cessation of intense short-term tapping in any case is accompanied by a reduction of pollen vitality. In trees with moderate shift of root-leaf relations, the improved pollen vitality is maintained for long. This can be seen from the results of test in BIN and Kutuzov sections. A significant reduction of pollen quality is noticed in highly notched Scotch pine trees.

143 Table 58. Vitality of pollen, %

Section, variant, year of test	Control	Test (disturbance)	
		moderate	intense
BIN, after 5-year tapping			
second	65.2	68.0	85.0
fourth	66.9	69.9	50.7
Kutuzov, 39th	46.3	54.2	41.0
"Scotch pine", notching, 8th–10th	68.0	53.1	28.9

The change of pollen vitality correlates well with its morphometric characteristics (Table 59). In trees in which intense tapping or notching has ceased and pollen has low vitality, pollen grains are smaller in size than in control. These changes are significant in the variants in which prolonged and intense interruption of root-leaf relations has been practiced. After moderate tapping, in some trees of Kutuzov section, pollen was found to be larger and, as shown above, more viable.

On the whole, the response of male and female shoots of trees is evidently different in the different stages of disturbance of their root-leaf relations. Initially, the reproductive activity of male as well as female shoots increased and pollen becomes qualitatively superior. With increasing duration and intensity of disturbance of the normal functioning of trees, the activity of processes changes in both the sexes (Fig. 43). It dips sharply in the female shoots after a significant disturbance but rises after a weak disturbance; in the male shoots, on the other hand, it increases in the first case and decreases in the second. Changes in the reproductive activity of

144 Table 59. Morphometric characteristics of pollen

Section, degree of damage	Size of pollen grains, µm				
	Total length of grains	Body length, A	Body height, B	Length of air sac, C	Height of air sac, D
			BIN section		
Control	69.6 ± 0.4	51.3 ± 0.3	43.5 ± 0.3	28.9 ± 0.3	36.6 ± 0.3
Tapping					
moderate	69.4 ± 0.4	45.8 ± 0.3	41.0 ± 0.3	28.6 ± 0.3	36.3 ± 0.4
intense	62.3 ± 0.3	41.4 ± 0.3	37.2 ± 0.2	24.0 ± 0.2	33.1 ± 0.3
			Kutuzov section		
Control	69.5 ± 0.4	47.7 ± 0.3	39.9 ± 0.3	23.3 ± 0.2	25.4 ± 0.3
Tapping					
moderate	74.0 ± 0.4	51.0 ± 0.4	44.4 ± 0.3	25.9 ± 0.3	38.5 ± 0.4
intense	68.4 ± 0.4	47.7 ± 0.3	39.2 ± 0.3	23.7 ± 0.2	34.0 ± 0.3
			"Scotch pine" section		
Control	64.5 ± 0.3	49.9 ± 0.3	43.3 ± 0.3	29.5 ± 0.3	38.9 ± 0.4
Notching					
moderate	60.6 ± 0.3	43.6 ± 0.3	36.8 ± 0.3	24.0 ± 0.,3	36.2 ± 03
intense	58.9 ± 0.3	40.1 ± 0.3	32.4 ± 0.3	22.4 ± 0.2	31.2 ± 0.3

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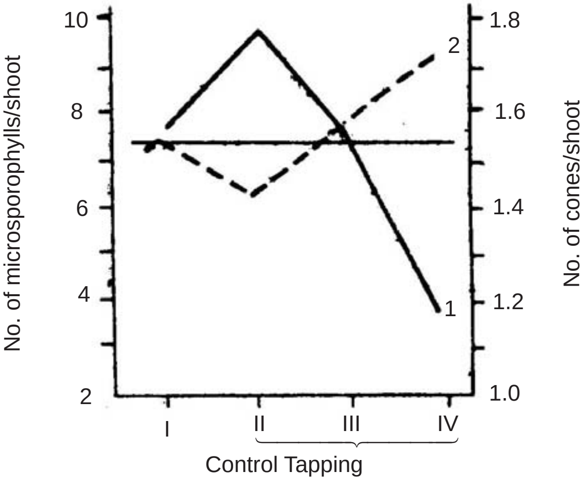

Fig. 43. Trends in the reproductive activity of shoots:
1—female; 2—male.

145 shoots in experiments with sealing-type cuts suggest the active adaptation of trees to the new conditions; in experiments with maximum damages, the changes point to the state of regenerative processes before the death of the tree.

Thus, the shift of root-leaf interrelations on mechanical cuts exerts varying influence not only on growth processes and regenerative development of shoots but also on the state of male and female shoots of trees individually. The latter, as seen from the preceding discussion, ultimately weaken.

A comparison of information presented also shows that changes in the reproductive process of trees under the conditions studied reveal several features which, on one hand, point to the nature of the influence of a particular factor and, on the other, provide an idea of the response of its individual phases to the variation of overall metabolism.

In particular, the embryonic phase (phase of primordia formation) is most affected under these conditions. The number of primordia in well-developed trees under test conditions increases distinctly, not the average number per shoot but for the tree as a whole. This occurs essentially due to a shift of female sex development of shoots that remained barren earlier. The identification of this effect showed that a change of physiological-biochemical processes on the disturbance of root-leaf relations facilitates involving new shoots in the cone-bearing process but these processes cannot significantly enhance their reproductive capacity. This signifies that the application of mechanical cuts for inducing cone-bearing may offer only a one-sided effect. Different measures are needed to raise the reproductive energy of shoots.

On excessive mechanical interferences, the formation of primordia falls sharply and, in the present case, because of a reduction in the energy of their formation of each shoot. In other words, while there is increased female sex development of shoots that were barren before and the total number of primordia on the tree as a whole rises under optimum shift of root-leaf relations, the excessive disturbance of the latter reduces the formation energy of primordia on shoots so much that it causes a significant drop of yield of the tree as a whole in spite of the fact that the number of cone-bearing shoots remained almost the same as in the control. The data for Tomsk section suggest that, as a result of such an effect, the yield of affected trees fell by 30% toward the end of the 10-year tapping period. A similar reduction of yield of tapped Scotch pine trees was reported when using
146 stimulators of resin exudation (Drochnev, Vishnevskaya, and Khuden'kikh 1978).

During post-embryonic development of reproductive organs in the pollination and cone-bearing periods, some crop losses arise but are not significant. An insignificant increase of cone fall points to the absence of significant disturbances during pollination and cone bearing. The normal course of the latter is confirmed by the presence of the same number of seeds in the cones as in control at the end of prolonged tests.

Further, a study of embryogenesis of seeds showed that a shift of root-leaf relations mainly exerts a positive influence on their development and maturity. This is confirmed by the absolute weight of seeds, their oil content, and viability. These results clearly show that the metabolism in the tree altered thus promotes excellent growth of seeds. This is also seen even when the formation of primordia has already commenced to fall significantly. As can be seen, the activation of the reproductive system of the affected tree by the improved planting qualities of seeds is a far more adaptable property than increasing their number.

Physiological Features of the State of Trees

Water Regime

A study of water regime under conditions of changing root-leaf relations studied is useful from different viewpoints. On one hand, growth conditions and cone bearing of shoots in the crown and, on the other, the overall condition of the plant relative to the disturbance of transport system in the tree depend on the water regime.

Mechanical damages of the trunk reduce the water content above the cuts in the phloem tissues and increase its content in xylem tissues (Table 60). While the former is associated with a total cutoff of the phloem, the latter is evidently related to the increased transport of water in the much deeper layers of the wood. Such a relationship of the water content of tissues above

147 Table 60. Water content of tissues in the cut region of trunk and roots, % of control

Organ, tissue	Siberian stone pine, tapping			Scotch pine, 8th year, Sept., notching	
	moderate		intense	moderate	intense
	July, 9th year	March, 9th year	June–July, 4th year		
Above cut					
phloem	90.1	96.1	87.0	94.3	89.4
xylem	101.5	111.6	102.3	125.8	110.9
Between cuts					
phloem	102.4	97.0	110.3	125.4	105.9
xylem	80.1	71.7	93.6	96.4	76.6
Roots	93.1	—	93.0	92.2	71.3

the cuts makes for favorable conditions of resin formation—a much higher concentration of cell sap is formed in the phloem, xylem is supplied with adequate water that is evidently used in the synthesis of terpenes in larger amounts in the tapped than untapped trees.

In the region of so-called "nutrient belts", water supply to phloem and xylem are contrasting. Increased material transport to this section of trunk also causes increased water flow mainly through the phloem. Water content of xylem falls, more significantly in the highly damaged trees in the autumn-winter period. Similar observations were reported for Siberian stone pine when using chemical stimulants for resin exudation (Khlebodarov,
147 Maksimchuk, and Manakov 1978). Such changes in xylem are confirmed by the reduced content of water in the roots. Significant losses are noticed in Scotch pine after an 8-year intense metabolic shift.

Water supply to the crown is more than in the control throughout the 10-year period (Table 61). This is true equally well for all its organs—needles, axis, and cones. Increased water content is more perceptible in one-year-old formations compared to the two-year-old. Water content determinations of buds, needles, phloem tissues, and one-year-old shoots of winter crops in early March showed that, after nine years of tapping, water in them was 12–34% more than in two-year-olds.

147 Table 61. Water availability to female shoots, % of control

Organ, tissue	Siberian stone pine, tapping		Scotch pine, 8th year, Sept., notching	
	moderate, 9th year, August	intense, 4th year, June–July	moderate	intense
Needles	103.2	104.1	100.5	99.4
Two-year-old cones	101.1	102.2	113.1	103.7
Axis of shoots	101.2	104.4	—	—

The shift of root-leaf relations also improves the water retention capacity of tissues (Table 62). This is well perceived on the example of needles of shoots of different genders under conditions of disturbance of transport channels of trunk tapped by cuts as well as by making notches. In either case, the most significant changes occur in the needles of female shoots. Here, water losses by evaporation per hour are 18–28% less than in control while they are also considerably less in needles of male shoots but are not significant in those of vegetative shoots.

The disturbance of root-leaf relations also improves water availability to
148 the female regenerative organs (Vorob'eva 1974). Better water availability to them is noticed throughout the growth period. Differences from the control levels in some phases are insignificant but are quite perceptible in others.

148 Table 62. Water retention capacity of needles, %

Test variant, type of shoot	Moisture, %	Moisture loss from initial value after, hr					Water losses/hr in first 6 hr of test
		2	4	6	12	24	
		Tapping, fourth year					
Female							
control	53.3	6.5	8.7	10.7	13.3	18.8	1.9
test	54.5	4.0	6.2	8.0	11.3	15.3	1.4
Male							
control	51.3	6.3	7.9	9.9	13.0	17.6	1.6
test	51.0	2.9	4.9	7.6	10.9	14.4	1.2
Growth							
control	54.5	3.2	5.9	6.7	9.9	12.8	1.1
test	53.7	3.3	5.1	6.2	9.1	12.3	1.0
		Notching of trunk, 8th–10th years					
Female							
control	51.7	7.3	10.3	13.4	16.6	18.6	2.2
test	52.0	6.1	8.5	11.3	14.5	17.3	1.8

The high water content of tissues of female organs in the period of growth completion of one-year-old cones, during the fertilization of ovules, and during maturity of seeds is noteworthy. In seeds that have matured, water content differences are insignificant but what is more important is the presence of better supply in the most required periods of growth of female organs. Judging from the available data, the noticed variation of root-leaf relations generates such conditions for the seeds.

On the whole, the change of transport channels in the tree caused by tapping and similar cuts enhances water supply to the surface organs by improving their water retention capacity as well as by the increase of water flow from the root system. The shift of water balance toward better supply to the crown, and less so to the roots, is more intense, the more significant the interruption of transport channels. On their exceptional breakdown, moisture deficiency arises in the roots and, on moderate interference, water supply to roots and crown is maintained at the normal level for a long period. Increased water flow to the surface organs proceeds through the "nutrient belts" as also, evidently, through the more inner layers of active wood under the cuts.

Content and Ratio of Plastid Pigments in the Leaf Apparatus

A study of the pigment system in conifers, specially in Siberian stone pine, is necessary as only some stray information is available on this subject

149 (Larionova 1968) although quite some work in this sphere has been reported on Scotch pine (Mamaev 1965, Ollykainen and Kozubov 1967, and Kozubov 1971) and Norway spruce (Tsaregorodtseva 1970).

The pigment content of two-year-old needles of Siberian stone pine is more than in the one-year-olds, even in the period of latent growth (Fig. 44). It has, however, been noticed that young needles even in mid-July differ little from the two-year-olds in the amount of chlorophyll *a* than chlorophyll b, and more so with respect to the total of carotenoids. In all probability, the relations and participation of pigments in the life of the young needle do not remain static from the moment of its appearance until cessation of growth. By tracing the dynamics of this process in the data of A.M. Ollykainen and G.M. Kozubov (1967), it may be seen that, in June, the young needle contains 25% green and 33% yellow pigments of the formed needles which, by August, rise to 95% and 79%, respectively. Such a reorganization in the pigment system of young needle is well-reflected by the variation in the ratio of green and yellow pigments: in the first case, it is less than 1.0 and, in the second, more than 2.0. It may also be seen in Fig. 44 that while the nature of differences between needles of first and second years in shoots of different genders is identical, the pigment content is different.

Compared to the vegetative shoots, needles of regenerative shoots contain less of pigments, especially chlorophyll *b* (Fig. 45). This difference is

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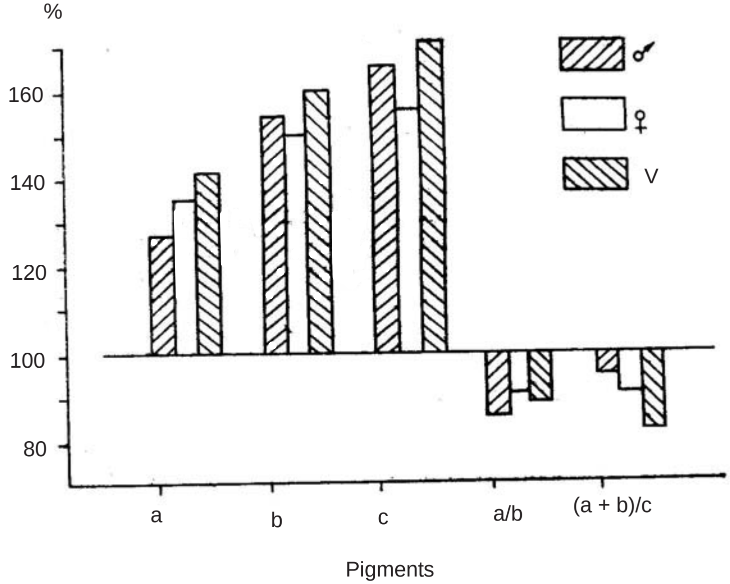

Fig. 44. Pigment content of two-year-old needles of different types of shoots (relative to one-year-olds).

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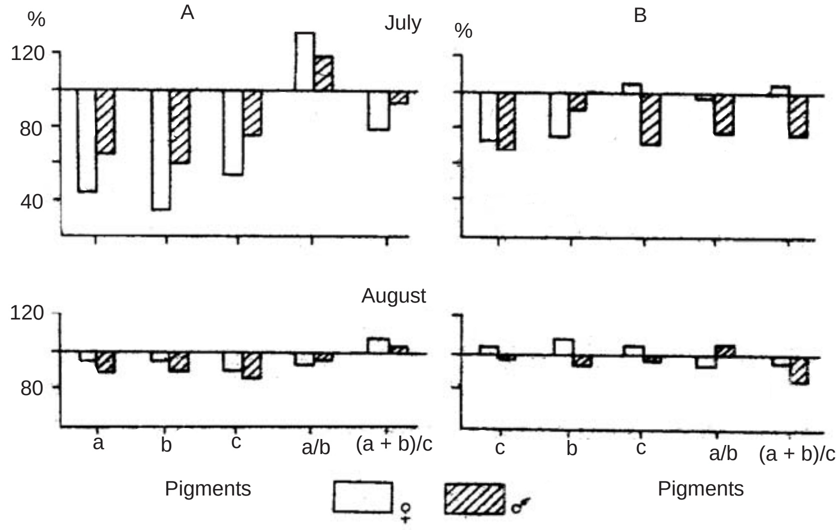

Fig. 45. Pigment content in needles of regenerative shoots (relative to growth shoots): A—two-year-old needles; B—one-year-olds.

perceptible in June, especially so in July. In August, its content is insignificant but their ratio varies. While the pigment content in the growth period is low in the needles of female shoots, in August after growth completion, it is on the contrary low in the needles of male shoots. The nature of these changes has also been detected in one-year-old needles in which, incidentally, it is more perceptible in July than in August. Insofar as the reasons for changes of
150 the possible role of needles of different ages are concerned, for the present, their association with differentiation of reproductive organs may be suggested. In the male shoots, this differentiation commences in July and terminates by autumn of the same year while, in the females, it proceeds mostly in the following spring.

Thus, needles of reproductive shoots differ from those of vegetative shoots in a lower content of pigments. As in Scotch pine, the needles of male shoots of Siberian stone pine contain more pigments than needles of female shoots in the summer period (June–July). Further, it is significant that ratio a/b rises from the vegetative to the female shoots but the value of (a + b)/c falls. In the first case, this is explained by a greater reduction of chlorophyll b content then chlorophyll *a* and in the second, on the contrary, more of greens than yellows.

These contents and ratios of pigments in needles of shoots of different sexes shows their wholly definitive and significant association with sex development.

In this context, data on pigment content of needles before and after pollination are interesting. It has been pointed out above that, in Scotch pine, such a phase is initially accompanied by pigment accumulation, specially of carotenoids, followed by their sharp reduction (Ollykainen and Kozubov 1967).

A similar response of pigment system to pollination is also traced in Siberian stone pine but the pigment content of needles of different shoot types change differently: in female shoots, it rises before falling but, in male and vegetative shoots, rises all the time (Fig. 46). It is possible that these
151 differences are associated with the fact that, in the year when the observations were made (1970), the pollen output of male shoots was poor and a greater energy was manifest only in tapping tests, this reflecting on the increased content of pigments at all levels of the crown. It is also possible that the state of the pigment system in the tree depends on the reproductive activity, not only in the male but also female shoots, as was noticed in Scotch pine (Tuzhilkina and Veretennikov 1981). So far, not much information is available not only for Siberian stone pine but for other conifers as well.

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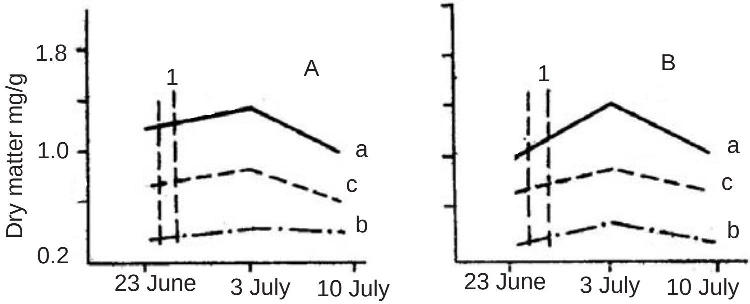

Fig. 46. Pigment content of two-year-old needles of female shoots before and after pollination under conditions of normal (A) and disrupted (by tapping) (B) root-leaf relations: 1—release of pollen.

A study of the pigment system is also of considerable interest in the context of activation of reproductive activity. In tests on the stimulation of cone-bearing in Scotch pine by the application of mineral fertilizers, significant variations of pigment content were detected in the needles of fertilized trees (Kozubov 1971). Even in the first year of test, the content of green pigments rose by 35% and of yellow pigments dropped by 20% as a result of which their ratio rose so much (over 4.0) that the needle acquired a dark-green coloration. At the same time, the ratio of chlorophyll *a* to chlorophyll *b* rose, evidently being associated with the increased photosynthesis. Three years later, the pigment content rose everywhere and their ratio changed as follows:

ratio a/b fell due to high content of chlorophyll b and (a + b)/c was less than in control as a result of increased content of carotenoids. Consequently, even after a short duration of the effect of mineral fertilizers, the pigment system in the coniferous tree undergoes a sharp change of its activity under their influence as well as by the inducing effects in the states of vegetative growth, pollen-bearing, and seed formation.

In the author's test conditions when the activation of the reproductive activity of Siberian stone pine was effected by a shift of root-leaf relations as a result of mechanical damage of the trunk, the pigment content of needles also changed sharply.

Early tests in this regard showed that changes of pigment content depend
152 on the extent of interruption of the transport system in the tree. On weak interruption, the amount of green pigments decreases slightly (statistically insignificant) but of yellow pigments increases (Table 63). As pointed out before, the conditions of this test predominantly activated the growth processes. On moderate shift of root-leaf relations, there was a significant increase of green and specially of yellow pigments. These changes in the pigment system were accompanied by increased cone production and improved seed quality.

152 Table 63. Pigment content of two-year-old needles of female shoots at the commencement of tapping

Tapping, extent, period	Chlorophyll				Carotenoids c	a+b+c	(a+b)/c
	a	b	a + b	a : b			
			First stage				
Weak, 3rd–4th years	1.02/ 97.3	0.32/ 98.1	1.35/ 97.6	3.18/ 99.0	0.72/ 111.9	2.07/ 102.2	1.88/ 87.4
Moderate, 3rd–4th years	1.30/ 123.2	0.39/ 118.8	1.69/ 122.1	3.32/ 103.4	0.86/ 134.2	2.55/ 125.9	1.96/ 91.2
			Second stage				
Intense, 3rd year	0.53/ 105.0	0.23/ 116.5	0.76/ 107.9	2.31/ 90.2	0.48/ 113.7	1.25/ 110.0	1.56/ 94.5
Scotch pine section, moderate, 7 years	0.81/ 101.9	0.20/ 117.7	1.02/ 130.8	3.91/ 90.9	0.62/ 117.4	1.65/ 108.6	1.66/ 89.2

Note. Numerator, mg/g of dry matter; denominator, % of control.

A comparison of the resultant effect with the test on stimulating cone-bearing in Scotch pine (Kozubov 1971) showed, in both cases, a perceptible rise of green pigments. Insofar as yellow pigments are concerned, their content in the author's test rose to a greater extent than that of green pigments. The latter content on moderate interruption of root-leaf relations does not exceed the level of carotenoids since their sharp increase is evidently associated with the strengthening of the protective functions of the affected tree (Ozolina and Mochalkin 1972).

On enhancing the intensity of prolonging the interruption of root-leaf relations, the effect of activating the pigment system begins to weaken (see Table 63, second stage). Most noticeable is the return of chlorophyll *a* content to the control level while the contents of chlorophyll *b* and carotenoids remain high. Under these conditions, ratio a/b falls to the lower level (2.31) which is evidently associated with the increased stability of the tree and its adaptation to the new environment. This ratio later rises higher (3.91) than in the
153 unaffected trees suggesting a possible breakdown of relations between the pigments.

Interestingly, in tests to increase cone-bearing in Scotch pine by ringing, a reduced content of green pigments was detected in the 2nd–3rd years of test, i.e. earlier than in Siberian stone pine (Ronis 1978).

The weakening of the activity of pigment system, judging from the content of green pigments, has been noticed in the other crown levels as well (Table 64). The amount of yellow pigments continues to remain higher than in control but not as significantly as at the commencement of the shift of root-leaf relations. The relation of green pigments to the latter drops fairly low, specially

153 Table 64. Pigment content in needles of different shoots at the commencement of weakening of the vitality of tree (notching, 5th–8th years)

Shoot	Chlorophyll				Carote-noids	a+b+c	a+b/c
	a	b	a + b	a/b	c		
			One-year-old needles				
Female	0.49/96.8	0.19/96.9	0.68/96.8	2.58/100	0.25/99.2	0.93/97.5	2.71/98.5
Male	0.48/95.0	0.16/96.0	0.64/95.4	2.86/99.3	0.28/118.9	0.93/101.6	2.30/90.7
Vegetative	0.46/91.6	0.14/80.0	0.61/88.5	3.12/114.2	0.31/130.8	0.93/99.5	1.92/67.6
			Two-year-old needles				
Female	0.67/96.8	0.28/97.8	0.96/97.1	2.31/99.1	0.40/102.5	1.36/98.6	2.38/95.5
Male	0.60/93.1	0.22/85.0	0.83/90.8	2.67/110.8	0.41/104.5	1.24/94.9	2.01/87.0
Vegetative	0.62/86.9	0.25/87.1	0.88/87.0	2.41/100	0.45/103.6	1.33/86.6	1.93/84.2

Note. Numerator, mg/g of dry matter; denominator, % of control.

in vegetative shoots. Needles of male shoots, one-year-olds as well as two-year-olds, occupy an intermediate position with respect to this index: needles of female shoots exhibit the least deviation from the normal value.

The subsequent stage show further weakening of the activity of the pigment system (Table 65). Under conditions of intense five-year tapping, approaching the effect of ringing and on 7–10 years of notching of trunk, the pigment system of damaged trees is characterized, apart from a reduced level of green pigments, by a drop of total carotenoids. The manifestation of this feature has been detected in needles of shoots of both
154 sexes but commences from the upper part of the crown, i.e. from the female shoots.

Table 65. Pigment content in needles of different shoots of Siberian stone pine at the
154 stage of significant weakening of the vitality of the tree

Test variant, duration	Chlorophyll				Carotenoids	a+b+c	a+b/c
	a	b	a+b	a/b	c		
				Female			
Intense tapping, 5 years	1.05/81.1	0.30/76.9	1.36/80.1	3.44/105.5	0.70/83.9	2.07/81.4	1.92/95.5
				Female			
Notching of trunk, intense, 7–10 years	0.94/71.2	0.24/61.8	2.18/69.0	3.76/115.4	0.64/77.0	1.83/72.0	1.85/87.9
				Male			
	1.21/74.8	0.34/71.0	1.56/73.9	3.47/104.8	0.80/94.5	2.36/79.8	1.91/76.7
				Growth			
	1.29/79.8	0.33/68.7	1.63/77.2	3.84/116.3	0.81/94.7	2.44/81.9	2.01/82.9

Note. Numerator, mg/g of dry matter; denominator, % of control.

The detected trends reveals considerable deviations from the normal value but do not reach the limits detected in larch weakened by Siberian silkworm (Girs 1970).

The result in brief of this section of investigations may be stated in the form of the following conclusion:

The ratio of shoots of different sexes of Siberian stone pine does not remain constant or invariable in pigment content but depends on the duration and extent of activation of vegetative and reproductive processes.

154 The transition of vegetative shoots into the reproductive state is accompanied by a reduced pigment content of the needle. Their activation of reproduction, judging from the ratio of reproductive load on male and female shoot reveals further intensification of this tendency—needles of female shoots in the period of active and latent growth have a lower pigment content than male needles. In the period of completion of growing season when the activity of reproductive processes falls in the female shoots but remains at a high level in the male as a result of differentiation of primordia, the ratio of shoots changes in a reverse direction: at this time, needles of male shoots record a lower content of pigments.

Before undergoing different phases of reproductive process, specially of microsporogenesis, the pigment system in Siberian stone pine, as also in Scotch pine, sharply intensifies its activity. A raised pigment content before pollination is noticed in needles of different shoots of first as well as second year.

The ratio of shoots with different sex development is characterized in the direction (v → ♂ → ♀) by two basic tendencies: increase of the ratio of chlorophyll *a* to chlorophyll b(a/b) and reduction of the ratio of green to the yellow pigments (a ÷ b/c) (sic!).

The optimum shift of root-leaf relations according to the type "root-crown" does not alter the ratio of shoots but influences the pigment content of the needle in such a way that it correlates in a definite manner with the vegetative and reproductive relations. Under conditions of insignificant damage of trees, the content of green pigments slightly falls but of yellow pigments increases (Fig. 47). These changes are not prominent, brief, and are mainly associated with the activation of growth processes. On a fairly significant shift of metabolism, the content of green, specially of yellow pigments,

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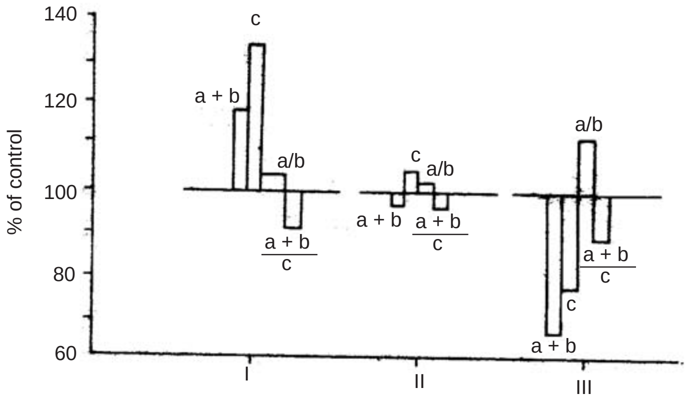

Fig. 47. Dynamics of the state of pigment system:
I—commencement of intense, II—moderate and prolonged, and III—prolonged and intense disturbance of root-leaf relations.

increases perceptibly and correlates with the increased reproductive activity of the tree.

Pathological changes in the state of pigment system are noticed under conditions of prolonged or exceptional disturbance of root-leaf relations; the content of green pigments falls at first, followed by that of yellow pigments, the ratio of chlorophyll *a* to chlorophyll *b* rises as a result of disturbance for the subsequent normal conditions of synthesis. Significant variations in the ratio of green and yellow pigments are evidently noticed in the much later stages of the death of tree, suggesting that disturbances occur at first in the photosynthetic system of pigments which later extend to the protective system.

The characteristics of relations of the pigment system in Siberian stone pine with processes of growth, reproduction, and survival point to the
156 prospects of further study by field and remote laboratory methods. It is possible to evaluate not only a weakening of the pigment system, as generally done by phytopathologists, but also its activity relative to the intensification of growth and reproductive processes. The latter aspect helps in evaluating the standing crop as well as the prognosis in good time.

Content and Ratio of Nitrogen in the Main Organs and Tissues of the Tree

A study of nitrogen metabolism under conditions of mechanical disturbance of root-leaf relations is also of wide interest. The variation of growth and reproduction relations under these conditions necessitates establishing its precise dependence on the content and direction of the metabolism of nitrogen compounds. Of particular interest in this context is a study of the dynamics of nitrogen metabolism in the roots and leaves on the extent of influence of this factor. Its knowledge is essential for comparing the changes of root-leaf correlations with the dynamics of the state of growth and reproductive processes.

Under conditions of the present tests, attention was essentially devoted to the ratio of protein and non-protein forms of nitrogen. Their optimum ratio is an excellent index of the normal vitality of the organism: deviations arising for one or the other reasons are usually associated with changes in the relations between growth and development.

According to V.O. Kazaryan (1969), growth activation is determined by the increase of protein synthesis in the leaf apparatus. An increase of its proportion in leaves is explained by their high availability to the roots and points to intense supply of root metabolites required for protein synthesis in the crown. The activation of the synthesis of protein compounds in the crown describes the intensification of root-leaf relations.

The protein nitrogen is an excellent index of the synthesizing activity of roots. An increase of their metabolic activity is noticed, for example, in the years of abundant yield when the current flow of assimilates is reduced but the trees are assured of them from the autumn reserves (Kazaryan and Arutyunyan 1966).

The predominance of non-protein nitrogen generally points to the breakdown of protein synthesis. This may occur due to underutilization of non-protein compounds, mainly free amino acids, in the growth process or due to pathological disturbances of protein synthesis in the weakened trees (Girs 1967). The latter are of a different type and closely associated with the type of weakening of root-leaf relations.

Nitrogen metabolism relative to the reproductive activity of conifers was studied by T.P. Nekrasova (1967). Differences in nitrogen adequacy of shoots of different sexes have been pointed out. Maximum nitrogen content is seen in male shoots, specially before the pollen matures. In the dynamics of nitrogen content, its maximum values are associated with processes of the type of growth and minimum values with processes of internal differentiation.
158 Thus, the initiation of female primordia in the buds occurs in the period of nitrogen deficiency in summer with a relatively high protein fraction. The data available so far suggest a pattern of nitrogen content in Siberian stone pine as shown in Table 66. It may be seen that the contents of total and protein nitrogen are a maximum in the reproductive organs—seeds, pollen, and buds containing male and female primordia. Nitrogen is less in the vegetative organs, specially in roots and xylem tissues of the trunk. The leaf system of Siberian stone pine is ensured of a fairly high supply of nitrogenous matter.

At the commencement of a weak shift of root-leaf relations, the content and ratio of nitrogen does not change significantly in all the organs and tissues of Siberian stone pine (Table 67). Applying sealing-type cuts causes, toward autumn, accumulation of total nitrogen in the crown and its corresponding reduction in the roots. Such variations are noticed over a fairly prolonged period and are confirmed by nitrogen content in the phloem tissues of the trunk above and under the cuts. The ratio of protein and non-protein forms of nitrogen in the leaf system points to the active synthesis of protein and a corresponding intensification of root-leaf relations. This tendency also characterizes an increased proportion of protein nitrogen in
159 the roots. Observations on the growth of shoots reported above revealed their maximum rise under conditions of this test while the effect of activation of the reproductive activity here was the least. From qualitative characteristics like the content of organic matter, oil content, and vitality, the values for seeds of weakly tapped trees only slightly exceeded the control. In nitrogen content, these as well as shoot axis revealed low protein synthesis and correspondingly higher proportion of non-protein nitrogen. Depending on

157 Table 66. Content and ratio of nitrogen in the main organs and tissues of Siberian stone pine

Organ, tissue	Nitrogen, % of dry matter			Ratio of protein nitrogen to	
	total	protein	non-protein	total	non-protein
Seeds					
M ± m	2.90 ± 0.12	2.61 ± 0.11	0.29 ± 0.03	0.90 ± 0.06	9.0 ± 0.2
σ	0.18	0.18	0.49	0.33	1.4
C_v	6.5	7.0	16.9	3.7	16.5
Buds					
M ± m	2.06 ± 0.10	1.89 ± 0.09	0.17 ± 0.04	0.91 ± 0.01	11.1 ± 2.0
σ	0.23	0.21	0.10	0.01	4.7
C_v	11.1	11.1	58.8	1.1	36.8
Pollen					
M ± m	1.77 ± 0.14	1.30 ± 0.10	0.48 ± 0.09	0.73 ± 0.03	2.7 ± 0.1
σ	0.36	0.26	0.22	0.09	0.1
C_v	20.3	20.0	45.8	12.7	7.0
One-year-old cones					
M ± m	1.12 ± 0.08	0.85 ± 0.12	0.27 ± 0.08	0.76 ± 0.11	3.2 ± 0.8
σ	0.16	0.25	0.15	0.22	1.6
C_v	14.3	29.4	55.0	28.9	51.0
Two-year-old cones					
M ± m	1.05 ± 0.05	0.84 ± 0.06	0.21 ± 0.03	0.80 ± 0.03	4.4 ± 0.6
σ	0.12	0.16	0.07	0.07	1.6
C_v	11.9	19.3	35.2	9.4	13.8
Axis of two-year-old shoots					
M ± m	0.72 ± 0.04	0.55 ± 0.04	0.17 ± 0.03	0.76 ± 0.02	3.2 ± 0.6
σ	0.10	0.09	0.08	0.05	1.2
C_v	14.3	16.3	41.2	7.0	40.0
Phloem of trunk					
M ± m	0.47 ± 0.04	0.31 ± 0.04	0.16 ± 0.02	0.65 ± 0.01	1.9 ± 0.5
σ	0.13	0.13	0.07	0.02	1.5
C_v	27.6	43.2	42.5	3.6	83.1
Conductive roots					
M ± m	0.46 ± 0.04	0.32 ± 0.03	0.14 ± 0.02	0.69 ± 0.03	2.3 ± 0.5
σ	0.13	0.13	0.07	0.12	1.7
C_v	29.0	40.6	50.0	18.0	70.0
Xylem of trunk					
M ± m	0.15 ± 0.02	0.10 ± 0.02	0.05 ± 0.02	0.66 ± 0.07	2.0 ± 0.2
σ	0.05	0.03	0.05	0.23	0.8
C_v	33.3	30.0	100.0	35.0	40.0

Note. Nitrogen content of buds after T.P. Nekrasova (1973); values for needles and shoots given for the female part of crown in the vegetative period.

158 Table 67. Content and ratio of nitrogen in Siberian stone pine under conditions of a weak disturbance of root-leaf relations

Organ, tissue, year of tapping	Total nitrogen, % of dry matter			Ratio of protein to non-protein nitrogen		
	control	test	% of control	control	test	% of control
Two-year-old needles (E)						
3rd	1.0	1.1	108	1.8	4.5	250
9th	0.9	1.2	129	0.4	0.9	222
Two-year-old needles (G)						
3rd	1.1	1.4	128	1.5	1.7	113
One-year-old cones						
3rd	1.2	1.4	116	0.8	1.7	212
Axis of two-year-old shoots (E)						
3rd	1.8	2.1	111	3.1	0.9	29
Seeds						
3rd	3.0	3.3	111	11.1	2.9	26
9th	2.0	2.6	127	0.9	0.9	101
Pollen						
9th	1.7	1.9	112	0.6	0.9	145
Phloem above cut						
3rd	0.2	0.3	120	1.4	5.2	371
Phloem under cut						
3rd	0.3	0.2	70	1.5	0.8	53
9th	1.0	0.4	39	4.3	4.0	93
Roots						
3rd	0.5	0.4	80	0.8	1.5	173
9th	0.4	0.3	68	2.1	5.0	238

the effect of the tapping factor, these trends began being weakened—the ratio of protein and non-protein compounds in seeds came to the normal and even exceeded it in pollen. Toward the end of the 10-year period of moderate tapping, no significant variations were detected in the vegetative organs.

Under conditions of a sharp disturbance of root-leaf relations, changes of nitrogen metabolism are of essentially a different type (Table 68). Here, on the contrary, compared to the control trees, surface organs contain less nitrogen and underground organs more. Information on the accumulation of total nitrogen under the cuts suggests a weakening of the transport of
160 nitrogen compounds into the crown. Figure 48 depicts well these patterns. It shows the change of total nitrogen content relative to the degree of damage of material transport.

159 Table 68. Content and ratio of nitrogen under conditions of intense disturbance of root-leaf relations

Organ, tissue, year of tapping	Total nitrogen, %		Ratio of protein to non-protein nitrogen	
	test	% of control	test	% of control
Two-year-old needles (♀)				
3rd	0.8	80	5.1	283
6th	1.0	101	8.3	163
Two-year-old needles (♂)				
3rd	1.0	93	6.3	420
Two-year-old needles (v)				
3rd	0.8	95	6.9	627
One-year-old cones				
3rd	1.3	102	1.2	1480
Seeds				
3rd	2.8	98	81.4	275
6th	1.8	90	11.4	135
Pollen				
6th	1.7	77	5.1	340
Phloem above cut				
3rd	0.2	96	1.8	128
Phloem under cut				
3rd	0.3	120	2.0	1133
6th	0.4	110	0.8	165
Roots				
3rd	0.6	110	0.5	88
6th	0.4	110	2.1	87

The ratio of nitrogen under the present test conditions also reveals intense protein synthesis but proceeding far more sharply than in the preceding case. Significantly, the products of reproductive phase—seeds and pollen—also have a high protein content. These changes in the crown occur in the background of a weakening of protein synthesis in the roots.

Growth under these test conditions, as stated before, is slightly better only in the first 2–3 years of test but the energy of growth processes in the crown later weakens significantly. For the reproductive activity in this case, a characteristic feature is the improved qualitative values of seeds, intense primordia formation, and involvement of new shoots in fruiting. Thus, a significant interruption of transport ducts in the tree causes such a sharp intensification of root inadequacy that the entire direction of nitrogen

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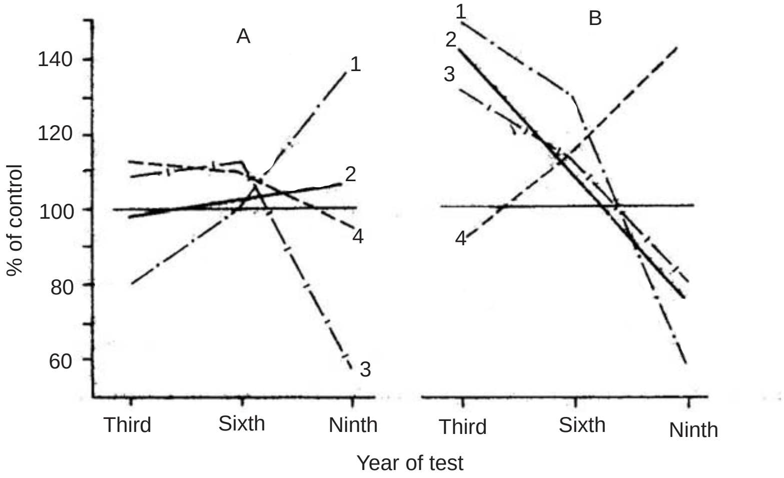

Fig. 48. Dynamics of the content of total (A) and protein (B) nitrogen under conditions of intense tapping in the different tests years:
1—needles, 2—seeds, 3—phloem, and 4—roots.

metabolism in the crown and trunk of the tree is pre-dominantly associated with activizing the regenerative and resin-forming processes. Further, growth processes reach the optimum level for a short period since the progressive intensification of protein synthesis no longer supports it and, on the contrary, inhibits it. Such an accumulation of protein nitrogen in the surface organs, in all probability, is associated with the effect of ringing (Kazaryan and Gevorkyan 1974) and, under unusual tendencies, can be regarded as unfavorable not only for growth but also for reproductive processes, specially for primordia formation. Ringing of ash shoots, for example, suppresses the ability of buds to flowering which, according to the above investigators, is explained by the high protein content. 161

Results of cleaving of trees suggests a more prolonged and optimum shift of root-leaf relations (Table 69).

It has been established in cleaving tests that the synthesis of protein compounds in the surface organs during cleaving weakens compared to intense tapping but, as before, remains more active than in the control trees. The content of protein nitrogen in the roots differs from the normal only insignificantly. This state of nitrogen metabolism correlates with the high energy of growth and reproduction of shoots as shown before.

A comparison of the state of nitrogen metabolism under conditions of test (tapping and cleaving) and natural (productive year) shift of root-leaf relations would be of interest (Table 70). Data reflecting increased cone yield were used for the variant with tapping. 162

161 Table 69. Content and ratio of nitrogen under conditions of prolonged and optimal disturbance of root-leaf relations (cleaving)

Organ, tissue	Total nitrogen, %		Ratio of protein to non-protein nitrogen	
	test	% of control	test	% of control
Two-year-old needles of female shoots	1.2	133	2.7	112
Axis of two-year-old female shoots	0.4	115	12.0	248
One-year-old female cones	1.0	85	12.4	120
Seeds	2.5	95	9.1	135
Phloem	0.3	110	5.6	180
Xylem	0.1	120	2.2	96
Roots	0.5	110	0.8	90

161 Table 70. Ratio of nitrogen forms and content of amino acids in protein hydrolyzates under conditions of natural (productive year—numerator) and artificial (tapping—denominator) shift of root-leaf relations

Organ	Ratio of protein to non-protein nitrogen		Total of amino acids	
	test	% of control	mg/g of dry matter	% of control
Needles of two-year-old female shoots	6.2/5.1	82/283	172.8/116.2	174/139
Seeds	5.1/31.4	121/275	161.4/266.8	102/115
Roots	2.3/0.5	121/88	8.6/13.7	95/120

The ratio of nitrogen and the content of amino acids in the productive Siberian stone pine trees reveals the same rise of metabolic activity of roots as in fruit-bearing apple trees compared to barren trees (Kazaryan and Arutyan 1966). In either case, the activation of protein synthesis in the roots is associated evidently with the predominant use of reserves as well as with some supply of current assimilates in spite of their intense utilization in the period of raising the crop. Under conditions of intense disruption of root-leaf relations, the supply of assimilates as well as their reserves have diminished in the preceding years (Vorob'eva 1974). As a result, the metabolic activity of roots in such trees is suppressed. On moderate reduction of assimilates supply, as in the cleaving tests, protein synthesis and the content of amino acids record the same parameters as under conditions of natural shift of root-leaf relations.

Their unusual disturbance, however, causes not only a sharp variation in the root system but also in the leaf apparatus in which a significant shift toward the predominance of protein compounds is noticed. The latter is caused probably due to a significant reduction of the supply of assimilates required by the root system.

Protein synthesis in the needles of an unaffected cone-bearing tree is somewhat weakened since it is evidently associated with the predominant use of current metabolites and reserves in it are not as much as in the needles of a damaged tree. In spite of this, the activity of the bonding of amino acids in both the cases is high as also in seeds in which the overall effect conforms to the content of protein nitrogen. Judging from the features of nitrogen metabolism in these variants, the search for optimum shift of root-leaf relations to activate reproductive processes should combine moderate intensification of the metabolic activity of roots with the possibilities of a greater supply of leaf metabolites to the crown. Data on nitrogen metabolism under cleaving conditions generally conform to such a variant. The application of such values and the method of disturbing the root-leaf relations help achieve a positive effect for a fairly prolonged period. Excessive root inadequacy, although causing a high activation of reproductive activity, is only for a brief period. Later, it saps the vitality of the organism.

The data on the content of amino acids in protein hydrolyzates demonstrate the specificity of nitrogen metabolism under conditions of weak and intense interruption of root-leaf relations (Table 71).

On weak disturbance of root-leaf relations when the flow of assimilates from the crown is evidently adequate, the root system activates the metabolism by increasing on one hand the synthesis of protein and on the other the amount of mobile compounds. The latter causes their increased flow into the crown and weakens the bonding of amino acids in the roots. Under these test
164 conditions, with the exception of arginine, the content of all other amino acids falls significantly compared to the control level. In the surface portion of poorly damaged trees, the amount of bound amino acids is not high. This is evidently associated in this case with the utilization of mobile compounds in the accelerated growth of the vegetative part of the crown. In the reproductive organs, specially in seeds, this state is characterized by a reduced content of protein and bound amino acids.

Under conditions of a more significant reduction of flow of assimilates, the metabolic activity of roots is weakened: the content of protein nitrogen falls and there is some lag in the transport of compounds to the area of cuts. All of this causes intense bonding of amino acids in the roots. In the surface organs of greatly affected trees, as a result of very significant restraint of assimilates and, evidently, adequate root metabolites, there is increased protein synthesis and reduction of the content of non-protein nitrogen compounds. The change of ratio between nitrogen forms brings about favorable conditions for the course of regenerative processes. The latter are accompanied in all the organs by a greater amount of protein nitrogen as

163 & 164 Table 71. Content of amino acids in protein hydrolyzates (control, mg/g of dry matter; tests, % of control)

Amino acid	Variant, disturbance by tapping	Needles	Seeds	Phloem	Roots
Lysine	Control	5.6	12.6	2.3	0.9
	Test				
	Weak	94	96	100	97
	Intense	141	119	121	122
Histidine	Control	2.6	6.0	0.8	0.3
	Test				
	Weak	115	116	112	70
	Intense	150	146	150	233
Arginine	Control	5.7	31.5	1.6	0.4
	Test				
	Weak	85	95	137	150
	Intense	136	112	162	250
Asparagine	Control	9.2	24.7	2.7	1.3
	Test				
	Weak	94	90	96	84
	Intense	125	114	118	100
Threonine	Control	4.2	8.4	1.3	0.7
	Test				
	Weak	100	101	84	57
	Intense	138	130	115	100
Serine	Control	4.8	15.9	1.7	0.9
	Test				
	Weak	85	92	82	77
	Intense	125	122	111	100
Glutamine	Control	10.7	37.5	3.4	1.7
	Test				
	Weak	93	92	97	76
	Intense	138	116	123	88
Proline	Control	4.5	11.1	1.6	0.6
	Test				
	Weak	111	90	87	83
	Intense	142	126	137	133
Glycine + cystine	Control	3.7	8.7	1.1	0.6
	Test				
	Weak	94	82	100	66
	Intense	140	114	109	90
Alanine	Control	6.3	10.8	1.7	0.9
	Test				
	Weak	79	95	94	50
	Intense	107	121	111	90

(*Table 71 contd.*)

(*Table 71 contd.*)

Valine	Control		5.0	11.7	1.8	0.9
	Test					
		Weak	100	90	88	50
		Intense	125	104	122	100
Methionine	Control		0.6	2.8	0.5	trace
	Test					
164		Weak	70	71	80	trace
		Intense	280	80	50	trace
Leucine	Control		8.4	17.5	2.7	1.4
	Test					
		Weak	90	91	85	71
		Intense	135	112	103	107
Tyrosine	Control		3.2	10.1	1.2	trace
	Test					
		Weak	96	102	108	trace
		Intense	162	115	133	trace
Phenylalanine	Control		5.3	13.7	1.6	0.8
	Test					
		Weak	94	78	106	112
		Intense	516	91	175	113
Total of amino acids	Control		83.6	231.8	27.3	11.4
	Test					
		Weak	93	93	97	75
		Intense	139	115	124	120

also intense bonding of amino acids. These changes are noticed more significantly in the shoot system where the total of amino acids increases by almost 40%.

In the lower part of the trunk, phloem tissues contain 24% more amino acids and seeds 15% more. The noticed changes are typical of most amino acids and organs. There are differences too. While methionine content in the needles rises by 180%, it falls by 20% and 50% in the seeds and phloem of trunk, respectively. In the roots, methionine is present (as in control) only in
165 traces. In the seeds, the greatest increase is noticed in the case of lysine, histidine, threonine, serine, proline, and alanine. However, apart from methionine, the content of phenylalanine also decreases. In the case of arginine, its content increases sharply in the trunk and roots under conditions of weak as well as intense disturbance of root-leaf relations.

Prolonging intense tapping eliminates the initial effect of the disturbance of root-leaf relations. Even toward the sixth year of test, protein synthesis in the needles begins to fall (see Table 68). Similar trends gradually extend to other organs, leading finally to the death of the tree (Table 72, see Fig. 48).

165 Table 72. Ratio of protein to non-protein nitrogen in the dying trees

Organ, tissue	Test variant			
	1st	2nd	3rd	4th
Needles of two-year-old female shoots	2.7/60	2.6/52	7.1/46	4.1/35
Axis of two-year-old female shoots	1.8/66	—	3.5/55	5.3/91
Two-year-old female cones	2.3/74	—	2.7/45	0.6/60
Pollen	2.6/76	3.7/48	3.5/70	1.8/53
Phloem	0.7/54	3.4/79	2.3/72	0.2/53
Xylem	4.5/346	—	—	3.1/148
Roots	4.1/372	3.2/152	13.5/201	1.0/200

Note. Tapping variants of Siberian stone pine: 1—sample collection 33 years after intense tapping, in 1935 and 1938; 2—four years after five-year intense tapping; 3—in the ninth year of intense tapping; and 4—8–10 years after severe notching of Scotch pine.

Numerator, test values; denominator, % of control.

In tests with intense disruption of root-leaf relations, the first effect of metabolic shift, as pointed out before, occurs quite rapidly. Transition from abundant supply to roots by the shoot system to its reduction occurs in the 4th–6th year of test. In the needles of affected trees, the ratio of protein and non-protein nitrogen varies in favor of the latter, causing an increase of total nitrogen content. In the roots and phloem of trunk, the amount of total nitrogen falls. An increase of the proportion of protein compounds is characteristic of the ratio of nitrogen in the roots of the weakened tree. This rise may be associated with the activation of the steadily shrinking root system (only live roots were included in the sample) as well as with the specific breakdown of proteins.

166 According to G.I. Girs and L.N. Kaverzina (1971), the initial weakening of larch damaged by fire is accompanied by intense protein synthesis and deficiency of amino acid composition in the phloem tissues of trunk. A greater content of amino acids is noticed on the breakdown of protein compounds. This is noticed only after the bast fiber tissues have turned brown and the carbohydrates in them are depleted.

Such variations of nitrogen metabolism accompanied by cell breakdown probably describe the last stage of its disturbance. Under the author's test conditions, the breakdown of constitutional proteins of plasma can evidently be noticed only in the notching test of Scotch pine. The protein nitrogen content around the root cuts was 6% of control in June, compared to 50% in the so-called "nutrient belt". The ratio of protein and non-protein nitrogen compared to unaffected Scotch pines was 14% in the first and 20% in the second case.

The increased protein nitrogen in the roots and xylem tissues of the lower part of trunk of oppressed trees foretells clearly the breakdown of constitutional proteins. Such a ratio was noticed in the author's tests during severe cleaving, after short and intense tapping, and after many years of thoughtless notching of trees (see Table 72). In all cases, surface organs were characterized by diminished protein synthesis and higher non-protein nitrogen content, i.e. very early charactristics of the breakdown of nitrogen metabolism than in the roots. Changes in the crown reflected the general features, affecting also the output of the reproductive organs. The vitality parameters of pollen and seeds in these cases were impaired.

On the whole, the experimental shift of root-leaf relations, depending on the degree of impairment of transport ducts in the tree, exerts varying influence on the state of nitrogen metabolism.

On lesser damage, the total nitrogen content in the surface organs increases, protein synthesis intensifies in the shoot system and metabolic activity of tissues in the underground organs is activated and is accompanied by a reduced amount of bound amino acids. These changes characterize the intense root-leaf bonds, temporarily activating the growth processes. Later, depending on the continuation of metabolic shift, protein synthesis in the crown is activated to an extent that promotes the optimum course of growth and cone production. Such a condition of nitrogen metabolism is characteristic of trees with moderate cleaving.

On intense damage of root-leaf relations, nitrogen availability to the crown is affected but conversion of nitrogen compounds into protein increases sharply. These changes are mainly noticed in trees with a high reproductive activity. The activation of protein nitrogen synthesis in the latter case proceeds in a background of suppressed metabolic activity of roots, leading ultimately to a pathological modification of bonds between them.

167 The breakdown of protein metabolism is accompanied in the crown, firstly, in the leaf apparatus by a weakening of protein synthesis and increase of the proportion of non-protein nitrogen and, in the roots, by initial stabilization of higher content of protein nitrogen and later by its degeneration in the dying tissues.

These step-wise changes of nitrogen metabolism relative to the varying extents of shift of root-leaf relations open up wholly definitive possibilities of their control so to establish optimum relations between growth and reproduction of trees by the application of mechanical cuts and other means.

State of Carbohydrates in the Main Organs and Tissues of the Tree*

Carbohydrate metabolism, its intensity and direction, play a leading role in plant metabolism. Being the first free product of photosynthesis (Turkina 1959 and Dogman 1959), carbohydrates are utilized to form ultimately all the materials essential for plant life. The importance of carbohydrates is particularly significant in the metabolism of conifers in the light of the natural ability of these species to form resins. G.V. Pigulevskii (1939) established that 2/3 of photosynthetic products in conifers are used in resin formation and only 1/3 directly in sustaining growth and reproduction. Many investigators (Pigulevskii 1939, Ivanov 1940, Kossovich 1939, and Neiman, Prokof'ev, and Shantarovich 1951) regard that products of anaerobic breakdown of carbohydrates comprise the direct source of resin formation. The abundant availability of carbohydrates at the sites of resin formation activates the course of their synthesis (Zubkova, Kolmazon, and Okuneva 1948). Further, resin formation proceeds most vigorously from the moment of the blossoming of buds to the cessation of needle growth (Pigulevskii 1939). By promoting resin liberation and correspondingly its formation, tapping should invariably result in an increased utilization of carbohydrates, leading either to their additional formation in the course of photosynthesis or to a redistribution of the available reserves.

Thus, in the totality of processes studied during tapping, the study of carbohydrate metabolism as a link most closely related to the level of resin formation should be regarded as one of the core aspects.

The information available in the literature on carbohydrate modifications in tapped trees is rather uncoordinated and contradictory and could be thoroughly systematized on the basis of step-wise changes in the life of tapped trees discussed above (Vorob'ev 1974b).

In the leaf apparatus of tapped trees, most investigators have noticed a 168 reduced content of readily soluble sugars (Gavrilov 1953, Frolov 1971, and Shul'gin 1973). B.I. Gavrilov showed that this reduction was caused by increased outflow of sugars from the needles of tapped trees and suggested the possibility of a bond between this process and the high activity of photosynthesis. Direct observations of photosynthesis confirmed the increased assimilates formation (Mogileva and Rastorgueva 1963, and Shul'gin 1973) and also established the increased outflow of sugars from needles from the very next day of making the tapping gashes (Shul' gin 1973).

The accumulation of assimilates in the leaf apparatus has been noticed only under conditions of ringing when the outflow of plastic matter in the

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*N.A. Vorob'eva collaborated in the preparation of this section.

roots has practically ceased and their utilization in resin formation on routine cuts was not much (Mogileva 1965 and 1970, and Cameron 1970). A similar effect is also noticed in fruit-bearing plants (Kolomiets 1966) and suggests a common response of plants to such influences.

The state of carbohydrates in the tissues of bast and wood has been studied somewhat in better detail than in needles. N.L. Kossovich (1939) for example showed that starch content of bast around the cut falls and altogether disappears in the parenchymatous cells of resin ducts. Starch concentration under these conditions is detected only in the "nutrient belts" (Kossovich 1939). At some distance from the cuts, under conditions of weak (Sinitskii 1940 and Gavrilov 1953) and even severe (Kraevskii 1955) tapping, no significant reduction of starch was observed. Only after a prolonged 12-year tapping, the starch content of sapwood, according to the data of A.N. Shaternikova (Ivanov 1940), decreased by almost 40%. Moreover, as also pointed out by N.L. Kossovich (1939), starch is concentrated in the bast of nutrient belts".

It is clear from the above discussion that the reduction of starch content is detected on the exhaustion of starch reserves in the tree and hence this information can serve as an important diagnostic indicator when studying the condition of tapped plantations.

Starch accumulation in the bast and wood during tapping has been noticed only in young tree (Gavrilov 1953 and Mogileva 1970) and is evidently associated with the specific response of the young organism to its disturbed survival conditions.

The content of readily-soluble sugars is known to decrease most often above the tapping holes (A.N. Shaternikova, cited after Ivanov 1940, Umpelev and Tereshina 1963, and Pilipenko 1965) and stands at the same level as in untapped trees only under conditions of a single or minor tapping of young trees (Mogileva 1970).

Sugar content under the tapping holes depends on the nature of cuts: on minor radial load, the level of readily-soluble carbohydrates remains unchanged at the original level (Umpelev and Tereshina 1963) while, on maximum load, it falls distinctly (Mogileva 1965). In the latter case, a sharp reduction of sugar level under the cuts is the result of a reduction of their supply from the crown.

169 Carbohydrates in the root system of tapped trees have been studied the least. According to the data of E. Ostrom and W. Warih (1946), the amount of stored carbohydrates in the roots of pitch pine decreased after four years of tapping.

Thus, the state of carbohydrate complex under tapping conditions was studied before only in some organs without involving the whole plant and ignoring the process dynamics in spite of the diverse influences of tapping on the body of the tree. Its impact on the content of carbohydrates in the tissues of the trunk is determined mainly by their utilization in resin formation. In the crown of the tapped tree, it depends on the relation between the extent of breakdown of outflow to the root system and the extent of utilization of the products of carbohydrate metabolism in resin formation. On one hand, the more the transport ducts in the tree are cut off (radial load), the greater the sugar retention in the crown and upper part of the trunk and, on the other, the higher the intensity of resin exudation (load caused by greater frequency of cuts), the more is the consumption of assimilates for terpene synthesis. Depending on the combination of these factors, various trends of sugar content variations are noticed in the crown (Vorob'eva 1974; Vorob'ev, Vorob'eva, Sviridenko, and Kolesov 1979).

The change of root-leaf relations primarily affects the condition of the root system and imposes some extent of isolation under such test conditions. The amount of carbohydrates in the roots is important for their survival as also for the normal functioning of the plant as a whole since a considerable proportion of compounds used *in situ* as also in the surface part of the tree is synthesized with their involvement (Kazaryan 1969).

According to the available data, short-term tapping of pitch pine reduces the content of carbohydrates in the roots (Ostrom and Warih 1946). Similar changes occur in Siberian stone pine in the third year of intense tapping (Vorob'eva 1974). Further, starch as well as readily-soluble carbohydrate contents decrease (Table 73). Among the readily-soluble carbohydrates, maximum changes were noticed in saccharose which is the main
170 carbohydrate that ensures the normal course of metabolic processes in the roots (Uait 1949).

169 Table 73. Carbohydrate content of roots, mg/g of dry matter

Test variant	Saccharose	Glucose	Fructose	Total	Starch maltose
Commencement of growing season, June 5					
Control	84.2	11.3	22.8	118.3	42.8
Tapping	51.7	15.9	18.3	85.9	4.0
End of growing season, September 9					
Control	28.1	trace	6.0	34.0	119.0
Tapping	16.7	4.6	1.6	22.0	76.0

Judging from the above data, the breakdown of root-leaf relations, on one hand, promotes the utilization of disaccharides and starch in the growth period and, on the other, impairs the accumulation of reserve compounds until the end of growing season. In the first case, the change of carbohydrates suggests evidently an acceleration of hydrolytic processes and, in the second case, the reduced availability of metabolic products to the roots. Their depletion in the root system reduces their absorbing capacity, ultimately weakening the synthesizing faculty of leaves (S.M. Ivan 1953).

Observations of this trend under conditions of maximum disturbance of root-leaf relations (BIN section, variant V) showed it to be unchanged in the course of a five-year test (Table 74). Later, in view of reduced resin exudation and sharp weakening of growth and reproductive processes, tapping was discontinued. This reduced the consumption of sugars and starch. The effect of the fall of metabolites requirement and the possibilities of restoring root-leaf relations was manifest in a rather brief increase of sugar and starch contents in the roots and phloem of the trunk. However, there were new signs of carbohydrate deficiency in the fourth year. In this case, these were evidently associated not with the utilization of carbohydrates in resin formation or reproductive processes in the crown but with pathological changes of metabolism in the dying state of the tree. The absolute content of sugars and starch in this period did not still reflect noticeable features of carbohydrate deficiency although the indexes of growth and cone yield were extremely low. The commencement of suppression of these processes is evidently best judged from the falling initial deficiency of carbohydrates, specially of starch. Having examined these different conditions of trees after the cessation of a weak interception of root-leaf relations (BIN section, technology of sealing-type cuts), it can be said that the carbohydrate content in the phloem tissues of the trunk and in the roots remained as before, at the original level (Table 75). Starch is not reduced under these conditions. Thus, root-leaf relations here have reverted to the 171 original level.

Table 74. Carbohydrate content in roots and phloem (% of control) at the commencement of intense tapping and after its cessation, July

170

Organ, tissue, carbohydrates	Year of tapping		Year after tapping		
	3rd	4th	1st	3rd	4th
Phloem					
Starch	5.9	114.7	117.4	84.5	70.5
Readily-soluble	66.4	74.3	115.2	80.9	—
Roots					
Starch	9.3	63.9	97.5	223.9	56.4
Readily-soluble	72.6	94.3	106.8	117.8	—

Unlike the preceding situation, the damages observed in the leaf apparatus cause sugar deficiency, mainly of monosaccharides, with simultaneous increased growth of needles, specially of shoots. The

171 Table 75. Carbohydrates content after cessation of weak tapping, July

Organ, tissue, carbohydrates	Year after tapping, % of control		
	1st	3rd	4th
Phloem			
Starch	107	95	93
Readily-soluble	105	107	—
Roots			
Starch	—	107	147
Readily-soluble	143	106	—

content of monosaccharides actively utilized in the growth processes decreases by 40–50%. Their deficiency is not uniform in shoots of different genders (Vorob'eva 1974). In needles of vegetative shoots, the deficiency is in spring at the time of their active growth. In needles of male shoots, the shortage is mainly found in autumn as a result of the differentiation of microsporophylls accompanied by increased flow of reserves from needles to primordia. In needles of female shoots, in which reproductive processes constantly take place, sugar shortage is noticed throughout the growing season.

The prolonged shift of root-leaf relations causes the accumulation of carbohydrates, predominantly by larger fructose and saccharose contents (Table 76). Simultaneous with the change of sugar concentration, increased moisture and reduced catalase activity are noticed in the needles. The reduction of catalase, pointing to the shift of redox regime of cells toward oxidation, suggests that the accumulation of mobile carbohydrates in the

171 Table 76. Carbohydrates content, catalase activity, and moisture content in two-year-old needles of female shoots

Date	Test variant	Moisture, %	Catalase activity, O_2, cm^3/min/ g of green matter	Content of easily soluble carbohydrates, mg/g of dry matter			
				total	saccharose	glucose	fructose
July 10	Control	54.7	9.3	51.2	8.6	1.5	41.1
	Test (4th year of tapping)	60.1	8.5	85.5	10.0	1.0	74.5
July 7	Control	52.5	10.8	46.3	8.1	2.0	36.2
	Test (8th–10th year of notching)	53.0	7.4	92.4	10.0	1.4	81.0

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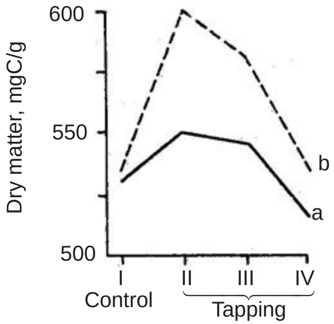


Fig. 49. Carbohydrate content in two-year-old needles of female shoots in the fourth year of tapping:
a—July 1; b—July 10.

needle is a result of hydrolytic breakdown of starch and not due to accelerated
172 photosynthesis (Krasinskii et al. 1955 and Subbotina 1961). Observations on the course of photosynthesis confirmed its weakening in the actual year of tapping (Fig. 49). In Siberian stone pine, subjected to notching, a similar state of mobile sugars, catalase activity, and intensity of photosynthesis have been noticed. A similar situation, i.e. accumulation of soluble carbohydrates and reduction of photosynthesis in the needle, has been reported by G.A. Mogileva (1965) on the ringing of Scotch pine. According to I.E. Malyugin (1970), a simultaneous reduction of photosynthesis and catalase activity in the needle suggests a weakening of the vitality of the tree, accompanied by reduced carbohydrates in the bark and wood (Solov'eva, Pochinok, and Okanenko 1962).

The above changes in carbohydrate content were accompanied in Siberian stone pine by the commencement of growth inhibition of shoots and increased reproductive activity. However, these observed trends in the conditions of intense shift of root-leaf relations are very rapid. The changes described above proceeded in the second and third years of tapping, respectively (Table 77). In the fourth year of test, the excess of carbohydrates began shrinking and simultaneously the ratio of saccharose and monosaccharides changed—former began to fall and the latter showed increase.

The stage of weakening of the vitality of trees was marked in the leaf apparatus by clear features of carbohydrate depletion—a simultaneous deficiency of monosaccharides and saccharose. The latter content in the needle throughout a year after test did not exceed 1/3 of the normal value.

172 Table 77. Carbohydrate content in two-year-old needles of female shoots at the commencement of intense tapping and after its cessation, % of control

Test year, date of observations	Total readily-soluble carbohydrates	Saccharose	Monosaccharides
Stage I—deficiency of sugars			
2nd year of tapping			
May 25	86.4	93.8	59.8
June 27	84.0	88.5	69.6
September 27	72.2	71.6	77.8
Stage II— excess of sugars			
3rd year of tapping			
June 5	140.0	652.0	60.9
Stage III—transition to acute carbohydrate shortage			
4th year of tapping			
July 10	163.8	116.3	179.6
Stage IV—acute shortage of carbohydrates			
1st year after tapping			
July 24	58.6	57.8	63.5
September 2	39.0	30.8	64.6

The duration of the different identified stages may vary depending on the extent and duration of the shift of root-leaf relations. For example, carbohydrate accumulation which was observed in Siberian stone pine under conditions of maximum tapping in the third year of test, was found in the eighth year in Scotch pine on moderate interference. In the female needles of Scotch pine, affected by notches, the saccharose content in September was 173 186.2% of control and of monoses 35.8%. A slight modification of root-leaf relations thus extends the period of initial reduction of carbohydrate level, generating a more prolonged interval of time for the activation of growth processes. The change of the quantitative content of carbohydrates in the shoot system is significantly reflected on their conversions in the reproductive structures.

Starch in the tissues of two-year-old cones in the third year of strong interruption of root-leaf relations increases by more than 300%. In the period of proembryonic development, the availability of assimilates and accumulation of metabolites rises in the seeds and, later during maturity, carbohydrate utilization in the synthesis of reserves is increased (Vorob'ev, Vorob'eva, and Rush 1971).

174 Table 78. Dynamics of the content or readily-soluble carbohydrates in the ripening seeds after the third year of tapping

Readily-soluble carbohydrate	Date of observation		
	June 15	July 28	August 9
Saccharose	16.1/304	17.0/144	7.5/95
Fructose	trace/-	0.1/16	1.1/110
Glucose	trace/-	0.2/100	0.3/100
Raffinose	trace/-	trace/-	1.2/600
Total	16.1/304	17.3/187	10.1/108

Note. Numerator, % of dry matter; denominator, % of control.

The active flow of carbohydrates to the ripening seeds may be judged from the accumulation of saccharose under the influence of tapping in July (Table 78). The content of glucose at this time does not practically change but fructose is distinctly lower than in the control. It is significant that the change of root-leaf relations is reflected mainly in the amounts of fructose and saccharose, i.e. carbohydrates, which are most closely involved in starch synthesis. Considering that this period is characterized by the formation and accumulation of the latter, it may be suggested that the seeds of tapped trees accumulate more of plastic matter than untapped trees by the commencement of increased fat formation.

In August, in the period of conversion of metabolites into reserves, seeds of tapped trees show a high amount of raffinose at nearly the same content of disaccharides. Thus, while the initial content of the latter in the seeds of tapped trees was 17% and in untapped trees 11.8%, these differences became insignificant in the present stage. The content of glucose and fructose was also equalized.

174 The ultimate utilization of readily-soluble carbohydrates in the seeds is associated with the intense formation of fat, its precursors being the products of anaerobic dissociation of carbohydrates (Newcomb and Stumpf 1953, and Pontovich 1959).

As established before, starch, the main source of carbohydrates, undergoes in this period increased hydrolytic breakdown (Sveshnikova 1957). The fall of saccharose content used in fat formation as was established above is found to be more pronounced in the test trees than in control. This suggests increased fat formation which accumulates in the seeds of tapped trees in a larger quantity than in controls (Table 79).

Changes in the intensity of carbohydrate utilization under tapping conditions lead to different ratios of readily-soluble and reserve carbohydrates in the mature seeds. Values in Table 80 show that tapping reduces the content of readily-soluble carbohydrates and starch. The sum of mobile sugars

174 Table 79. Oil content of seeds, % of dry matter

Year of tapping	Average for the tree			Stand		
	Control	Tapping		Control	Tapping	
		moderate	intense		moderate	intense
1st	60.4 ± 0.3	61.0 ± 0.4	62.8 ± 0.3*	61.3 ± 0.4	62.3 ± 0.6	62.7 ± 0.8
2nd	55.8 ± 0.4	60.4 ± 0.6*	62.1 ± 0.8*	54.0 ± 0.6	61.2 ± 0.8*	62.2 ± 0.7*
3rd	53.9 ± 0.5	57.8 ± 0.6*	61.7 ± 0.8*	59.1 ± 0.4	58.3 ± 0.6	59.6 ± 0.5

175 Table 80. Carbohydrates contents in mature seeds

Variant	Saccharose	Raffinose	Fructose	Glucose	Total	Starch maltose
Commencement of tapping, 3rd year						
Control	4.0	4.7	0.2	0.3	9.2	5.9
Tapping						
moderate	40	70	150	70	58	50
intense	82	35	50	100	70	40
End of tapping, 8th year						
Control	8.7	0.5	0.1	0.2	9.5	1.9
Tapping						
moderate	40	60	300	150	50	68
intense	28	20	100	200	31	52

Note. Control, % of dry matter; test, % of control.

decreases with the simultaneous fall of saccharose and raffinose. The pattern of these changes, however, is not uniform: the reduction of raffinose content is noticed right until maximum intensity of tapping and of saccharose only up to a moderate interruption of root-leaf relations. Under intense tapping conditions, the amount of saccharose is at first more than average. In the eighth year of test when a weakening of greatly affected trees began being noticed, the amount of saccharose in seeds, like total sugar, was significantly
175 below not only the control but also compared to the seeds of moderately tapped trees.

Throughout these stages, starch content decreased in proportion to the tapping intensity. Since starch is the main source of fat formation, it was suggested that its reduction was related to the increased fat synthesis (Fig. 50). This relation prevailed until the weakening of the vitality of trees and reduction of the oil content of seeds commenced in the fourth

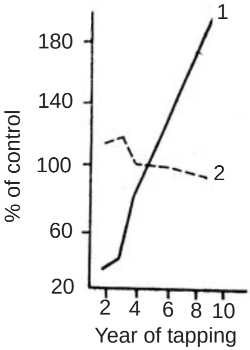
173 

Fig. 50. Fat and starch ratio in the seeds in different years of tapping: 1—starch; 2—fat

year of test with intense tapping. Under these conditions, the starch content began to rise and approached the control level. The course of this trend was traced in the eighth and ninth years of tapping at different severities (Table 81). By this time, under weak tapping conditions, fat content continued to remain higher than in control, but starch was correspondingly lower. On moderate tapping, the fat rise in the seeds was the same but of starch higher than in control. Finally, in tests with intense tapping of oppressed plantations in Tomsk district (IV quality index; VII class of age), a significant reduction of the oil content of seeds and a sharp rise of starch content were detected. Readily-soluble sugars in all the cases were invariably less than in control.

By first activating the vitality of the tree, tapping thus promotes the biochemical conversions of carbohydrates by reducing the starch content and increasing the oil content of seeds. In the period of weakening of vitality, the synthesis of reserves in the seeds is disturbed and oil content decreases gradually and starch content rises sharply. The biochemical conservation of carbohydrates in seed suggests a stable relation between the reproductive system and the condition of the tree and thus facilitates the use of combined oil and starch contents as a diagnostic tool not only for tapped 176 trees but also for plantations affected by other methods.

On the whole, the shift of root-leaf relations in the woody plant initially causes a deficiency of carbohydrates in the surface organs mainly due to additional consumption in resin formation and creates more favorable 177 conditions for growth. The weaker the shift, the longer is the duration available for optimum growth of surface organs, vegetative as well as reproductive.

176 Table 81. Ratio of fat and carbohydrates in seeds under tapping conditions, % of dry matter

Composition	Control	Test	
		%	% of control
Weak tapping, 8th year, Balandu-kol′ section, Gornyi Altay			
Fat	64.0 ± 0.5	65.2 ± 0.7	101.8
Starch	1.9 ± 0.1	1.0 ± 0.1*	52.3
Total readily-soluble carbohydrates	9.45 ± 0.09	4.73 ± 0.11*	50.0
saccharose	8.77 ± 0.08	4.17 ± 0.10*	47.5
raffinose	0.30 ± 0.09	0.29 ± 0.04	96.6
fructose	0.22 ± 0.02	0.19 ± 0.03	86.3
glucose	0.16 ± 0.002	0.18 ± 0.004	112.5
Moderate tapping, 9th year, Ozup section, Gornyi Altay			
Fat	53.4 ± 0.6	55.5 ± 0.8*	103.9
Starch	2.8 ± 0.1	4.0 ± 0.4*	143.7
Total readily-soluble carbohydrates	12.01 ± 0.13	10.33 ± 0.11*	86.0
saccharose	7.53 ± 0.09	6.34 ± 0.08*	84.2
raffinose	4.32 ± 0.03	3.87 ± 0.01*	89.4
fructose	0.05 ± 0.002	0.03 ± 0.005*	53.7
glucose	0.10 ± 0.01	3.98 ± 0.04	89.3
Intense tapping, 9th year, Yarinsk island, Tomsk district			
Fat	64.9 ± 0.4	62.4 ± 1.0*	96.1
Starch	4.5 ± 0.1	10.1 ± 0.1*	224.4
Total readily-soluble carbohydrates	9.93 ± 0.11	6.22 ± 0.09*	62.7
saccharose	5.12 ± 0.17	4.05 ± 0.15*	74.5
raffinose	3.56 ± 0.14	2.08 ± 0.14*	58.4
fructose	0.76 ± 0.05	0.09 ± 0.002*	11.5
glucose	0.18 ± 0.01	0.01 ± 0.001*	6.2

When the shift of root-leaf relations is more significant, the deficiency of sugars in the crown, mainly in the shoot system is only for a short period. Later, it is succeeded by the accumulation of carbohydrates, mainly saccharose, by the reorganization of the ratio between monoses and saccharose in favor of the latter, and intensification of starch utilization. These changes impede the growth processes and create favorable conditions for reproduction. In this environment, the supply of assimilates to the roots is steadily reduced and the consumption of their reserves increases. On extreme interruption of transport ducts, these changes ultimately not only depress the positive effect on the intensity of reproductive activity but also result in the overall weakening and death of the tree.

On moderate shift of root-leaf relations, a high consumption of sugars does not lead to pathological consequences of carbohydrate metabolism but promote the active advance of processes of growth and reproduction for a very prolonged duration.

* * *

The nature of response of trees to the mechanical damages of trunk described above may be examined from three view points: control of the reproductive activity of conifers, relative to the problem of stability of woody plant against damage of its entirety, and in the context of biological principles of integrated utilization of pine forests.

Damage to the whole plant on mechanical cuts on the trunk disturbs the equilibrium state of the polar system of the trunk—roots and crown—and causes a shift of their interrelations in favor of weakening of the activity of roots.

The set of physiological processes accompanying these changes is characterized by the following features on moderate shift of root-leaf relations:

a) increase of water availability to the organs of the crown by enhancing the water retention capacity of tissues and increased water flow through the undamaged phloem as well as under cuts through the inner layers of wood; under these conditions, roots suffer moisture deficiency;
b) activation of the pigment system manifest in an increased chlorophyll content, specially carotenoids, which determines the strengthening of the protective response of damaged trees;
c) primary manifestation of the deficiency of carbohydrates in the surface organs, later their accumulation and reorganization of the ratio between monoses and saccharose in favor of the latter by increased starch utilization; flow of assimilates to the roots is affected under these conditions and the utilization of reserves increases;
d) greater bonding of nitrogenous compounds into protein in the surface organs and weakening of the metabolic activity of roots; and
e) variation of terpene ratio in favor of a higher content of compounds possessing better protective properties.

On weak and severe shift of root-leaf relations, these processes possess in the first case the features of *brief intensification of the activity of roots and, in the second case, following optimum weakening, of the pathological state.*

Several stages can be recognized in this scheme of dynamics of root-leaf relations in the vitality of damaged trees. These stages provide an idea of the course of changes of reproductive and growth processes.

The stage of growth *activation*, predominantly of regenerative processes: involves hitherto vegetative shoots in the reproductive activity, thus enhancing the overall yield of the tree, and significantly improving the conditions for seed growth as well as their qualitative characteristics.

The stage of *adaptation* of the tree to the altered metabolism: return of growth indexes to the original level, weakening of the stimulating effect in the activity of regenerative spheres, and maintaining the improved seed characteristics at optimum combination of the extent and duration of the shift of root-leaf relations; the body of the fully grown tree successfully adapts to the new conditions of survival and provides more seeds of better quality than before the application of the stimulating factor; at a non-optimal combination of test conditions, the vitality of the tree weakens.

The stage of *weakening* of the processes of growth and development: distinct reduction of the energy of shoot growth, formation of female primordia, transition of some shoots from the reproductive to the vegetative state, and manifestation of adverse changes in the course of seed growth.

The stage of the *critical state* of the tree and significant weakening of growth and development processes: perceptible and progressive reduction of the energy of growth processes, reduction of the photosynthetic tissue of the tree, sharp fall of the energy of reproduction in the shoots and the tree as a whole due to the reduced number of female shoots, noticeable deterioration of seed quality, and reduced level of resin formation.

The stage of the *death* of the tree: causing minimal linear growth of shoots, fall in the number of needles and the resultant sharp reduction of the framework of the crown, and reduced number of cone-bearing female shoots to a few while preserving an adequate number of male shoots characterized by high formation energy of microsporophylls but low viability of pollen, significant reduction of the sizes of cones and seeds, and later their planting quality, and inhibition of resin-formation processes.

The duration of stages and their precise characteristics under different test conditions depend on the original state of the object and the intensity and duration of interruption of root-leaf relations. On stronger shift of plant metabolism, these stages proceed over 5–7 years but, on a weaker shift, take several decades to enter the second or third stage. In the older trees and impaired growth conditions, the stimulating effect of the changes of root-leaf relations is brief and insignificant. Such trees lose their vitality rapidly and
179 consequently are unsuitable either for comprehensive utilization for producing galipot or for inducing reproductive activity.

In the species of pine characterized by very active metabolism (Scotch pine), the positive and negative responses to the variations of growth and reproduction are more significant and faster than in those characterized by less labile metabolism (Siberian stone pine).

Under these conditions of shift of root-leaf relations, the change of physiological processes promotes at first the activation of growth processes and later inhibit them before promoting the reproductive activity. On extreme starvation of roots as noticed during ringing or strangulation of trees, this stage results in their death, and thus these measures cannot be viewed as stimulants of prolonged cone yield.

Activation of regenerative processes stands at an optimum level on moderate weakening of root-leaf relations, mainly by involving a large number of shoots in reproduction and improving the conditions of seed formation. This does not, however, result in greater primordia formation per shoot or balanced cone yield dynamics in the same manner as during the stimulation of reproduction processes by other means, specially on the application of fertilizers, improvement cutting, or trimming the crown or roots. To resolve these problem, other methods require to be used, most probably those associated with better breeding possibilities and control of ecological conditions.

From the viewpoint of the theory of adaptation and stability of plants to the damaging environmental factors, a study of the corresponding responses of tree to the mechanical damages points to the need to devote attention not only to weakened but also the active state of plans. Further, the range of processes analyzed should be extended to studying the response of growth and regenerative development. Under the author's test conditions, the manifestation of the mechanism of plants stability included the inhibition of growth processes in the crown and activation of reproductive (cone yield) and protective (resin exudation) systems. Further, the tree constantly tended to return to the original state of root-leaf relations through activation
180 of cambial activity in the intact sections of trunk. Such response of the tree points out, on one hand, to the mechanism acquired over the evolutionary course and, on the other, the manifestation of cybernetic properties of root-leaf relations. The application of these aspects to the problem of stability of coniferous plants and crop control, as will be shown below, is of positive interest for theoretical studies as well as for resolving field problems.

Based on the above discussion, crop control in coniferous plants should be based on controlling root-leaf relations which are responsible for the prevailing dynamics of relations between growth and reproduction. The mechanism of this control should primarily lead to conditions conducive to the activity of the plant as a whole and later to the periodic intensification of processes of growth and reproduction while maintaining in general the principle of *dynamic equilibrium* between them.

Taking these premises into consideration, the stages of experimental control of reproductive activity in coniferous plants should cover the following program of operations:

a) preparation of plants to the reproductive activity by applying methods for activating the growth processes while impeding the reproductive processes at this stage. Enlarging the volume of crown, trunk, and the root system should result in the formation of a significant number of shoots potentially capable of male or female shoots (depending on the objective of stimulation). The set of measures applied at this stage is related to the strengthening of root activity. Without appropriate preparation of plants to the reproductive activity, acceleration of intensification of their cone yield is purposeless;

b) prepared plants enter reproductive activity by a shift of root-leaf relations toward an optimum inadequacy of roots. For this purpose, the prevailing methods including mechanical cuts can be selected. In fully grown trees, such a shift can be attempted by normal tapping 10 years before cutting down. A more prolonged and moderate effect of stimulation is realized by adopting sealing-type cuts. A special technology needs to be developed for young plants providing for a one-time cut but not covering more than 50% of the circumference of the trunk, immediately after the formation of female strobili;

c) in the next stage, efforts are made to support and intensify the reproductive faculty of shoots, specially lateral shoots, by improving the nutrition of trees and protecting strobili in the period of non-seed cycles of cone formation. This is achieved by using the methods of mechanical protection from the adverse effects of ecological factors, mainly spring frosts, and physiological inhibition of phenophase using antitranspiration agents, and optimum combination of early- and late-
181 developing forms. The desirable size and duration of enhanced yields, i.e. the smoothing of cone forming dynamics, is determined at this stage; and

d) the first cycle of controlling the reproductive activity of trees ends in a temporary activation of growth processes, i.e. to intensify afresh the root activity. The performance of this objective determines the conditions for the next cycle.

The above suggested scheme may be regarded as a first guide to conducting tests for stimulating cone yield and as a plan for studying the aspects associated with this problem. In this respect, the data examined point to the need for repeating the investigations for studying the conditions of equalizing the cone forming dynamics without emphasizing on its intensity. This is not a contradiction of the objectives but achieving moderate stable yields, according to the author, is more important than achieving record but rare crops. For this purpose, a further study of the state of growth and reproductive processes is necessary under conditions of naturally prevailing dynamics of their ratio as also its modification under the influence of varying root-leaf relations.

From the viewpoint of ensuring *comprehensive economy* in Siberian stone pine forests, the data presented above suggest the possibility of prolonging the tapping duration and different permissible combinations with nut production. Depending on the type of comprehensive utilization of the stand (short or prolonged duration), the duration of tapping, its technology, and correspondingly the effect of stimulating cone formation, are determined. A combination of tapping and nut production (production of commercial nuts) is realized for several years before cutting down the stand.

CHAPTER V

Comprehensive Utilization of Siberian Stone Pine

Brief Description of the State of the Problem

Although the concept of comprehensive utilization of forest resources, including non-timber products, is quite well-known and acknowledged at present (Pozdnyakov 1975, Tupytsya 1976, A. Petrov 1978, and Plyakov 1978), its practical implementation in the Siberian stone pine forests is far from an optimum solution.

The timber industry approach oriented mainly toward timber production continues to prevail and, as usual, no attention is paid to fulfill the requirements of conserving the genetic resources or the environment and several other features and advantages. Forest exploitation is combined only rarely with the production of galipot, nuts, berries, and game products but this too ultimately ends in a total cutting down of the trees.

Attempts to restrain the felling of Siberian stone pine trees do not meet the objectives because of economic considerations and the incorrect approach based on an assessment of current and immediate prospects of forest produce and not on the scientific principles of organizing the forest economy. It is sufficient to say, without going into all the aspects of forest management, that the commercial exploitation of timber which is otherwise unsuitable for long-term comprehensive utilization is essential and justified in many cases but the point is that this approach is being adopted universally without regard to the other features or benefits. As a result, the better and productive pine forests are being felled together with inferior trees thoughtlessly. The general age limit laid down for felling (within a given group of forests) is not, and cannot be, an optimum if it is not based on a thorough evaluation of the forests (Semechkin and Vorob'ev 1980). The problem with Siberian stone pine forests thus is not the difficulty of resolving any technological issue in their exploitation or forest restoration—they are being solved and will be solved in future—but lumbering trends predominate in the most valuable sections of the pine forests of Siberia and the Far East and this manner of exploitation and the resultant poor attention to conservation make for a generally unsatisfactory situation.

When evaluating the state of economy in the Siberian stone pine forests, not only the several techno-economic problems hitherto unresolved should be tackled but also the insufficient theory of comprehensive utilization of 183 forest resources must be corrected. This theory at present is based, on one hand, on the principle of the prospects of utilizing all the benefits from the forest and, on the other, the timely recovery of more productive, accessible, and profitable resources, for example, timber. Holding blindly to one or the other principle with respect to the pine forests and attempting their formal separation or combining different forms of economy, lack of theoretically justified recommendations for assessing the stands—all of these are factors contributing to the present unsatisfactory state of the utilization of forest resources (Vorob'ev, Spiridonov, and Saeta 1979, Semechkin and Vorob'ev 1980, and Vorob'ev 1981).

A study of these factors with a historical perspective shows that all of them are associated with extreme situations of evaluating the pine forests.

Originally, even in the Prerevolution period, Siberian stone pine was recognized as a "cash" tree, a source not only of nuts but also a habitat for useful birds and game animals (Slovtsov 1892, Andrianov 1909, Borzenko 1910, and Baryshevtsev 1917, all cited after Krylov 1961). Attention was therefore mainly devoted to organizing nut collection and fur preparation. An important practical outcome of this and the later periods is the extensive organization of pine forest plantations which represent even at present shining example of the effectiveness of improvement cutting (Petrov 1971 and Alekseev 1979).

Under the Soviet rule, specially in the '30s, pine forests continued to be regarded as a source of nuts and, in many cases, even the question of their more extensive utilization began being posed (V. Ivanov 1934 and Petrov 1936). The governmental approach to exploiting the pine forests comprised the organization of several specialized establishments, and specially the Karakokshin unit in Gornyi Altay. However, the predominantly commercial attitude of organizing the establishment and several years of crop failure became a reason not only for closing down this and other similar establishments but also sliding back to the concept of pine as a common forest species. As pointed out by I.A. Bekh and I.V. Taran (1979), while felling of pine was prohibited in Siberia until 1936, it is being practiced thereafter in the name of developing comprehensive utilization of pine forests as well as for commercial production of timber.

Nevertheless, attention to rational utilization of pine forests did not diminish (Adamovich 1948, Tikhomirov 1949, Petrov 1952, and

Gorchakovskii 1955). The works of these and later investigators (Pentegov 1957 and Znosko 1960) made several suggestions toward the end of the ’50s. These were reported in 1959 at the first conference on the problems of Siberian stone pine (Krylov and Mukin 1960) and formed the basis for organizing afresh in Gornyi Altay the first ever establishment in the country for the comprehensive exploitation of taiga pine named “Kedrograd”.

184 The great advance of scientific investigations on the subject of Siberian stone pine including the comprehensive utilization of forest resources commenced in the ’60s. Basic studies were concentrated at the V.N. Sukachev Institute of Forests and Timber under the directorship of Acad. A.B. Zhukov (Motovilov and Shcherbakov 1962, Shcherbakov 1965, Spiridonov 1965, Zhukov 1965, Sokolov 1966, Lebkov 1967, and Semechkin 1971) and at the Institute of Biology, Siberian Division, Academy of Sciences, USSR, with the participation and directorship of Prof. G.V. Krylov (Krylov and Mukin 1960, Krylov 1971, Nekrasova 1960, Krylov, Pryazhnikov, and Vorob’ev 1965, Pryazhnikov 1966, Surov 1968, Vorob’ev 1968, and Kulakov 1973). The Ural forest scientists led by B.P. Kolesnikov, Corresponding-Member, Academy of Sciences, USSR, made significant contributions towards solution of problems concerning comprehensive utilization of Siberian stone pine forests (Kolesnikov and Smolonogov 1960, Kolesnikov 1966, Zubov 1960, Petrov 1966 and 1968, Petrov and Kirsanov 1968, Yurchikov, Trusov, Teten’kin, and Petrov 1962, Kirsanov and Trusov 1968).

The scientific investigations carried out during this period pointed out that the program should cover diverse aspects: preparation of nuts, medicinal-industrial raw material, fur, timber, galipot, etc. The realization of these objectives in “Kedrograd” acquired a commercial bias for the first time. As in the ’30s, experience showed the promise of this approach for utilizing the pine forests as the main method for such organizations. Subsequent inclusion of tapping and timber preparation, on one hand, stabilized the techno-economic indexes and, on the other, led to a predominant timber industry approach, the consequences of which were discussed above. The results of this period, specially the activities of experimental units have been reported in various general publications (Khlatin 1966, Telegin 1966, Saeta 1971, and Parfenov 1979, and Talantsev, Pryazhnikov, and Mishukov 1978). Having evaluated this period in the present context, it may be said that a program largely dealing with the short-term utilization of poorly and moderately productive parts of Siberian stone pine forests has by now been worked out and introduced into practice. Insofar as the better exploitation of plantations is concerned, more so their long-term exploitation, such a program is not only unsuitable but impermissible. In the plan of the overall organization of economy, convincing proof has surfaced in favor of multidisciplinary approach in pine forests (Spiridonov 1965, Saeta 1971, and Parfenov 1979).

By the end of the '70s, it became evident that the comprehensive utilization of pine forests, primarily their stands, should be organized of differentiated basis by an optimum combination of the intra- and interplantation features. This approach is theoretically based on the principles of relations between growth, yield, and resin output of Siberian stone pine at the intra- and interpopulation levels (Vorob'ev 1968, 1973, and 1981).

185 A definite step toward organizing differential exploitation within a stand has been taken by the Ural forest scientists V.A. Kirsanov and P.F. Trusov (1968) who proposed the felling of unproductive sections of plantations in the nut producing zones after taking into consideration the resin productivity and the yield of trees. Their differentiation was based on the Kraft categories and functional relations between these productivity indexes. Reliance on this form of relations due to poor understanding at the time of the variability of these characteristics, methods of their determination, and relations at the intrapopulation level did not permit the investigators to depend on this form of relations and arrive at a final solution to the problem since a fairly large volume of timber production resulted in corresponding losses of crop and yield of galipot. When producing timber only from a small section of the stand, selective felling did not hold promise from the economic or forestry management viewpoints since it did not take care of the structure of the entire plantation.

Appropriate investigations carried out at the Institute of Biology and later at the Institute of Forests and Timber helped propose a system of comprehensive utilization of not only the nut producing zones but also the pine forest as a whole on the principles of differential combination of the elements and types of the complex (Vorob'ev 1968, 1973, 1981, and 1982, Vorob'ev, Saeta, and Kulakov 1978, Vorob'ev, Spiridonov, and Saeta 1979, and Semechkin and Vorob'ev 1980).

Principles of Comprehensive Utilization

The diversity of benefits of pine forests, comprehensive utilization, and the nature of their preceding exploitation point to the clear desirability of organization and management of economy of a differential basis.

The principle of integrated utilization determines the nature of management, differential combination of the various elements of utilization, i.e. its content. These principles should be implemented at all levels within the management and within the regional organizations. The approach within the management is based on the differential utilization of the plantation while the intraregional approach is based on the appropriate consideration of the specific properties of trees. On the whole, the differential approach should be practiced throughout the system of utilization of the pine forests, from establishing the optimal ratios between the different divisions of forest produce to the individual trees.

An outline of the history of utilization of pine forests and the subsequent evaluation of their benefits reveal the prevalence of several types of complexes which may be recognized either in the form of individual managements or the sumtotal of areas, functionally combined into a common system of utilization. Taking into consideration the extant practice and suggestions for its rationalization, three basic types of complexes in use within a unit, region, or for interregional organization of the utilization of pine forests can be tentatively recognized. Apart from this, three additional types of complexes are proposed, mainly for organization within a unit.

Timber industry (lumbering) type complex (TIC) is based on the exploitation of non-pine, mixed, poorly and moderately yielding pine plantations by conducting preliminary short-term tapping and collection of nuts and ancillary material, followed by timber recovery as the main product (group III of forests) or felling "depending on the level of cone yield (group I of forests—nut producing zone). When collection of nuts (less than 30 kg/ha) and galipot (less than 25 kg/ha) is not profitable, pine plantations of group III can be preferentially used for timber followed by afforestation or promoting the undergrowth. Forest stands with "very low" and "low" productivity fall in group III and "very low" stands in the nut collecting zone in group I (classification of categories discussed later).

The basic purpose of the complex is to produce timber and generate a techno-economic base for the organization. Depending on the structure of forests and the type of management, it may occupy a leading or subordinate position among many other types of complexes.

Forest-economy complex (FEC) is earmarked for prolonged active utilization of the more productive sections of pine forests, not falling in the category of a protected regime, breeding, or for producing forest seeds. Forestry type complexes include plantations in group III of forests with "moderate" and "high" productivity and those in group I with "low", "moderate", and "high" productivity (nut collection zones). These are predominantly pure, very dense plantations, in the form of large massifs with good internal and external transport network for organizing intense ancillary activities and production of galipot and timber. The organization of this complex provides for a prolonged combination of specialized tapping, nut collection, and selective felling of trees on the basis of the condition of cone yield and suitability of trees for comprehensive utilization based on visual evaluation for selection on economic considerations (growth, yield, and resin productivity).

In plantations with a low content of Siberian stone pine in which the collection of nuts and galipot is not profitable and the older trees require to be replaced by younger generation, selective or gradual felling, largely for

purposes of forest organization, needs to be widely practiced. In either case, ancillary material is collected in the complex, and measures for forest restoration and other types of activities are organized. On the whole, the
187 purpose of a forestry complex is to maintain and promote long-term utilization of the more productive part of pine forests.

Plantations that are not ready for commercial utilization with respect to their age (I–III age classes) represent the base for the formation of pine stands for purposes of comprehensive utilization in case of their diverse composition and importance as well as specialized stands for producing mostly timber in some cases (from dense undergrowth), nuts or galipot in other cases or for performing protective and other functions as for example genetic selection. This section of the plantation should be integrated and regarded as a distinct *forest-forming complex* (FFC). It forms the base for changeover from a combination of all elements of utilization within the same plantation at present to raising complex systems on the principles of an optimum combination of specialized natural and developed stands.

Game type or hunting-game complex (HGC) integrates game economy and ancillary utilization. These are organized in different types of forests: protected, reserve, poorly accessible areas with respect to their territory as well as technologically, in the zone of the activities, i.e. TIC and FEC. The game type complex may provide a base for organizing specialized units or it may be integrated with TIC or FEC types in a unified management system.

Apart from the main types, there are also “seed selection” and “specially protected” complexes.

The *seed-selection complex* (SSC) or essentially the seed base contains the genetic reserves, plus category of plantations marked for some specific features, permanent and temporary seed sections, plantations or beds along with plus category of trees. This complex is marked out in all groups of forests on the basis of systematic principles and is integrated with forestry measures aimed at conserving and improving its functions.

Specially protected complex (SPC) is organized at the base of forest categories spread over a fairly extensive territory which is important for water and soil conservation or for some other purpose. In the mountains, subalpine pine forests under bald peaks and plantations of other species accompanying them form the base of these complexes. On the plains, these include northern taiga pine forests. The composition of this complex also includes different types of specially protected sections marked in the effective zone of lumbering and forestry complexes. The basic purpose of the specially protected complex is to guarantee the conservation of the major regional (river sources in the mountains and their riparian sections in the plains) ecological functions of pine forests. For management purposes, the SPC is preferentially integrated with the game type of complex and is regulated by an appropriate system of forestry measures aimed at conserving and improving the protective functions.

188 The dominant type of complex is determined according to the structure of pine and other forests and the form of established activity: lumbering (predominance of timber complex), forest combine (commercial activity with an optimum combination of different complexes), forestry (dominance of forestry, mainly forest restoration activity), and cooperative game management (game type).

The dominance of one type of complex should not be a reason for irrational exploitation of other resources—the management of pine forests should be an integrated system independent of their organizational affinities (Semechkin and Vorob’ev 1980).

Integrated multidisciplinary systems represent the basic form of management in the pine forests. These are organized predominantly in the management system in forests for optimal combination of all types of activities. The main problem in such systems is the management of forestry type organization of activities. The timber industry section is included in them as a techno-economic base of the unit, permitting it to handle large-scale activities that are more cumbersome, like forest restoration, as well as develop the nut producing zone. Under these conditions, game activity provides additional products and helps in developing largely inaccessible sections of pine forests.

The territory of such organizations is managed on the basis of premises discussed above and appropriate evaluation of pine forests in the course of setting up and design of the complex taking into consideration the techno-economic conditions (Vorob’ev, Saeta, and Kulikov 1978, Vorob’ev, Spiridonov, and Saeta 1979, Semechkin and Vorob’ev 1980, and Vorob’ev 1981).

A special problem in the comprehensive utilization of pine forests is the development of nut producing zones which cover 9.1 million ha in Siberia and Far East (Yurchikov et al. 1962, Petrov and Krisanov 1966, Zubarev 1964, Vorob’ev 1968 and 1973, and Vorob’ev, Saeta, and Kulikov 1978). So far, these zones fulfilled their primary objective by providing a guarantee for protecting some forest sections from total felling. Insofar as comprehensive utilization is concerned, apart from game and occasional collection of pine seeds, no other management measures have been recommended other than activities relating to conservation (Motovilov and Shcherbakov 1962).

The present state of the timber industry calls for a more intense exploitation of forest resources, including group I forests (Vasil’ev 1972, Krest’yashin 1972, Melekhov 1975, and Sinitsyn 1977). The extension of such activities to the nut producing zones until recently has been restrained for want of appropriate theoretical support.

189 Development on the lines of the above concepts and principles will help approach the utilization of nut producing zones on a commercial basis by involving all the segments of the complex (Yurchikov, Trusov, Teten'kin, and Petrov 1962). A shift to this basis will eliminate the domination of the game complex becoming uneconomical and also the danger of exploiting these zones on the lines of the timber industry by shifting the activities between groups I and III as and when the resources are depleted in any one of them.

The nut producing zones should be marked out for conservation and active utilization of the most productive part of the pine forests, primarily with a high productivity. The most important task in the nut producing zones is the conservation of the genetic resources of pine forests and utilizing them as the main seed base.

Depending on the management problems, the nut producing zones may be subdivided into two categories:

one, the type of timber and cone-yielding plantations (pine forests around settlements and similar ones) with different types of locations and areas and characterized by high yields (over 100 kg/ha in an average year), and

two, the type of compact pine plantations which promote, along with the exploitation of forests of groups II and III, the organization of an integrated system of those of interest for independent management of hunting-game activities or for conserving the valuable massifs.

The main task in the nut producing zones of the first category, specially in pine forests with settlements around, is their conversion into a seed base of a transitional type (before developing seedlings for growing) by

190 a) carrying out an inventory of breeding activities, selection and utilization of valuable forms, mainly nut yield;
b) practicing improvement cutting aimed at preparing the plantations to mechanized collection of cones and improving nut output not only by weeding out extraneous species but also the minus category of pine trees;
c) adopting measures for improving the yield and balancing its dynamics by the application of fertilizers and other measures;
d) adopting mechanization of preparation and processing of cones;
e) organizing the prognosis of the quantity and quality of crop; and
f) better crop protection from pests.

When organizing the forestry complex in the above zones, tapping and cleaving are not permitted. T.P. Nekrasova (1968) and Yu.B. Alekseev (1979) dealt with some of these problems.

The main principles for distinguishing the nut producing zones of second category are: overall value, primarily high seed productivity, compact disposition, and suitability for commercial adoption and for organizing transport facilities. The criteria for classifying the nut producing zones of this category are:

a) the availability in the organization of a single block (about 5000 ha) or some groups or blocks or sections (up to 2500 ha) of pine plantations of 'high' and 'very high' productivity and forming a single transport network;
b) domination in these plantations of I–III quality classes and III–IV age classes with a composition of over five units, density exceeding 0.5, and with nut output of more than 75 kg/ha in an average crop year;
c) the possibility of the optimum combination of different types within the complex into a single territory (150,000–200,000 ha or more): 'seed selection' (2%) and forestry (50%) in the most productive section of pine forests; game sanctuary (30%) predominantly in mixed dense and open coniferous forests as well as in pine forests of average productivity; timber section (10%) mainly in the low-yielding pine sections unsuitable for prolonged integrated utilization; young seedlings (8%);
d) setting up an overall nut producing area covering not less than 30% of the territory of the organization; and
e) the nut producing zone should not include protected pine forests of local importance (flow of large rivers in mountains and watersheds on the plains); the area of such zones is regarded as an independent category.

When a complex satisfying these conditions is not available, the most productive pine plantations are identified as fragmented sections ('blocks') in the nut producing zones of first category.

A ready criterion for identifying nut producing zones is the proportion of participation of good pine trees as determined from their complex evaluation discussed below.

According to the purpose of the nut producing zones of second category, a combination of the types of complexes is established taking into consideration the evaluation of the pine forests and recommendations for groups of forests.

The main type of complex is FEC type in the zone of utilization of fully grown plantations and objective raising of young plants as well as in the nut producing zone that is essentially exploited on commercial basis. Its use extends to pine forests of appropriate rank, high yield, and resin productivity. The most productive part of such pine trees can be assessed as genetic reserves based on selection.

TIC under these conditions is best permitted together with FEC when developing 'blocks' of plantations for rationalizing their use and organizing transport network. The main objective of TIC in the nut producing zone is the elimination of unproductive pine trees on the basis of age, composition or formation characteristics like narrow crown in which selective felling and organization of FEC type complex is not desirable. Felling of such plantations may be carried out gradually in due course "based on the state of cone yield 191 in one stage (in the absence of a second level) or two (when it is present). The rank and size of yield and resin productivity can also serve as a criterion for adopting such a type of complex. In the TIC group are placed larch, dense and open coniferous forests (excepting those required for organizing game) with felling ages conforming to the nut producing zones.

HGC and SPC types are combined with the above types with due consideration of their objective and dominant role in the nut producing zone.

The following are the main techno-economic considerations for developing the nut producing zones on a commercial basis:

a) enlarging the activities of the unit by including timber preparation and preliminary tapping,
b) achieving total interpretation of the activities of the complex within as well as between different plantations,
c) concentrating expenses on minor but fairly productive sections,
d) possibility and need for setting up a network of regular forestry and timber transport roads (for zones located not more than 50 km away from the site of working),
e) availability of a techno-economic base for the unit (volume of timber processed in group III forests not less than 50,000 m^3/year), and
f) establishing a ratio of 1.0:0.1 between the volume of timber processing in group III forests and nut producing zones.

When these conditions are not satisfied, the nut producing zones are developed as a game type and combined with the conservation of genetic reserves and protective functions. Scattered bodies with nut producing sections having poor access are similarly organized.

On the whole, the organization of nut producing zones should also take into consideration the above premises, integrated assessment of pine forests, and special structures and projects.

Methods of Selection and Integrated Evaluation

Among the diverse benefits of comprehensive utilization of pine forests, the important ones are timber, nuts, and galipot, which represent products of growth, regenerative, and resin forming processes. An analysis of their relations at inter- and interapopulation levels showed a positive statistical correlation which allows genetic or phenotypic exceptions like poorly or highly developed properties of some trees and plantations (see Fig. 36).

These patterns of correlations between the characteristics are applied to samples of trees and plantations selected for one or the other highly developed properties; the basis of an integrated management system is the optimum combinations and short-term exploitation of highly weakened and minus 192 category of trees and plantations as well as those in which the indexes required for active utilization (yield and resin output) are poorly developed but timber mass is well formed. In other words, there is a possibility of differential utilization of the structure of relations between the characteristics in poorly, moderately, and highly productive sections, with respect to the distribution of a particular leading feature. In such an approach, exploitation assumes a selective or theoretical basis of differentiation in the organization and management of comprehensive economy.

For evaluating individual trees and plantations, selection and integrated rank can be adopted (Vorob'ev 1974, 1979, 1981, and 1982).

The rank for selection purposes was studied before when analyzing the relations between growth, yield, and resin productivity. In this case, it must be emphasized that it is established only for the pine section of the stand and, in the case of a mixed-age plantation, for the main generation. Selection rank is calculated separately for each of the characteristics.

The integrated or complex rank comprises several forestry or other ranks calculated (when evaluating plantations) with allowance for the overall timber resources. Its value on the example of the characteristics of trees under study is determined according to the following formula:

$$R_c = R_y + R_{re} = \frac{Y_x \times d_{\bar{x}}}{Y_{\bar{x}} \times d_x} + \frac{Re_x \times d_{\bar{x}}}{Re_{\bar{x}} \times d_x} = \left(\frac{Y_x}{Y_{\bar{x}}} + \frac{Re_x}{Re_{\bar{x}}}\right) \times \frac{d_{\bar{x}}}{d_x} : 2,$$

where R_c—complex rank,

R_y— rank according to yield,

R_{re}— rank according to resin productivity,

$Y_x / Y_{\bar{x}}$ — relative yield,

$Re_x / Re_{\bar{x}}$ — relative resin productivity,

d— diameter for evaluating the trees (or m^3/ha for a plantation), and

x, $\bar{x}$ — partial and average values of characteristics.

The comprehensive assessment of trees or plantations in the above form takes into consideration only the favorable aspects of pine stands and is designed mainly for distinguishing their short-term (TIC) or long-term (FEC) exploitation by comparing the characteristics that determine the desirability of their felling (for timber) or retention (yield and resin productivity).

The principle of comprehensive evaluation of pine forests should reflect the entire gamut of their advantages, i.e. examining broadly and simultaneously all aspects. At present, because of the non-availability of quantitative indexes for several characteristics, for example ecological significance, such an assessment is difficult but nevertheless not impossible, if estimated (in balls) values are taken as the basis.

For example, when making the ecological evaluation of plantations (E), the quality of game resources (G), and overall index of the productivity of
193 medicinal-technical raw material (MT), the assessment assumes the following form:

$$R_c = \left[\left(\frac{E_x}{E_{\bar{x}}} + \frac{G_x}{G_{\bar{x}}} + \frac{MT_x}{MT_{\bar{x}}} + \frac{Y_x}{Y_{\bar{x}}} + \frac{Re_x}{Re_{\bar{x}}} + \ldots + \frac{N_x}{N_{\bar{x}}} \right) \times \frac{M^3_{\bar{x}}}{M^3_x} \right] : \; n,$$

where N is the successive index and n the total number.

The actual overall rank represents the sum of indexes of relative productivity of many characteristics with its correction for the reciprocal relation of timber mass of test and average plantation.

The rank thus arrived at represents the biological evaluation of the sumtotal of all the variable characteristics covered in the plan of calculation, systems of relations as well as the equivalent administrative factors. For purposes of management, it is possible to use the coefficients of 'preference' which strengthen a given index depending on the current context and the objective of forest exploitation. The application of such coefficients is quite a complex task since it may involve subjective treatment of some elements. In order to avoid it, a select or particularly high value of a given index may be considered. For example, if the relative productivity with respect to some index is maximum or minimum, an appropriate factor of 'preference', 1.5, 1.0 or 0.5 (or some other value) may be used. When an index, primarily genetic or ecological, is overassessed, the other factors may be ignored.

On the whole, the evaluation of plantations and trees should take into consideration the intra- and interpopulation variations of characteristics and appropriate criteria used (Table 82). The classification of selection and forestry categories of productivity is based on the extent of mean square deviation (sigma, σ) which, in the present case, has been taken as 1.

Plantations of rank less than $\bar{x} - 1\,\sigma$ are regarded as poorly productive (minus category, $\bar{x} - 1\,\sigma$ up to 1.0 as low (normally) and from 1.0 to $\bar{x} + \sigma$ as average (normally good), from $\bar{x} + 1\,\sigma$ to $\bar{x} + 2\,\sigma$ as high (good), and above

Table 82. Criteria for evaluation and selection of Siberian stone pine plantations and trees

Category of selection	$\bar{x} \pm \sigma$	Forestry category of relative productivity	Rank of selection for			Integrated rank of overall productivity	Type of complex	Forestry category according to forest groups	
			growth	yield	resin productivity			I	III
Plantations									
Minus	$< \bar{x} - \sigma$	Very low (1)	< 0.70	< 0.65	< 0.80	< 0.75	TIC	1	1–2
Normal	$\bar{x} - \sigma$	Low (2)	0.71–1.00	0.66 –1.00	0.80–1.00	0.76–1.00			
Normally good	$\bar{x} \pm \sigma$	Moderate (3)	1.01–1.30	1.01–1.35	1.01–1.20	1.01–1.25	FEC	2–4	3–4
Good	$\bar{x} + \sigma$ to $\bar{x} + 2\sigma$	High (4)	1.31–1.60	1.36–1.70	1.21–1.40	1.25–1.50			
Plus	$> \bar{x} + 2\sigma$	Very high (5)	>1.61	>1.71	>1.41	>1.51	SSC	5	5
Trees									
Minus	$< \bar{x} - \sigma$	Very low (1)	< 0.80	< 0.50	< 0.60	< 0.55	TIC	1	1–2
Normal	$\bar{x} - \sigma$	Low (2)	0.81–1.00	0.51–1.00	0.61–1.00	0.56–1.00			
Normally good	$\bar{x} \pm \sigma$	Moderate (3)	1.01–1.14	1.01–1.50	1.01–1.40	1.01–1.45	FEC	2–4	3–4
Good	$\bar{x} + \sigma$ to $x + 2.5\sigma$		High (4)	1.15 –1.75	1.51–2.25	1.41–2.00	1.46–2.12		
Plus	$> \bar{x} + 2.5\sigma$	Very high (5)	>1.76	>2.26	>2.01	>2.13	SSC	5	5

Note. The categorization of highly productive part of plantations and trees is based on the assessment of individual selection characteristics.

$\bar{x} + 2\sigma$ as very high (plus category). For trees in the last category, a criterion of 2.5 σ is possible because of the high variability of characteristics.

The limits of relative productivity for selection and integrated evaluation shown in Table 82 are approximate. They should be refined for a given case based on the actual mean square deviation.

The selection criteria for plantations and trees for comprehensive utilization established relative to a group and category of forests for organizing seed cultivation are few.

For short-term or tentative TIC in group I forests, mainly in the nut collection zone, only poorly productive pine trees are placed. Plantations of average productivity should be included in group III. Long-term exploitation 195 of good forests under FEC plan may be organized in plantations of average and high productivity group I forests and only in highly productive plantations in group III forests.

Seed selection base or the SSC type is formed from different types of seed sections as well as the plus category of plantations that have been recognized as genetic reserve for some or the other criterion. They are regarded as a category of forests (group I) having "scientific or historic importance".

The plantations are distributed according to the types of complexes as described below. It must be emphasized here that the groups of forests and types of complexes are more correctly established after their evaluation since the prevailing division of pine forests in many cases has not been carried out properly. According to the data of B.S. Spiridonov (1975), in Krasnoyarsk region, for example, most of the nut producing zones do not serve the purpose because of the predominance of high altitude pine forests, bald peaks, and subalpine meadows.

The evaluation of pine forests according to productivity should precede the marking out of protected sections, and later the selected stands. In the rest of sections, an overall rank is established for organizing the forest exploitation.

Evaluation for selection or the inventory of selected forests has so far not been prescribed as an essential recording procedure. In most cases, it is done by discussion of the management with the scientific subdivision which is managed by a single or, at best, two workers in a region. This work is sometimes carried out by the project organizations but largely routinely without methodical or organizational support. Good pine trees are sometimes felled which, according to the data of A.I. Iroshnikov (1975), not only theoretically depletes the genetic reserves of forests but in practice results in a significant loss of productivity of a newly organized plantation since the seeds from them are selected from stands of III and IV quality indexes.

In this context, the entire complex of measures for selection starting from the evaluation of characteristics is essential specially for Siberia, where the magnitude of forest felling is not commensurate with the rate and methods of the above discussed inventory preparation. In this respect, the marking out of plus category of plantations, not of plus category of trees, is particularly important which, for several reasons, has remained so far only as an object of experimental investigation and did not provide a basis for organizing the plantations on a commercial scale (Vorob'ev 1981).

Evaluation for selection should be made separately for the different levels (in the mountains) and subzones (on the plains) within the corresponding age limits—black soil subbelt and southern subzone (121–240 years),
196 mountain-taiga and central subzones (141–200 years), and subalpine and northern subzones (161–240 years). The priority and desirability of preparing the inventory of selected forests should be made conforming to these principles. Plantations of different quality classes are best grouped within the above subbelts and subzones as follows: I–II (III), III(IV), and IV–V.

This evaluation is carried out in three stages.

When preparing the inventory in the field at the time of organizing the forests (not below II order), sections that are significantly outstanding in the above features from the average plantations are identified and more accurately assessed; examples of good stands are included in the plan of model assessment; this stage concludes with compiling a preliminary list of sections that are useful for selection.

In the office, based on physical descriptions of sections and ancillary records of the pattern of growth, yield, and resin productivity, the productivity of plantations according to the different characteristics is determined and, later, on the basis of selection criteria, sections valuable for selection are identified and their location plans compiled.

Field inspections of selected sections are repeated by the specialist groups of "Soyuzgiproleskhoz" (Central Institute of Commercial Forestry) partly by the scientific-industrial groups of the forestry board and scientific organizations and finalize the list of selected plantations, drafting the documents, and suggestions for transforming these sections into the appropriate categories of forests.

The sequence of work organization in the last, vital, stage of making the inventory of selected forests can be as follows.

Since the plus category of plantations is identified on the basis of rank-wise comparison of a given characteristic with the average value for the test series and also the proportion of the plus category of trees, these problems can be resolved by organizing standard test plots.

In the calculations, the pine trees are subdivided according to their major characteristics into plus, good, normally good, normal, and minus categories. The basis for classification is the deviation of the value of average tree from that of the selected value (see Table 82) or the actual gradation of relative productivity as well as the additional supporting data for plus category of trees with respect to this characteristic.

The value for selection of a body is established from the proportion of participating plus category of trees, more often not more than 3%, and also a comparison of the overall productivity of plus and average categories of plantations of the corresponding ranks.

Special attention is paid to the selection of average category of plantations. Their preliminary characteristics are established based on a study of the physical data for plantations that are as similar as possible. The test plots in average category of plantations should be formed and documented to serve as control for selecting the plus category of sections. 197

When selecting the plus category of trees by 'free exploration' (on foot), the operational sequence changes: test plots are formed around the probable trees of such category and the rest of operations are the same.

The selection of trees according to the characteristics under study has its own special features and hence should be studied individually.

Growth. The evaluation and selection of plus category of plantations and trees for accelerated growth of quality timber conform to the well-known premises.

In making an inventory of forests in the first as well as later stages, special and progressive attention is paid to plantations of I, II, III quality classes with high reserves of pine timber of relatively pure composition and high density, free of brushwood, predominance of spruce-like form of crown, and ancillary features as recommended in the “Guide for Selection ...” (1972) when evaluating trees according to growth and development.

Plantations and trees are evaluated for this characteristic taking productivity into consideration, i.e. by back comparison with the selection rank of timber mass and cone yield. Attention is further drawn to the age and quality of the stand since plantations with a poor cone yield but good reserves of timber may have an anomalously high rank of phenotypic state and are liable for elimination as not promising in the plan of long-term comprehensive utilization.

The criteria of the characteristic exceeding the average value are established with due consideration of the level of variability. According to the prevailing recommendations, the values should be regarded as exceeding at 20–30% higher diameter, 10–15% greater height, 35–70% broader extent of live crown, 20% more of brushwood-free zone, and 15–20% greater cross-section of upper portion of crown (Demidenko, Il’ichev, and Urusov 1979).

When looking for plus category of trees on foot, attention is paid to the characteristics of good growth (radial): few cleavages on the bark, predominance of whitish shade on it, and the less-branched and low crown.

The probable trees for plus category are inspected visually for the characteristics of female shoots for yield so to select clean timber, quite free from branches, fast-growing, but less productive forms.

Productivity. Visual and quantitative indexes are used for evaluating this feature.

The visual characteristics is based on a description of the cone-bearing (upper) part of the crown of trees (Vorob'ev 1974). In its assessment, age, genotypic, and phenotypic characteristics of crown formation of Siberian stone pine and Korean pine trees are taken into consideration (Pravdin 1964
198 and Izmodenov 1972). Summary characteristics of crown are thus obtained facilitating a preliminary evaluation of the productivity of trees (Table 83). Apart from the three main categories (in balls), a zero ball category has been provided for barren trees and 4 ball category for high yielding, potentially plus category of trees. The proportions of these categories are determined, when required, by combining the form and density of the upper part of the crown.

The productive category on the ball scale is recorded for each tree when exploring for plus category of specimens. A similar assessment is used for marking trees for selective felling. In this case, as well be demonstrated later, several other factors which provide an overall comprehensive evaluation are taken into consideration.

During inspection tours of plantations in the period of organizing the forest or the game facilities or performing special tasks for listing of selected forests, the general yield of the plantation in balls is established based on the dominant form of the cone-bearing portion of the crown for the stand as a whole:

ball 1—more than 3/4 of trees with narrow-cylindrical spruce-like sparse crowns,

ball 2—ratio of different crown types equal, and

ball 3—more than 3/4 of trees with chandelior-type well-developed dense crown tops.

This system proposed by I.V. Semechkin (Semechkin and Vorob'ev 1980) is integrated in the record of physical features and used later for more precisely calculating the productivity of forest sections and for drawing up appropriate tables.

When selecting plantations for a given objective, productivity in balls is compared with the timber reserve using the nomogram shown in Fig. 51. Plantations approaching selection class '4' of productivity and reserves of
199 pine timber are marked as probables for the plus category and studied by quantitative methods. With allowance for their overall timber resources, the rest are classified into the other economic types and appropriate methods for felling are identified.

Table 83. Scale in balls for evaluating the yield of trees (compiled by A.I. Iroshnikov and V.N. Vorob'ev)

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Scale in balls	Overall evaluation of cone-bearing portion of crown	Shape	Crown size		Fullness of central cone-bearing shoots and needles content (density index as % of gaps)
			extent, %	cross-section, m	number of shoots
1	Poor (weakly formed or aging)	Sharply conical or distorted obconical asymmetric (spruce-like)	Varying	Varying, below center	Sparse (above 50)
2	Moderate	Sharply ovoid, chandelier-shaped (intermediate)	25	Up to 4, at center	Up to 30 Moderate (15–50)
3	Good (very good)	Chandelier-shaped (pine-shaped)	30–50	Above 4, above center	30–100 Dense (up to 15)
					Over 100

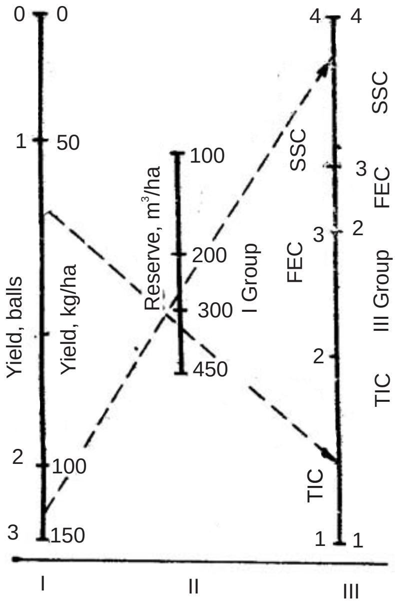

Fig. 51. Nomogram for integrated evaluation and selection of Siberian stone pine plantations: I—average yield of nuts, II—timber reserves, III—selection according to the category of overall productivity; 1 (low)—timber complex (total felling of forest), 2 (moderate)—forestry complex (partial forest maintenance), 3 (high)—forestry complex (selective felling for comprehensive utilization), and 4—probables for the plus category of plantations.

The quantitative evaluation of yield is based on counting the traces of fallen cones as described earlier (see Chapter II). While evaluating the overall yield of trees, all the cone-bearing shoots are taken into consideration for compiling the tables; when selecting the plus category of trees, only a certain number of ideal branches are considered (Nekrasov 1963). For arriving at the weight characteristics of the crop, 10 cones of the accounting year are selected randomly and the weight of seeds determined in the model trees and areas (kg/ha). As a result, the average yield characteristics for a 10-year period are ascertained (average number of cones and weight of seeds per tree as well as the number of cones on shoot, an index which describes the reproductive energy and dynamics).

In test plots, in preselected plantations or around the probable plus category of trees detected by 'free' exploration, the yield of all the trees is recalculated and presented in balls. These values for the selected tree and five average trees are compared with their radial growth used the nomogram shown in Fig. 52 which, like that for the plantation, is designed for selection and forestry functions.

When the preliminary assessment is confirmed, the yield is more accurately determined for all trees directly in their crowns by the method of

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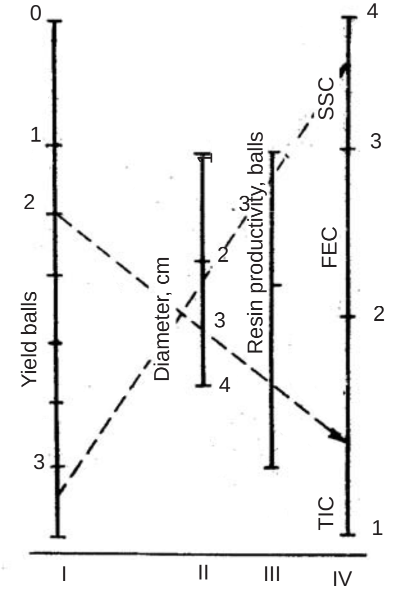

Fig. 52. Nomogram for integrated evaluation and selection of Siberian stone pine trees (in balls):
I—yield, II—diameter, III—resin productivity, and IV—selection according to categories of integrated productivity: 1 (low)—felling, 2 and 3 (moderate and high)—integrated utilization, and 4 (very high yield class)—probables for plus category of trees.

thorough counting of cones in the current and winter crops on all the cone-
200 bearing shoots, the traces for the past 10 years on 10 central skeletal branches.

Cone yield is calculated in the latter half of summer in a year of moderate yield or exceeding it. The average yield for two accounting years is determined from the total number of maturing and winter cones in the crown. This work is done at first on average model trees to get an idea of the general picture of cone-bearing shoots and method of calculating the cone traces and later repeated for probables for the plus category of trees. Simultaneously, the weight of seeds in an average cone is established in the plus and average categories of trees.

The rank of plus category of trees is calculated according to the following formula:

$$\frac{(\mathrm{Co}^{2}_{\mathrm{cr}} \times \mathrm{Co}^{10}_{\mathrm{mod}})^{+} \times (\mathrm{Co}^{2}_{\mathrm{mod}} \times g)^{x} \times d_{x}}{(\mathrm{Co}^{2}_{\mathrm{mod}} \times g)^{+} \times (\mathrm{Co}^{2}_{\mathrm{cr}} \times \mathrm{Co}^{10}_{\mathrm{mod}})^{x} \times d_{+}},$$

where

Co^{2}_{cr} —average number of cones in the crown in two successive years,

201 Co^{2}_{mod} —the same for 10 model shoots,

Co^{10}_{mod} —the same for 10 model shoots for 10 years,

g—average weight of seeds in the cone, g,

d—diameter of trees, cm,

+—plus category of trees, and

x—average tree.

The above criteria are used for evaluating the plus category of trees. Indexes of average number of cones per tree and per cm diameter (see Chapter II, Table 24) can be used as approximate data for pine forests on mountains.

Based on the results of counts of cone traces on ideal shoots, two most important indexes of independent importance are determined.

The first of these is the reproductive energy of shoots (number of cones per shoot). The selection and use of cuttings from shoots with high reproductive energy is one of the methods for enhancing the yield of grafted plantations. The criterion for selecting the shape using this characteristic is the average reproductive energy of shoots of more than 1.7 over 10 years (30% above average).

The second characteristic is the crop dynamics determined from the coefficient of variation of the index of reproductive energy. The selection criterion for stable cone yielding forms is less than 25%.

Resin productivity. Visual and theoretical indexes are used for evaluating this characteristic too.

Visual evaluation of resin productivity compiled with due consideration of the work of V.E. Kulakov (1979) is made predominantly for purposes of integrated management as its relation with morphological factors is moderate, as discussed in Chapter III, and characterizes mainly the suitability of trees for different methods of tapping within the plantation (Table 84).

202 The selection of the tapping method conforms to the assessed values of other indexes and is made in accordance with the nomogram for selecting trees for comprehensive utilization (see Fig. 52).

When making an inventory of selected plantations, the scale of resin productivity is used for preliminary evaluation, mainly established by the direct index (yield of galipot). Further, specific, biological, and technological resin productivities of trees and plantations are distinguished.

The yield of galipot recovered from a minimum standard cut (g/cm of renewal) is adopted as the unit of specific resin productivity of Siberian

201 Table 84. Scale of evaluation (in balls) of resin productivity of trees (compiled by V.E. Kulakov and V.N. Vorob'ev)

Description of trees	Ball (category)
Promising for long-term tapping, well-developed (up to 30 cm in diam.) trees	0 (unsuitable for tapping)
Poorly developed trees, suitable for felling in the first instance depending on the state of cone yield, of any age and diameter suitable for tapping	1 (can be used for short-term tapping)
Trees of moderate vitality and development (more than 30 cm) with normal crown	2 (suitable for long-term and short-term tapping)
Most developed, over 30 cm, with good growth, clean trunk (3 m), and generally dense crown	3 (suitable for long-term tapping)

stone pine trees according to the suggestion of V.E. Kulakov (1973) and Yu.N. Il'ichev (1979). A microcut 10 cm long made 1–3 times in a season (June 15 to Aug. 15) on the debarked surface of trunk (15 × 20 cm) is regarded as the standard cut. The specific resin productivity of plantations is determined in a sample of 35–40 trees. Before cuts, the trees are numbered, their bark removed on the same side, and fitted with a weighed resin collector. The galipot yield is checked after seven days and calculated per cm of cut length. The resin productivity of each tree is determined and later the average value calculated for the plantation.

The specific resin productivity characterizes the intensity of resin formation and exudation of the tree and is used as a primary characteristic of resin productivity forms and is the basic criterion for determining the resin productivity of trees in a plantation.

The biological and technological resin productivities of plantations are established based on the physical description of the section and the corresponding data of specific resin productivity of trees recorded during forest organization or special project operations carried out to draw tables of resin productivity.

The biological resin productivity of trees and plantations is a nominal summary index reflecting the potential yield of galipot during identical minimum cuts on the trunk. The evaluation of the biological resin productivity of trees includes: specific resin productivity (g/renewed hole), one renewal in a season, nominal opening of hole 100%, coefficient of conversion for the breadth of hole 1.25, covering the total circumference of trunk. The number of trees suitable for tapping and their diameter is determined from the assessed biological resin productivity of the plantation.

The technological resin productivity may vary depending on the method of tapping. Its evaluation is facilitated by the availability of the table of biological resin productivity of the plantation of the type compiled by the author from the data of V.E. Kulakov (Mishukov and Kulakov 1970, Il'ichev and Kulakov 1977, and others) (Table 85). The table shows the biological resin productivity of an actual division according to the physical characteristics. For the value of 10-year tapping as required in the timber 203 complex before complete felling, its value is multiplied by a constant coefficient of 7.2 which gives the anticipated yield per year. When combining 5- and 20-year tapping within the plantation for stands for felling and retention, corrections of 6.8 and 2.0 are made to the biological resin productivity. The number of trees for a given type of tapping is determined as a percentage of the ratio to the diameter of average tree in the plantation.

When tables are not available, biological and later even the technological resin productivity of plantations is determined from the specific resin productivity and physical description. On the whole, the compilation of resin productivity tables for organizing tapping and forest management is necessary for Siberian stone pine for many areas. For Scotch pine, such tables are available, for example, for the European North (Sukhanov 1977).

The evaluation and selection of plus category of plantations for resin productivity are made according to the above principles.

When organizing the forest or verifying the objects identified before, attention is mainly paid to the relatively pure pine stands distinguished by high timber resources, larger number of trees free from branches and diameter more than 24–28 cm (above 100/ha) with spruce-like and moderately developed chandelier-type crown shape. In the tapping regions, stands are considered that have existed for 1–5 years and characterized by high yield of galipot per hole and per unit area when adopting appropriate technology. Such sections are inspected more thoroughly and when the required selection indexes and the general conditions are good, they are withdrawn from tapping and marked as of plus category of plantations. The evaluation of resin productivity on a ball scale serves as a basis for the preliminary evaluation of plantations with respect to this feature.

The plantations are assessed theoretically from the quantitative indexes of biological or average specific resin productivity. When selecting good plantations by any method, the coefficient of resin productivity (CR) is adopted as the basis. The CR is calculated from the rank of selection with allowance for the growth indexes of trees and plantations. The general criteria of selection conform to the above premises. The values of specific (see Table 27) and biological (see Table 85) resin productivity of plantations may be taken into consideration as basic average values. The data of Yu.N. Il'ichev (1979) provide some support in this respect. He proposed classifying the plantations and trees in the selection categories according to the following

204 Table 85. Biological resin productivity of Siberian stone pine plantations of Gornyi Altay, kg/ha

Age, years	Pine proportion in composition	Black soil						Mountain taiga					
		Fern-tall grass						Green moss					
		II			III			II			III		
		1.0–0.9	0.8–0.7	0.6–0.5	1.0–0.9	0.8–0.7	0.6–0.5	1.0–0.9	0.8–0.7	0.6–0.5	0.1–0.9	0.8–0.7	0.6–0.5
121–160	10–9	20.4	16.8	13.0	14.9	11.0	8.5	21.6	17.7	13.8	12.8	10.5	8.1
	8–7	16.2	13.2	10.3	11.7	8.7	6.7	17.1	14.0	10.9	10.1	8.3	6.4
	6–5	11.9	9.7	7.5	8.6	6.4	4.9	12.5	10.2	8.0	7.4	6.1	4.7
	3–4	7.6	6.2	4.8	5.5	4.0	3.1	8.0	5.5	5.1	4.7	3.9	3.0
161–200	10–9	21.6	17.6	13.8	17.0	14.0	10.8	18.6	15.2	11.9	16.5	13.5	10.4
	8–7	17.1	13.9	10.9	13.4	11.0	8.5	14.6	12.0	9.4	13.0	10.7	8.2
	6–5	12.5	10.2	8.0	10.0	8.1	6.2	10.7	8.8	6.9	9.5	7.8	6.0
	4–3	8.0	6.5	5.1	6.3	5.1	4.0	6.8	5.6	4.4	6.1	5.0	3.8
201–240	10–9	17.2	14.3	10.8	16.5	13.6	10.5	12.3	10.1	7.6	15.9	13.1	10.2
	8–7	13.6	11.3	8.5	13.0	10.7	8.3	9.7	8.0	6.1	12.6	10.3	8.0
	6–5	10.0	8.3	6.3	9.6	7.8	6.1	7.1	5.8	4.4	9.2	7.6	5.9
	4–3	6.3	5.3	4.0	6.1	5.0	3.9	4.5	3.7	2.8	5.9	4.8	3.8
241–281	10–9	12.2	10.0	7.8	12.6	10.4	8.0	9.8	8.0	6.2	11.9	9.8	7.6
	8–7	9.7	7.9	6.2	9.9	8.2	6.4	7.7	6.3	4.9	9.4	7.8	6.0
	6–5	7.1	5.8	4.5	7.3	6.0	4.6	5.7	4.6	3.6	6.9	5.7	4.4
	3–4	4.5	3.7	2.9	4.6	3.8	3.0	3.6	3.0	2.3	4.4	3.6	2.8

values of resin productivity (g/cm of renewed cut): minus, up to 4.0; normal, 4.1–6.0; good 6.1–8.0, and plus, above 8.1.

The search for plus category of trees among untapped plantations is made by laying test plots, separating the stand into selection categories, followed by the determination and comparison of quantitative indexes of resin productivity of average model trees and those that hold promise as 204
genetic reserves. The primary object for their search is the tapping section. Trees known to tappers as 'outstanding' are investigated, their galipot yield compared with that of average trees in that group by evaluating in balls its volume in the container (Vink 1973) or by weighing directly. When the result is double that or more than the average and the condition of the crown, more particularly the quality of seeds, is good (Vorob’ev 1974a), such trees are withdrawn from tapping and marked as of plus category. By subsequently felling the stand around the plus category of trees, an oval-shaped protective zone of approximate radius 25 m is formed and stalked in the field as well as on the technological map of felling.

Broad grass						Bergenia			Reed grass		
II			III			III			III		
1.0–0.9	0.8–0.7	0.6–0.5	1.0–0.9	0.8–0.7	0.6–0.5	1.0–0.9	0.8–0.7	0.6–0.5	1.0–0.9	0.8–0.7	0.6–0.5
18.5	15.1	11.8	13.7	11.2	8.6	10.0	8.2	6.3	13.2	10.9	8.4
14.6	11.9	9.3	10.8	8.8	6.8	7.9	5.5	5.0	10.4	8.6	6.6
10.7	8.7	6.8	7.9	6.5	5.0	5.8	4.8	3.6	7.6	6.3	4.9
6.8	5.6	4.3	5.1	4.1	3.2	3.7	3.0	2.3	4.9	4.0	3.1
22.1	18.0	14.0	16.7	13.6	10.5	10.8	9.0	6.9	16.5	13.5	10.5
17.4	14.2	11.1	13.2	10.8	8.3	8.5	7.1	5.4	13.0	10.7	8.3
12.8	10.4	8.1	9.6	7.9	6.1	6.3	5.2	4.0	9.5	7.8	6.1
8.1	6.6	5.2	6.1	5.0	3.9	4.0	3.3	2.5	6.1	5.0	3.8
21.7	18.0	13.6	17.3	14.2	11.0	12.4	10.3	7.9	15.3	12.6	9.8
17.1	14.2	10.8	13.7	11.2	8.7	9.8	8.1	6.2	12.1	9.9	7.8
12.6	10.4	7.9	10.0	8.2	6.4	7.2	5.9	4.6	8.9	7.3	5.7
8.0	6.6	5.0	6.4	5.2	4.1	4.6	3.8	2.9	5.6	4.6	3.6
16.6	13.6	10.6	15.4	12.7	9.8	12.0	10.0	7.8	10.0	8.2	6.4
13.1	10.7	8.4	12.2	10.0	7.8	9.5	7.9	6.1	7.9	6.5	5.1
9.6	7.9	6.2	8.9	7.3	5.7	7.0	5.8	4.5	5.8	4.8	3.7
6.1	5.0	3.9	5.7	4.7	3.6	4.4	3.7	2.9	3.7	3.0	2.4

The *comprehensive evaluation* of plantations and trees is made with the above objectives, principles, methods, and criteria.

During inventory of selected forests which represents a component of comprehensive characteristics, their evaluation based on economically important characteristics is made in stages—during inventory preparation, planning, and exploitation of the plantation in between the reviews.

The primary evaluation is based on the standard physical description of the sections taking into consideration the yield in balls of plantations and preliminary indication of the type of their comprehensive exploitation.

The basic evaluation is made theoretically. The general procedure for Siberian stone pine forests on mountains can be drawn into a rough computer
205 program as follows:

a) the entire forest is divided into three sections according to the altitude of complexes and their corresponding classes of productivity: black soil, mountain-taiga, and subalpine subzone under bald peaks
(criterion of evaluation and selection—group of quality classes);

b) within each subzone, the overall variation series of sections containing Siberian stone pine are compiled
(criterion—composition);

c) plantations unsuitable, because of their age (up to 120 years), for commercial exploitation or not meeting the appropriate comprehensive and selection assessments are eliminated from each series (plantations older than 241 years are also not considered for selection assessment)
(criterion—age class);

d) statistical indexes of physical assessment and comprehensive (after preliminary investigation by independent methods) characteristics are derived from each series
(program—statistics);

e) from the initial series, sections are evaluated for selection taking into consideration the set of characteristics, criteria, and the sequence of their selection in the subzones, and a record of the most valuable portion of plantations and forest categories of scientific or historic importance is prepared
(criterion—selection ranks for each of the characteristics);

f) the entire series of subalpine forests and those under bald peaks and all 206 other plantations placed in the protected category of 'subalpine forest' comprising a significant proportion of the protected complex and representing at the same time an independent game section (including the preparation of medicinal-technical plant raw material); from among the complex evaluation, only the overall yield of the plantation is determined here
(criteria—group of quality classes, altitude, expert ecological evaluation);

g) in the series of black soil and mountain-taiga subzones, a complex evaluation of sections (based on complex rank) is made and they are classified into productivity categories—“very low”, “low”, “moderate”, “high”, and “very high” (plantations preliminarily classified as of high selection rank hold their priority in this evaluation and remain in the corresponding category)
(category—complex rank);

h) from the series of black soil and mountain-taiga subzones, sections with characteristics of protection types are excluded and placed in the protected category
(criteria—norms of distinguishing protected categories of sections and expert ecological evaluations);

i) based on the complex evaluation of plantations, they are classified into groups of forests, operational and nut producing zone, and the form of management is determined. For these purposes:

— regional "blocks" are formed according to freight flow at the level of river basins of 4th–5th categories (assuming for example Ob′ river as of 1st category)
(criterion—freight flow characteristics);

— within the "blocks", two groups of areas are compared: first, plantations valuable for selection and categories of "high" and "very high" overall productivity; second, of "very low" and "low" productivity and plantations of other species; when the first group is predominant, the area is regarded as a nut producing zone and the rest as group III of forests;

— predominance of the areas of one or the other "blocks" determines the main form of the complex: forests of nut producing zone—forest combine and group III—timber industry
(criterion—proportion of the areas of good Siberian stone pine plantations); and

j) plantations suitable for comprehensive utilization are grouped into a series within each block and later within the organization into basic types of management (FEC and TIC), including plantations of other species) according to the group of forests also determined simultaneously (the preceding operation is skipped when the groups of forests have already been identified). The identified FEC and TIC series in the nut producing zone and separately in group III forests serve as the basis for working out utilization and subsequent economic activity (taking into 205 consideration the other categories of forests classified into appropriate complexes)
(criterion—forest groups).

Based on the data of selection and complex evaluation of forests, the following charts can be drawn:

— chart of types of complexes with different selection sections colored,

— chart of yield of Siberian stone pine plantations colored according to the economic classes of yield: first, up to 25; second, 26–50; and third, above 51 kg/ha, showing sections accessible for nut collection; and

— chart of resin productivity with classes of biological resin productivity colored: first, up to 5; second, 5.1–15.0; and third, above 15.1 kg/ha, showing tapping sections classified according to the anticipated yield of galipot after separating the forest sections into TIC and FEC (examples of such charts are shown later).

The limits of yield and resin productivity classes are rendered precise when setting up the actual systems. Based on the productivity charts, the nut producing base is formed and nut collection organized. The chart of biological resin productivity serves as a base for locating current and prospective tapping operations. On the whole, the entire data of complex evaluation of pine forests serve as the basis for planning and subsequent management of diverse economic activities. The suggested approach based partly on the potential possibilities of pine forests corresponds to the modern practice of forest organization for comprehensive utilization of resources (Polyakov and Kanunnikov 1975, Antsukevich 1976, and Semechkin and Vorob'ev 1980).

When directly organizing the operations during reviews, the complex evaluation of plantations is used for more accurately assigning the sections to different types of complexes and also for identifying the forest sections for felling.

For this purpose, the nomogram of comprehensive utilization of plantations discussed before (see Fig. 51) is used. Stands with yield of 1 ball are marked for thorough felling, those of 2 balls for felling in due course, and of 3 balls in the selective felling category. The selection of the type of exploitation of a given section and the method of felling are identified more accurately by comparing the yield with the overall timber reserves on the principle that the higher the reserves and lower the yield of a plantation, the greater is the justification for its short-term utilization. When assigning a stand for selective felling, the marking of trees for felling is done on the basis of complex evaluation of their characteristics, primarily their yield.

Before covering the entire felling area is a plantation, a strip sample of up to 200 trees in a hectare is formed for understanding the structure of the stand and determining the optimum extent of first felling. The characteristics of the crown and the usefulness of trees for any method of tapping are examined using the scales for evaluating the characteristics given above and 208 the nomogram for selection. The parameters of an average tree are used as a reference for all the indexes.

A list is prepared according to the thickness stages and three grades (balls) of yield, showing in the numerator the trees that are left unaffected and, in the denominator, those marked for felling. Trees are marked for felling by visual inspection by comparing the grade (ball) of yield and diameter (see Fig. 52). Low-yielding trees and those unsuitable for prolonged tapping marked 1 on the ball scale are earmarked for felling in the first instance (ball of selection 1). In case felling falls in the tapping sections, oppressed trees with few "nutrient belts" are first felled.

Trees of 2 balls category are distinguished by the above principle: the lower the yield (1 or 2 balls) and greater the diameter (3 or 4 balls), the greater is the desirability for felling. The unsuitability of such trees for prolonged use and the possibility of their removal from the stand without affecting the density of the canopy determines the selection in favor of 1 ball category. The rest of trees of 2 balls class are retained unchanged in group 3 which includes trees that are most productive and suitable for prolonged tapping. Trees of 0 ball class, with good condition and growth prospects are saved and the rest felled. Trees of 4 balls category are inspected for plus categorization by the above method.

Data for felling are analyzed by the main forest organization taking into consideration the recommended felling technology, minimum loss of yield (not more than 20% of weighted mean value of evaluation in balls) and retaining an adequate number of trees that are productive and suitable for long-term tapping (not less than 70/ha of 30 cm stage) while maintaining the optimum density of the stand (0.5) and extracting an economically adequate quantity of timber (not more than 80 m^3/ha in the case of Siberian
209 stone pine) and determine the actual percentage of the first lot for felling. The entire timber felling is carried out as decided after correcting the preliminary selection either way.

Marking the trees for felling based on complex evaluation improves the structure of the stand as a whole and, compared with the selection of trees based on diameter, reduces the loss of yield of felled section by half. The results of selective commercial felling in Gornyi Altay Experimental Forest Combine led to the same conclusion (Fig. 53). This aspect will be discussed later in greater detail. On the whole, the selection of trees individually for felling conforms to the general trend of tackling this problem in other regions and with other species (Konovalov 1971 and Danilik and Isaeva 1972).

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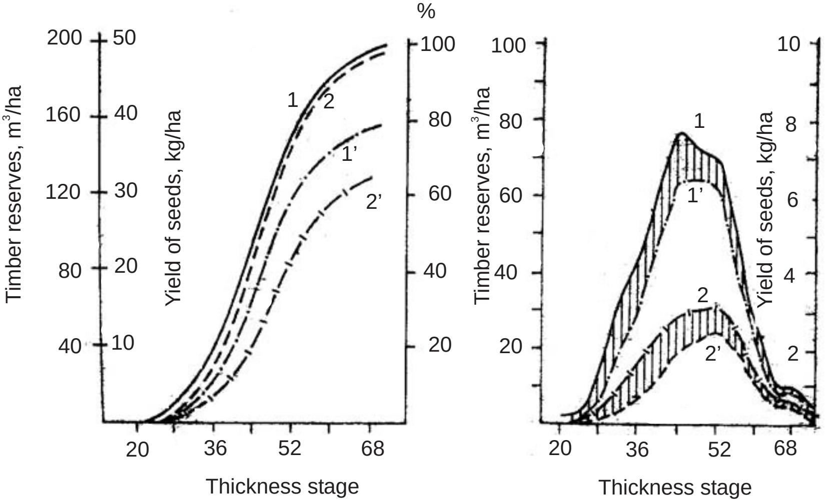

Fig. 53. Course of accumulation (left) of overall yield (1) and timber reserves (2) and the structure of their distribution (right) according to thickness stages before and after selective felling (1′ and 2′).

Examples of Comprehensive Utilization

Concepts on the nature of relations between the indexes of the main products of pine forests as well as the recommendations for their evaluation and exploitation distinguish examples of actual combination of elements and types of complex at three levels—within the stand, within the "block" of the plantation, and within the entire organization. It is further intended to demonstrate the characteristics of complex management in both the pine forests in general and the nut producing zones.

The data for calculations on product yield and approximate techno-economic indexes have been studied from the example of Gornyi Altay Experimental Forest Combine for Comprehensive Utilization of Taiga Pine Forests, the base unit of the Ministry of Forestry, Russian Soviet Federative Socialist Republic (RSFSR), and Institute of Forests and Timber, Siberian Division, Academy of Sciences, USSR.

Combination of the elements of complex within the plantation (FEC). The experimental section with a combination of the elements of the complex within the plantation (36 ha) was laid in 1973 in Kochesh area of Pyzha taiga of Gornyi Altay (Vorob'ev, Saeta, and Kulikov 1978). It practiced five-year intense tapping of stand marked for first felling and 20-year long-term tapping of remaining trees (commenced by V.E. Kulakov), selective felling of different intensities reviewed at 40-year intervals, and preparation of berries and nuts. The base indexes of the experimental section for the period of its best functioning (1971–1973) were adopted as the basis for evaluating the economic efficiency of combining the elements of the complex (Saeta 1971 and Parfenov 1979). In the recent years, the working plan was modified for several subjective as well as objective reasons. Although aware of the current and projected changes of prices of various products, the original level of calculations was maintained since they were related not with the overall techno-economic base of the organization forming a part of the problem for the special project and implemented at the "Soyuzgiproleskhoz" (Central
210 Institute of Commercial Forestry) but with a relative comparison of the different combinations of the elements of the complex at the level of similar production indexes.

The plantations in the experimental section consist of three divisions representing typological subclasses of central taiga pine forests. Conforming to the plan of age structure, these have been classified as of same age, approximately same age, approximately different ages, and different ages (Semechkin 1971). The characteristics of stands show that the trees belong to different types of age structure (Table 86).

Section 1. Plantation with predominance of pine, average age 185 years, main proportion in the stand comprises trees of III (181–220 years) and IV (141–180 years) generations, forming 78% of reserve. On the whole, the stand

211 Table 86. Assessed physical characteristics of stands in the test section

Level	Composition of generation	Area of section, m^2/ha	Density	Species	Age, years	Height, m	Diameter, cm	Reserves, m^3/ha
Section 1, Test Plot 1								
1	$2P_{II}$	19.7	0.46	P_{II}	230	28	49	40
	$5P_{III}$			P_{III}	195	25	35	91
	$2P_{IV}$			P_{IV}	165	22	24	56
	1S			S	110	22	24	35
2	7B	3.8	0.14	B	90	21	22	16
	3F			F	100	19	21	5
	$+P_{IV}$			P	120	17	16	0
	Total	23.5	0.60		188*	23*	30*	243
Section 2, Test Plot 2								
1	$7P_{I}$	16.5	0.30	P_{I}	275	33	60	157
	$3P_{II}$			P_{II}	240	32	56	65
	$7P_{III}$			P_{III}	195	26	33	77
2	$3P_{IV}$	8.9	0.18	P_{IV}	160	23	24	29
	7F			F	90	20	19	56
3	3S	8.6	0.26	S	110	21	26	27
	B			B	70	18	18	4
	Stray F			P_{V}	120	21	19	2
	Total	34.0	0.74		207*	27*	38*	417
Section 3, Test Plot 3								
1	$8P_{I}$	26.3	0.56	P_{I}	277	30	49	257
	$2P_{II}$			P_{II}	246	30	42	57
2	$5P_{III}$	3.0	0.08	P_{III}	205	25	29	33
	3S			S	110	23	25	22
	2F			F	90	22	21	12
	Stray P_{IV}			P_{IV}	163	20	20	1
	Stray B			B	60	16	16	1
	Total	29.3	0.64		253*	29*	43*	383

*Average values given for pine.

P—pine, S—spruce, B—birch, and F—fir.

is quite dense with trees which do not have much prospect for further growth. Due to their insignificant diameter, the overall felling in the plantation does not exceed 30%. Based on complex evaluation, the removal of 45% of

II generation trees has been recommended. The overall yield is moderate. The removal of poor cone-bearing trees would involve only an 8% loss of commercial nuts (Table 87).

Before felling, tapping of selected sections of plantations yielded 15 kg/ha and rest 20 kg/ha galipot in a season during 1974 to 1977. Timber recovery under these conditions was insignificant: within 60 m^3/ha of pine, about 80 m^3/ha including some spruce and fir. The initial density dropped to 0.4 and, considering only the trees with poorly developed female shoots that have been removed, the crown density dropped below the optimum, i.e. 0.5.

Selective felling in such stands permits the remaining more productive trees access to a significantly larger area of aerial space and root nutrition, a very important condition in the rather thin mountain soils and promotes the growth of cone-bearing part of the crown. In the present example, the low percentage of felling for timber is best compensated by a greater removal from plantations of section 2. A similar conclusion emerges from an analysis of the economic efficiency of combining the different elements of complex within these stands (Table 88).

These calculations show that the profit essentially is from galipot and nut production in section 1. The proportion of profit from the initial timber recovery was insignificant (around 25%) or its processing may even be unprofitable. This becomes particularly evident when the timber has to be hauled over a long distance to the depot below, which increases the overall cost of timber processing for some or the other reason. At such a cost of production and the expenses involved, as experienced before by the Gorno-Altay Experimental Production Combine, selective management in a part of the pine forests of the type of section 1, and specially of type 2, may be economically justified.

211 *Section 2.* Plantations in this section fall in the watershed area of the slope. The upper level consisting of I generation (over 260 years) is considerably sparse due to windfall and, moreover, are quite aged. Deadwood 215 is covered with moss, timber is mostly decomposed. In the number of trees, the first level comprises 30% and, in reserves, about 50% (see Table 86). The average diameter of this level is high, though on average not more than 40 cm since the plantation has many trees whose age is under 200 years. The sizes and state of the second level suggest a good replacement of the main generation. Under these conditions, thinning by eliminating trees with damaged crown with yield of 1 ball would be advantageous.

The original assessment of yield from this stand shows that thick trees of I generation bear an average of 37 cones and of II generation 60 cones. Trees yielding 28 cones or less are marked for selective felling, leaving trees of I generation yielding an average of 92 cones a year.

212 & 213 Table 87. Complex evaluation of stands in the test section (before first felling and thereafter)

Pine generation	No. of trees		Average diameter, cm	Total area of section, m^2/ha	Timber		Nuts				Galipot	
	No./ha	%			m^3/ha	%	Cones '000/ha	Cones %	Cone producing trees, No./ha	Cones/tree	Tapped trees, No./ha	In season, kg/ha
1	2	3	4	5	6	7	8	9	10	11	12	13
Section 1, Test Plot 1 Original Stand												
II	16	8	49	3.2	40	22	0.4	11	15	25	16	—
III	76	37	35	7.7	91	48	2.2	65	73	30	73	—
IV	107	53	24	5.2	56	30	0.8	24	36	21	54	—
V	5	2	16	0.1	0	0	0	0	0	0	0	—
Total	204	100	30	15.2	187	100	3.4	100	124	26	143	—
Selected Part												
II	9	54	44	1.4	18	45	0.2	36	8	19	8	—
III	16	21	29	1.1	13	14	0.2	8	13	14	13	—
IV	58	53	22	2.4	25	45	0.1	14	9	12	30	—
V	1	20	16	0.1	0	25	0	0	0	0	0	—
Total	84	41*	26	5.0	56	30*	0.5	12*	29	15	51	15
Part Left Out												
II	10	6	54	1.7	22	17	0.2	8	8	29	8	—
III	60	49	36	6.5	78	60	2.0	66	60	32	60	—
IV	50	41	26	2.8	30	23	0.7	26	28	23	24	—
Total	120	100	32	11.0	131	100	2.9	100	95	30	92	20
Section 2, Test Plot 2 Original Stand												
I	39	21	60	11.6	157	48	1.5	41	39	37	40	—
II	19	10	56	4.8	65	20	1.1	32	19	60	17	—
III	68	36	32	6.3	77	22	0.8	24	43	19	39	—
IV	55	29	23	2.5	29	9	0.1	3	16	8	3	—
V	6	3	19	0.1	2	1	0	0	0	0	0	—
Total	187	100	38	25.3	330	100	3.5	100	117	21	99	—
Selected Part												
I	35	88	60	10.2	138	97	1.0	68	35	28	35	—
II	8	43	54	1.9	26	40	0.2	22	8	31	7	—
III	17	25	30	1.4	17	22	0.2	12	7	15	7	—

(*Table 87 contd.*)

(*Table 87 contd.*)

IV	15	27	21	0.5	6	21	0	6	2	3	1	—
V	1	22	16	0.1	0	13	0	0	0	0	0	—
Total	76	41*	44	14.1	187	57*	1.4	38*	52	26	50	48
Part Left Out												
I	4	4	62	1.4	19	14	0.5	22	5	92	5	—
II	11	10	57	2.9	39	27	0.9	41	11	80	10	—
III	51	46	34	4.9	60	42	0.6	33	36	29	32	—
IV	40	36	24	2.0	23	16	0.1	4	14	7	2	—
V	5	4	20	—	2	1	0	0	0	0	0	—
Total	111	100	33	11.2	143	100	2.1	100	65	33	49	25
Section 3, Test Plot 3 Original Stand												
I	96	58	49	19.2	256	74	1.5	64	87	17	96	—
II	28	17	42	4.3	56	16	0.6	27	20	31	25	—
III	38	23	29	2.8	36	10	0.2	9	11	20	30	—
IV	3	2	20	0.1	1	0	0	0	0	0	0	—
Total	165	100	42	26.4	349	100	2.3	100	118	20	151	—
Selected Part												
I	75	79	47	14.1	188	73	0.8	51	66	12	74	—
II	9	32	26	0.5	6	11	0	2	2	7	6	—
III	12	32	26	0.8	9	27	0	7	2	7	9	—
Total	96	58*	43	15.4	203	58*	0.8	34*	70	11	89	70
Part Left Out												
I	21	30	55	5.1	70	48	0.7	47	21	34	21	—
II	19	28	49	3.8	50	35	0.6	38	18	34	19	—
III	26	38	30	2.0	25	17	0.2	15	9	22	22	—
IV	3	4	20	0.1	1	0	0	0	0	0	0	—
Total	69	100	42	11.0	146	100	1.5	100	48	32	62	—

214 Table 88. Economic effectiveness of combining different elements of the complex in a stand

Product	Yield/ha		Value, roubles		Expense, roubles		Profit, roubles	
	per year	over 40 years	per year	over 40 years	per year	over 40 years	per year	over 40 years
Section 1								
Timber, m^3	57	57	574	574	527	527	47	47

(*Table 88 contd.*)

(*Table 88 contd.*)

Galipot, kg								
in selected section	15	75	17	86	15.6	78.0	1.7	8.3
in rest of section	20	400	23	460	20.1	402	2.9	5.8
Nuts, kg								
in selected section	2.5	6.3	4	10	3.4	8.5	0.6	1.5
in rest of section	28	560	44	884	41.2	824	3.0	60
Total				2014		1839		175
Loss of nuts		43.8		69.2		59.6		9.6
Section 2								
Timber, m^3	187	187	1887	1887	1730	1730	153	153
Galipot, kg								
in selected section	48	240	55	276	50	249	5.4	27
in rest of section	25	500	28	576	26	518	2.9	58
Nuts, kg								
in selected section	6.5	163	10	25	9	22	1.5	3.8
in rest of section	22	440	34	696	30	598	4.9	98
Total				3456		3117		339.8
Loss of nuts		114		180		155		25
Section 3								
Timber, m^3	204	204	2054	2054	1887	1887	167	167
Galipot, kg								
in selected section	70	350	80.5	402	72.6	363	7.9	39
in rest of section	15	300	17.3	346	15.6	312	1.7	34
Nuts, kg								
in selected section	4	10	6.3	15	5.4	13	0.9	2
in rest of section	15	300	23.7	474	26.4	408	3.3	66
Total				3292		2983		309
Loss of nuts		70		110		95		5
Average for the sections (ratio of sections, area-wise 1:1:0.6)								
Timber, m^3	122	122	1228	1228	1128	1128	100	100
Galipot, kg								
in selected section	35	175	40.3	201	36.3	181	4	20
in rest of section	18	360	20.7	414	18.7	375	2	40
Nuts, kg								
in selected section	4	10	6.3	15	5.4	13	0.9	2
in rest of section	20	400	31.6	632	27.2	544	4.4	88
Total				2491		2241		250
Loss of nuts		70		110		55		15

Timber recovery from I generation trees was 87%; this is 57% or 187 m^3/ha for the stand as a whole. Loss of commercial nuts in this case was 22.8%.

Resin productivity of the plantation, including in the section selected for felling, was quite high. Short-term tapping of trees marked for felling at the first instance produced 48 kg of galipot per ha a year for five years. Fifty trees were found suitable for long-term tapping, these producing 25 kg of galipot each in a season.

Felling generally was quite intense although density did not drop below 0.5. In all probability, felling here is best restricted to 40–45% and about 130–140 m^3 of pine timber per ha recovered. The economic desirability of limiting the recovery theoretically lay in the range 80–100 m^3/ha. In this case, a large number of trees would be covered for prolonged exploitation and galipot yield raised as a result of prolonged tapping. The final solution to the most desirable felling level in such stands should be fixed with due consideration of felling in the adjoining stands. If, however, felling in the latter is low, the section can adopt the upper limit of permissible felling so as to achieve an overall profitability for the area as a whole. Such a need arises when comparing the economic effectiveness of exploiting stands of second and first sections (see Table 88).

Section 3. This section is located on the lower portion of the slope and hence, not withstanding their age (over 260 years), continues to maintain a compact canopy. Because of the onset of disintegration of the stand and considerable thinning of the crown, seed output is very low although the overall timber reserve is about 400 m^3/ha (see Table 86). The second level is rather poorly manifest and trees of III (181–220 years) and II (221–260 years) generations account for only an insignificant proportion. The content of associated species too is not much. The density of the stand at present is 0.6 and the reserves and state of windfall reveal that, until quite recently, it was a highly dense plantation with sharp domination of the leading I generation that is responsible for suppressing the growth of the second level, leading to a generally poor seed production.

The latter aspect is well-identified from the number of cones per tree as well as from the weight of yield/ha (2355 cones or 40 kg of seeds per ha).
216 In the same plantation, resin productivity is also low. On the whole, the complex evaluation of the stands points to the desirability of complete felling rather than recommending long-term and comprehensive utilization.

An analysis of the selective felling method showed that the first removal should be high 58% or 204 m^3/ha of reserves. The low crop losses in this case (biological product 34% and commercial product 21%) suggest that the selection covered the poor cone-yielding section of the plantation. This is evident since the average yield of selected trees was

11 cones a year while that of the remaining trees was 52 cones. In such selective felling, the density of the stand falls to 0.28, even after retaining all the associated species.

When this stand is growing on much thicker soils, the unaffected portion can be preserved and exploited later. However, when the soil under this stand is rather thin, fresh fall of trees even in nature as well as the experience of felling with a higher percentage of selection (70–80%) carried out under conditions of this region by E.V. Titov (1971) suggest that the standing trees will be fully destroyed. Under these conditions, the desirability of total felling is more obvious than selective felling. Such felling may be carried out even in the nut-producing zone. The economic effectiveness of differential approach to the utilization of such sections, as discussed here, would be high.

An evaluation of the solutions examined shows that the organization of combining the elements of the complex and, in particular, the felling operation, should be approached with due consideration of relations between the different characteristics of productivity of trees. In such a case, it would be possible to recover maximum timber from the poorly productive pine trees and optimum exploitation of the highly productive trees. The differential approach also helps in resolving the question of economically effective combination of the various elements of the complex.

Combining the types of complexes within a "block" of plantations can be studied on the example of Kochesh river basin (4th category of freight flow on the river system). The massif comprises 16 blocks of total area 4500 ha, more than 300 sections of predominantly typical same-aged, highly productive, and resin producing, relatively pure pine stands of above average density located mainly in the midportion of mountains (Table 89, Figs. 54 and 55).

The division of plantations according to overall rank distinctly divided the above categories of productivity (Fig. 56). The best section of pine plantations has an average yield of 120 kg/ha, biological resin productivity of 14 kg/ha, and timber reserves of 350 m^3/ha, which includes 345 m^3/ha of pine. The output of poorly productive section is low, unsuitable for tapping but has high overall timber reserves, suggesting its exploitation within the framework of a commercial timber complex without any significant loss of reserves of nuts or galipot in the basin as a whole.

218 Simultaneous evaluation for selection identified good plantations in terms of growth, yield, and resin productivity. Further, it was very clearly brought out that the selection characteristics of a pine plantation may vary widely for the same physical characteristics. The assessment used for this purpose reveals the contradictory nature of relations between growth, yield, and resin productivity even on the basis of standard physical descriptions. Earlier, while studying growth and cone yield

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Fig. 54. Yield of pine plantations:
1—0–25, 2—26–50, 3—above 50 kg/ha in an average year, 4—non-pine area, and 5—plus category.

(see Chapter II) as well as cone yield and resin productivity (see Chapter III), it was shown that the ratio between two characteristics can be
219 depicted in the form of a scissors-like model. Thus, as the leading characteristic intensifies to the level of selection importance, the ancillary feature fell to the average level. The behavior of the model of relations between three characteristics produces a scalene triangle in which one feature represents the selection characteristic, the second the average,

219

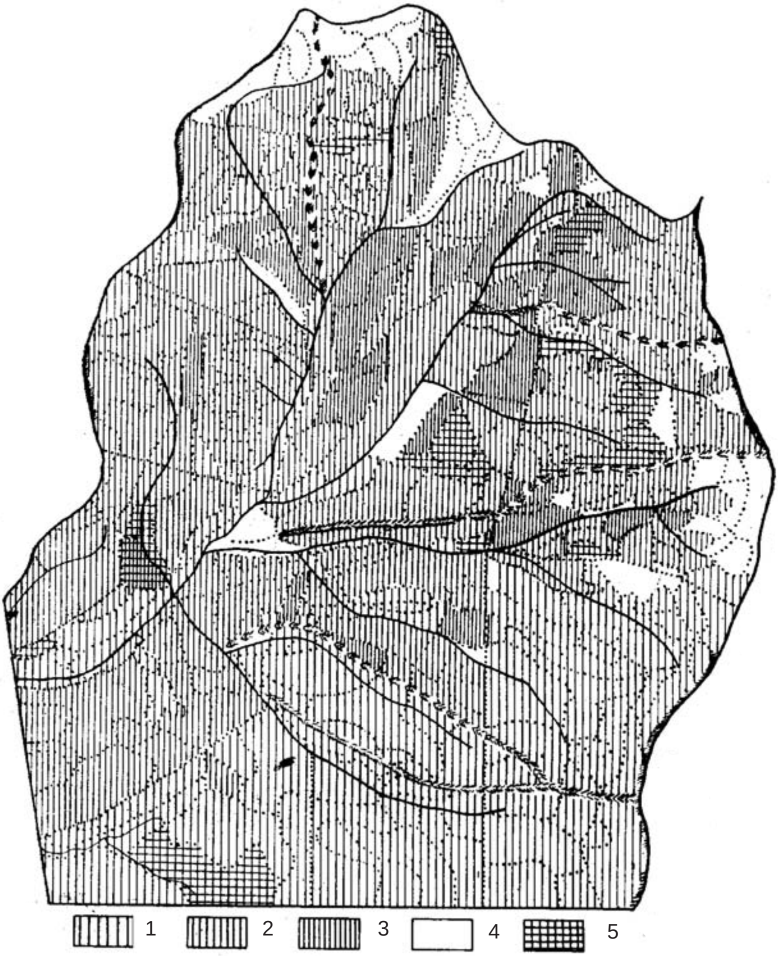

Fig. 55. Resin productivity (biological) of pine plantation:
1—0–5, 2—5.1–15.0, 3—above 15.0 kg/ha in a season, and 4 and 5—the same as in Fig. 54.

and the third the subnormal level. It may be seen from Table 89 that these models are effective at any combination of the characteristics. A knowledge of these principles is important for an objective selection of 220 features and for establishing their optimum combination for developing specialized plantations for integrated management in future on an essentially new basis.

The comprehensive utilization of taiga pine plantations, as stated above, should be based on a differential combination of the types of complex between the plantations. Their classification based on complex assessment of stands

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Fig. 56. Integrated and selection evaluation of pine plantations: productivity: 1—low, 2—moderate, 3—high, 4—possible plus category, 5—fir-spruce forest, and 6—subalpine pine forests.

reveals substantiates possibility for such an organization of management (Table 90).

FEC takes the dominant position in group I forests (nut producing zone)
221 (Fig. 57). Plantations forming this group cover 40% of the territory in this region, hold the main reserves of pine timber and record maximum output and resin productivity. Timber section comprises less than 10% of the area

Table 89. Integrated and selection evaluation of pine plantations

Category of integrated production and selection characteristics of plantations	Physical characteristics assessed									Integrated rank	Timber		Nuts		Galipot	
	Area, ’000 ha	Pine ratio in composition	Age, years	Quality index	Diameter, cm	Height, cm	Density	Pine, No./ha	Total reserve, m^3/ha		m^3/ha	rank	kg/ha	rank	kg/ha	rank
Mountain-taiga subzone																
Very low and low	0.5	6.8	170	II, 8	40	25	0.6	150	310	0.7	210	1.0	63	1.0	7	0.9
Moderate	1.4	9.1	160	II, 6	41	26	0.6	220	350	1.0	320	1.0	95	1.0	11	1.0
High	0.6	9.8	180	II, 7	42	25	0.6	230	350	1.2	345	0.9	120	1.1	11	1.1
Very high																
yield	0.3	7.9	170	II, 5	40	25	0.5	150	280	1.1	220	0.6	104	1.6	8	1.0
resin productivity	0.2	7.9	170	III, 0	43	24	0.5	160	290	1.0	230	1.1	68	0.9	12	1.3
growth (timber reserve)	0.3	8.8	160	III, 0	40	24	0.6	190	320	0.8	280	2.0	45	0.5	12	1.1
Total	3.3	8.8	170	II, 7	41	25	0.6	210	330	1.0	290	1.0	88	1.0	11	1.0
Subalpine subzone																
Total	0.9	9.6	160	IV, 2	32	20	0.5	340	250	0.6+	240	0.3+	51	0.7+	4	0.4+

Note. 0.6+—relative to mountain-taiga subzone; selection in the appropriate sections was made at 1.5 σ.

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Fig. 57. Types of complexes (variant of group I forests—nut collecting zone): 1—TIC, 2—FEC, 3—HGC and SPC, 4—FFC, and 5—SSC.

which is unsuitable for prolonged comprehensive utilization according to the above criteria.

FFC includes plantations which need objective care in the massif. SPC contains mainly the subalpine part of pine forests since the inclusion in it of protected sections on steep slopes and for other reasons was difficult due to adverse conditions of preparing the corresponding 222 material. The HGC includes not only the protected territory but also the

Table 90. Distribution of pine forests according to types of complexes

Type	Area		Proportion of pine in composition, %	Quality index	Pine, No./ha	Complex rank	Timber					Nuts		Galipot	
							total reserve		pine reserve						
	’000 ha	%					m^3/ha	’000 m^3	m^3/ha	’000 ha	rank	kg/ha	rank	kg/ha	rank
I group forests (nut-producing zone)															
Forestry	1.8	40	9.7	II, 6	220	1.1	350	629	340	611	0.9	105	1.1	12	1.0
Timber	0.4	9	7.1	II, 8	160	0.7	310	138	220	60	1.2	69	0.8	7	0.7
Selection-seed	0.7	15	8.8	II, 8	170	1.0	300	240	245	200	1.1	73	0.9	10.5	1.0
Forest-forming	0.4	9	8.1	II, 8	200	0.8	320	118	260	96	1.1	76	0.9	9.5	0.9
Specially protected	0.8	18	9.6	IV, 2	340	0.6	250	217	240	208	13	51	0.7	4.0	0.5
Game*	2.6	53	9.2	III, 0	200	0.8	360	638	240	589	1.0	68	1.0	7.0	0.8
III group forests (exploitation section)															
Forestry	0.6	13	9.8	II, 7	230	1.2	350	222	345	219	0.8	120	1.3	14	1.2
Timber	1.7	38	8.4	II, 6	150	1.8	310	540	260	453	1.1	76	0.9	9	0.9
Selection-seed	0.7	15	8.8	II, 8	170	1.0	300	240	245	200	1.1	73	0.9	10.5	1.0
Forest-forming	0.4	9	8.1	II, 8	200	0.8	320	118	260	96	1.1	76	0.9	9.5	0.9
Specially protected	0.8	18	9.6	IV, 2	340	0.6	250	217	240	208	1.3	51	0.7	4.0	0.5
Game	1.8	40	9.2	III, 2	250	0.8	260	452	240	417	1.1	59	0.8	7.0	0.8

*A part of other areas was included in this complex considering their suitability for game exploitation.

area of forestry complexes with a corresponding reduction of the quality index of game areas. On the whole, it comprises over 50% of the entire area of the "block" of plantations.

The distribution of pine forests according to the types of complexes taking into consideration the forest groups brings about changes in the proportions of FEC and TIC (Fig. 58). In group III forests, FEC occupies a subordinate position (13%), with TIC leading (38%). Moreover, it is significant that FEC comprises the good forests, i.e. "high" and "very high" categories of integrated productivity. This is confirmed by the characteristics given above.

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Fig. 58. Types of complexes (variant of group III of forests): 1—TIC, 2—FEC, 3—HGC and SPC, 4—FEC, and 5—SSC.

224 The timber section, as in group I, has practically the same low yield and resin productivity. Nevertheless, the reserves of pine timber are high which enhances the timber processing possibilities in this complex. The structure of other complexes stands essentially unaltered with the exception of game section, the conditions for its management worsening quantitatively as well as qualitatively.

Calculations of anticipated output in differential approach suggest its usefulness for group III as well as I of forests (Table 91). The data take into consideration the suggestions for 10-year tapping for TIC plantations and prolonged (5 + 20 years) for FEC type. These correspond in the first case to complete felling of the forest and in the second to selective felling (for group I—selection 30% and for group III 40%). Nut reserves were calculated on the basis of long-time average level allowing for natural losses (50%) and crop dynamics (crop possibility in 5 to 10 years).

These data for the given conditions show that, in the nut producing zone, the total utilization of 9% of the area under TIC may provide 30% of

224 Table 91. Projected volumes of output according to types of complexes

Type	Area		Timber				Nuts		Galipot	
	'000, ha	%	total reserve		pine reserve		tons	%	tons	%
			'000 m^3	%	'000 m^3	%				
			Group I forests (nut producing zone)							
Forestry	1.8	40	189	45	103	56	93	54	40	63
Timber	0.4	9	138	33	93	30	15	9	23	37
Selection-seed	0.7	15	66	15	24	7	29	16	—	—
Forest-forming	0.4	9	29	7	24	7	14	6	—	—
Specially protected	0.8	18	—	—	—	—	23	13	—	—
Game	2.4	53	—	—	—	—	—	—	—	—
Total	4.5	—	422	100	329	100	174	100	63	100
			Group III forests (exploitation section)							
Forestry	0.6	13	78	11	75	13	38	22	16	12
Timber	1.7	38	540	76	453	79	66	39	112	88
Selection-seed	0.7	15	66	9	24	4	29	17	—	—
Forest-forming	0.4	9	29	4	24	4	14	8	—	—
Specially protected	0.8	18	—	—	—	23	23	14	—	
Game	1.8	40	—	—	—	—	—	—	—	—
Total	4.5	—	713	100	576	100	170	100	128	100

timber reserves and 37% of galipot at a theoretical crop loss of 9%. Exploitation here of some parts of forests as a forestry complex would recover 56% of timber reserves, 54% of nuts, and 63% of galipot.

Timber exploitation of pine forests of group III would provide 79% of timber reserves and 88% of galipot at theoretical crop loss of 30% instead of 225 100% at present following completely indiscriminate felling of good and inferior plantations. Under these conditions, FEC occupies a small area, has some reserves of timber and galipot, the high yield of timber permitting its exploitation for a long period. An important aspect of the above discussion for group III is that good pine forests are conserved. The area of this complex is determined with consideration of its thorough assessment. Timber section is evidently associated with the less valuable pine forests but with fairly high timber reserves including pine timber.

The natural ratio of the types of complexes and correspondingly the areas of total and partial felling should evidently be regarded as an important basis in resolving the problems of managing pine forests. The data given for group III forests show that the ratio of FEC and TIC for this area was 1 : 3 which is evidently quite an optimum variant. Fluctuations of this ratio are possible in some blocks but in any case they should be based on an integrated evaluation of the pine forests and not on any arbitrary criterion. The optimization of the ratio of total and partial felling is at present regarded as a general solution to the problems of forests exploitation (Moroz 1975).

This approach is equally relevant for exploiting the nut producing zone. In this case, the ratio of the areas of these two complexes (FEC : TIC) is clearly in favor of long-term utilization (4 : 1).

These suggestions open up definite possibilities for long-term and rational utilization of pine forests in all forest groups. Data on combining the types of complexes within several blocks of plantations, i.e. within an organization, also lead to a similar conclusion.

Combination of types of complexes within a multidisciplinary organization* may be demonstrated on the example of several blocks of pine plantations of the type in Kochesh area representing FEC in various combinations with TIC and HGC (Vorob'ev, Saeta, and Kulikov 1978).

The following variants of current and prospective management methods in the organization have been examined:

1) timber and game complexes (TIC in group III of forests and HGC partly in group III and completely in I, the latter representing nut producing zone),
2) forestry and game complexes (independent exploitation of nut producing zone in group I), and

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*This section was prepared in collaboration with V.A. Saeta.

3) entire complex of operations (TIC in group III and FEC and HGC in groups I and III).

Taking into consideration the comprehensive evaluation of pine plantations by the simplified method (based on nut reserves, timber concentration, and anticipated yield of galipot), and also the freight flow, six sections or blocks were formed covering 11% of the entire area. These blocks 226 were regarded as an FEC base and nut producing zone or group III forests in the absence of group I (Table 92). Much of the territory of the unit including the nut producing zone has been provided for the development of HGC (64%); in group III forests, not more than 25% of total forest area has been provided for TIC considering that half of the area of slopes is accessible to tractors.

226 Table 92. Characteristics of forestry sections

Section	Area, '000 ha		Timber, million m^3			Nuts			
	total	forested section	total	mature area	access-sible area	area of cone-bearing trees, '000 ha		biological yield, tons	
						total	yielding over 40 kg/ha	total	yielding over 40 kg/ha
Kochesh	6.0	5.6	1.0	0.5	0.26	4.3	3.1	266	230
Evii	4.0	3.8	1.5	1.3	1.16	3.7	3.4	395	386
Uchal	3.8	3.5	1.0	0.2	0.18	3.1	1.9	184	150
Obogo	2.2	2.0	0.5	0.1	0.10	1.4	0.7	72	52
Bulandu-kol'	4.9	4.8	1.1	0.3	—	4.2	2.4	184	147
Malye Chili	7.8	6.3	1.2	0.3	—	4.5	1.6	169	96
Total	28.7	26.0	6.8	2.7	1.70	21.2	13.1	1270	1061

The characteristics of sections given above point to the predominance of pine plantations with high reserves of timber, nuts, and correspondingly high resin productivity.

Taking into consideration this section of forests and generally the nut producing zone earmarked for commercial exploitation, the anticipated additional output, expenses, and economic effectiveness have been calculated for combinations of different types of complexes as well as for the experimental unit. For the latter, as stated before, its base indexes for the best of productive years have been taken into consideration.

Production. One of the basic conditions of economic effectiveness of developing a forest territory for comprehensive exploitation as forestry and game types is the additional production. Its overall assessment suggests that the annual average production volume increases by 33.0% and for the FEC or nut-producing zone by 95.8% (Table 93).

The most significant increase of production would be in the case of live forest products: nut collection 286.7%, fur 160.3%, medicinal-technical raw material 352.6%, and tapping 96%. The rise in timber volume was projected
227 to be insignificant at 14.5%; the overall ratio between forestry and timber types of complexes for this undertaking was 1 : 7.

The additional output significantly improves the ratio of the elements of the complex within the unit, approximating to the optimum (Table 94). The proportion of timber products falls by 11%, tapping production rises by 4%,

227 Table 93. Average annual production volume with additional territory under exploitation

Product type	Unit of measurement	Actual volume (HGC)		Projected volumes (TIC+HGC)		Additional output		Increase of production volume in the undertaking, %
		quantity	price, '000 rubles	quantity	price, '000 rubles	quantity	price '000 rubles	
Timber	'000 m^3	—	—	11.6	116.8	11.6	116.8	14.5
Galipot	tons	—	—	113	130.0	113	130.0	96.0
Nuts	tons	7.5	11.8	115	181.7	107.5	169.9	286.7
Fur	'000 rubles		5.0		15.1		10.1	160.3
Medicinal and technical raw material	tons	0.9	2.4	4.3	10.7	3.3	8.3	352.6
Total			19.2		454.3		435.1	33.0
			4.2		100		95.8	

227 Table 94. Ratio of specific utilization of elements, %

Element of complex	Actual (TIC+HGC)	Additional (FEC+HGC)	Combined (TIC+FEC+HGC)
Timber	61	27	50
Timber processing	18	—	18
Tapping product	10	30	14
Nut collection	5	39	14
Game	1	3	2
Medicinal and technical raw material	1	1	2
Others	4	—	2
Total	100	100	100

and nut collection by 9%. The game economy and medicinal-technical raw material production also improve.

Prolonged exploitation of pine forest resources by the recommended system improves their utilization. As against the original level of 200 rubles income from 1000 ha of forest area, the anticipated yield is 4000–5000 rubles and 9000–11,000 rubles for FEC section. Depending on the increasing availability of productive plantations, with long-term combination of the 228 elements of utilization in the zone of regular availability of transport network, production quantum will rise in proportion to the territory exploited. Under the present conditions, however, roads predominantly service the timber sections which on increasing exhaustion will have to handle the remaining reserves farther away from the processing center. Ultimately, this increases the production cost and renders the unit uneconomic.

This practice has particularly led to the main undertakings in Gornyi Altay, including the experimental, becoming uneconomic resources.

Capital investment. The utilization of FEC resources or nut producing zone would facilitate improving this position but it depends largely on ensuring the required work force and capital investment. Without laying the roads, maintaining the overall well-being of the territory, required machinery and mechanisms, housing for workers, the commercial exploitation of this section of forest cannot be realized.

The approximate minimum of required capital investment is put at 851,000 rubles, including 91,000 rubles for improving industrial facilities, 312,000 rubles on forestry, and 448,000 rubles for non-industrial forest funds. Expense on raising housing has been worked out at 53% and for laying roads 32% of the above amount.

The scheme for improving transport in the new territory provides for: constructing forestry motorable, round-the-year roads with gravel topping, linking FEC sections with the main road (22 km), tractor roads for seasonal use in the comprehensive exploitation sections (total 116 km); approach pathways for implementing biotechnical measures for game management and for economic recovery of medicinal-technical raw material (over 100 km).

The entire housing is best concentrated in the central farmstead of the forest combine. A guard system for the settlement should be organized in the nut producing zone. A network of small permanent and temporary depots for nut storage should be set up directly in the sections. So far (20 years), expenses on the construction of temporary facilities (depots, tractor roads, pathways, etc.) amounted to 280,400 rubles that went into the recovery of nuts, galipot, and medicinal-technical raw material.

Economic effectiveness of the proposed solutions is reflected in the growth of profits and reduction of specific capital investments (Table 95). Its calculation may be represented in the following form:

229 Table 95. Volume and approximate price of products on combining different types of complexes

Product type	Unit of measurement	Volume for forest combine (TIC+HGC)			Volume of additional product (TIC+HGC)	Combined volume (TIC+FEC+HGC)			Increase of profits, '000 rubles
		quantity	cost '000 rubles	market product, '000 rubles		quantity	cost, '000 rubles	market product, '000 rubles	
Timber	'000 m^3	80	717.6	805.6	11.6	91.6	831.3	922.4	3.1
Galipot	tons	117.6	117.9	135.2	113	230.6	235.0	265.2	12.9
Processed timber, etc.*	'000 roubles	—	200.4	216.2	—	—	200.4	216.2	—
Total market product			1035.9	1157.0			1266.7	1403.8	16.0
Nuts	tons	37.5	51.6	59.3	107.5	145	197.8	229.1	23.6
Fur	'000 rubles	—	5.9	6.3	10.1	—	15.6	16.4	0.4
Medicinal and technical raw material	centners	9.5	2.0	2.4	33.5	43	9.0	10.7	1.3
Total byproducts			59.5	68.0			222.4	256.2	25.3
Grand total			1095.4	1225.0	435.0		1489.1	1660.0	41.3

*Timber processing has not been provided at present but is reckoned to be economically most promising.

$$\Delta P = (\Sigma CP_1 - \Sigma C_1) - (\Sigma CP - \Sigma C) \quad (1)$$

(1660–1489.1) – (1225–1095.4) = 41.3 thousand rubles,

where ΔP—the rise in profits per year, '000 rubles,

ΣCP and ΣCP_1—total of commercial product before and after organizing FEC, '000 rubles, and

230 ΣC, ΣC_1—total cost of commercial product before and after organizing FEC, '000 rubles.

$$E_{sp.\,cap.} = (En_n \times B \times P)/100 - En_n \times \Sigma_{cap} \quad (2)$$

$(0.15 \times 2567 \times 35.5)/100 - 0.15 \times 851 = 9000$ rubles, where $E_{sp.\,cap.}$—economy of specific capital investment, '000 rubles,

En_n—standard coefficient of capital efficiency (0.15),

B—book value of available basic industrial and non-industrial facilities, '000 rubles,

P—rise of production value, %, and

Σ_{cap}—total capital invested in the extended activities, '000 rubles; and

$$S_{an} = \Delta P + E_{sp.\ cap.}, \qquad (3)$$

$$41.3 + 9.0 = 50.3 \text{ thousand rubles,}$$

where S_{an}—total of annual earnings of the plantation.

On the strength of additional profits, the entire capital invested in exploiting the FEC area is recouped, according to the author's calculations, in 16.9 years, including the component of basic industrial facilities in 9.5 years.

The cost of main facilities in the experimental area per ha in 1971–1973 was about 10 rubles. Taking into consideration the additional capital investment, the basic facilities in the area may rise by 35%.

Calculations show that the exploitation of a part of pine forests by the FEC route is economically justified. Efficiency of capital utilization for the organization as a whole rises by 9.5%, the output of total forest produce per unit of forest area rises by 35.5%, and net profit by 30.2% (Table 96).

230 Table 96. Economic indicators of the organization on partial and total combination of types of complexes

Description	TIC+ HGC	TIC+ FEC+HGC	Increase, %
Output of total forest produce per ha of forest area, rubles	5.47	7.42	35.5
Expenses per ruble of commercial product, kopecks	89.3	89.7	0.4
Profit, '000 rubles	130.6	170.1	30.2
Output of commercial product per ruble of basic industrial investment, kopecks	137	150	9.5

The economic indexes of experimental and more so of another organization will differ quantitatively depending on the conditions of exploitation and actual combination of types of complexes and corresponding
231 product costs. In this case, it is not important that the forestry exploitation of the best part of forests including the nut collection zones should be undertaken simultaneously on the basis of TIC in group III forests. Uncoordinated economic management is undesirable for the independent exploitation of a given group of forests as well as generally for an integrated organization. Moreover, the continuation of unilateral exploitation of some forests and

reservation of others would lead in both the cases to their felling since the exhaustion of timber reserves in group III forests with growing industrial requirement will be compensated by converting good plantations of group I into group III that are unsuitable for felling and converting an equal or even larger area from group III into group I. According to the author, this would be the further course of exploiting pine forests of Gornyi Altay even in the other regions of Siberia and Far East.

A real and scientific solution to the problems of pine forests, according to the author, could only be in organizing differential management based on a thorough complex evaluation of pine forests. This shows that differential approach to combining the elements and types of complex would result in modern methods of exploitation in group III forests conforming to their overall value; in group I, in this case, the nut producing zone, facilities are provided for exploiting them on a commercial basis and generate a significant amount of additional produce without much expense or affecting conservation and ensuring long-term utilization of resources.

This approach should be followed first of all by working out appropriate instruction manuals, followed by specialized forest organization operations and developing a network of complex pine plantations. A vital step in this direction is the Guide for Organizing and Economic Management of Pine Forests (1982) worked out by the Institute of Forests and Timber, Siberian Division, Academy of Sciences, USSR. It takes into consideration the above suggestion and has been approved by the Ministry of Forestry, Russian Soviet Federative Socialist Republic.

Conclusion

The great diversity of useful resources and the high environment-influencing functions of Siberian stone pine forests necessitate their management to satisfy not only the utilization aspects of their valuable products but also to ensure their conservation and reproduction.

The contemporary utilization of pine forests predominantly reflects the timber exploitation approach which is generally unsatisfactory and arouses anxiety about the future of pine and about the efforts that are going into its conservation. Attempts to tackle this complex situation by prohibiting the felling of pine do not serve the purpose as such a solution is not practical and scientific and economic problems cannot be resolved in this manner. Suffice to say that exploitation of a part of pine forests for timber that are not suitable, for example, for long-term comprehensive utilization would be entirely justified. Although this approach is followed everywhere, good, primarily productive, pine forests are felled along with the inferior ones and, what is more particularly objectionable, long before they stop producing cones.

The essence of the pine problem thus is not whether it should be cut down or not but to provide a competitive solution to the various techno-economic problems for which we have so far no scientific system of management in these forests.

The investigations carried out showed the desirability of examining the prevailing principles of organizing and managing the forest economy more thoroughly and provide satisfactory solutions to the problems of forest products and the society at large.

A fairly convincing example, according to the author, is a study of the biological aspects of relations between the characteristics of growth and development of pine on a theoretical as well as practical basis for comprehensive utilization of forests.

A thorough analysis of the structure of relations between growth characteristics, cone yield, and resin formation showed a positive statistical correlation, making it possible for the presence of genotypic and phenotypic exceptions in the form of poorly or highly developed properties of some specimens and populations.

The biological principle of statistical relation between the characteristics 233 of growth and development lies in the commonality as well as contradiction of their genotypic and phenotypic origin.

Positive correlations are noticed between the distribution series of the leading characteristics in the poorly and moderately productive parts. The formation of such a correlation and its persistence over time bears a moderately cyclic variation pattern of optimal and non-optimal parameters of growth and development at which the spurt of one factor suppresses the prevailing condition of the other factor but also promotes the subsequent features. When the parameters of growth or development run beyond the range of ecologically desirable limit, they affect the dynamic equilibrium or the phenotypic relations between the characteristics. Short-term upward deflections of the optimum gradually revert the organism to the normal but prolonged (below the optimum) variation results in a pathological condition.

The steady accumulation of positive deviations of one of the characteristics opens up its leading genotypic feature leading to the formation of phenotypic association with the associate feature in the highly productive part of the series of the distribution of individuals or a population with highly developed properties which, although faint, are nevertheless adequate for their manifestation.

The mechanism of statistical correlation between the features of growth and development is similarly manifest at different levels of organization of the tree and its population. During the ontogenetic development of young trees, the commencement of the reproductive phase is preceded by a spurt in the activity of growth processes and later their inhibition resulting ultimately to a 25–28-year growth cycle. A further combination of the activity of growth and regenerative development, on the example of 100-year cone-yielding pine branches, proceeds such that the ascending branches of apical growth cycles induced by solar activity impede the on-going cone formation process but promote its further rise. In the seasonal context, the morpho-physiological course of growth and reproductive development of shoots is adjusted such that, in the period of maximum intensity of reproductive processes (June), growth phenomena are impeded and compensated later under favorable ecological conditions (July). In their absence or profuse crop, the growth inhibition of shoots and trees is manifest in reduced final parameters of seasonal increment. In the first case, the optimum growth inhibition promotes the subsequent course of cone formation of shoots and, in the second, when inhibition is excessive, this course weakens causing a shift of its cyclic variations. The recorded data and concepts on the role of growth inhibition in the course and control of reproductive processes largely agree with the corresponding hypothesis of G.M. Kozubov (1974).

The morpho-physiological, ecological, ontogenetic, and other aspects of the time-related mechanism of interrelations between the characteristics of growth and development proceed in space in all the individuals and the population growing in consonance with their variations and intercorrelations. The labile structure of interrelations of characteristics 234 between growth and development determines the need for its differential utilization for resolving the various field problems.

It would be advantageous to study the patterns of relations between growth processes and reproductive development as an overall theoretical basis for controlling the reproductive activity of coniferous trees. The concepts existing in the field and the results of factual crop stimulation predominantly result in creating the conditions for female sex development due to better nutritional conditions for plants aided by improvement cutting, mineral fertilizers, trimming of crowns and roots, use of mechanical cuts of trunk, etc. A significant increase of yield is possible in this manner in the years of favorable weather conditions. As far as balancing the crop dynamics is concerned which, according to the author, is a more urgent and complex problem, it cannot be implemented since, under better overall trophic conditions, the upward growth of plants along the "vertical" and time-related correlations of growth processes and cone yield (along the "horizontal") remain the same as when stimulation was not applied. It would therefore be advantageous in the first instance to approach differentially not only for creating favorable conditions for growth and cone formation but also, individually to apical and cambial activity of tissues as well as to the female and male shoots. The solution to the second problem should be probably related to controlling the effect of hormonal factors which pertain not so much to ensuring stable formation of female primordia as to a weakening of their partial predisposition to fall at the commencement of postembryonic development. It has been suggested that apical domination plays a vital role in this process. The program for this domination in all likelihood is developed simultaneous with the formation of female primordia and is often realized in the form of an extremely large number of shoot growths (from the viewpoint of sexual reproduction). The application of hormonal control under these conditions for a greater realization of the potential possibilities of cone formation and optimum seasonal and ontogenetic growth inhibition should be related to the action of the physical factors of environment which, judging from the influence of solar activity, largely set the seasonal rhythm of life processes.

Thus, crop control in conifers should lead, on one hand, to controlling root-leaf relations which determine the cyclicity of overall productivity of growth and reproductive development of trees and, on the other, to a shift of their internal cycles toward less favorable conditions while generally maintaining the principle of dynamic equilibrium.

Non-compliance of this principle is undesirable not only in the context of crop control but also from the viewpoint of plant stability to sharp changes of root-leaf relations, for example, due to immoderate application of 235 mechanical cuts on the trunk, trimming of crown and roots or the effect of unfavorable environmental factors.

Under conditions of the present experiments, the mechanism of stability of the tree comprised the inhibition of growth processes in the crown and activation of reproductive (cone-bearing) and protective (resin-forming) systems. Further, the tree constantly endeavored to revert to the original root-leaf relations by boosting the cambial activity in the undamaged portions of the trunk. This manner of response of the tree suggests, on one hand, the protection mechanism acquired over the course of evolution and, on the other, the manifestation of cybernetic properties of root-leaf relations. The utilization of these aspects in solving the problems of crop control and stability of conifers is of positive interest. In the latter case, for example, not only the weakened state of the plant will have to be studied, the aspect covered by phytopathology, but also its active state which opens up the mechanism and limits of protection of the tree will have to be understood. Enlarging the range of the study to analyzing the response of growth and reproduction processes is also important.

The application of statistical correlations between the growth and development characteristics of pine in organizing integrated and specialized management systems is based on a differential consideration of the structure of their distribution series. In the first case, this would mean exposing forest exploitation to considerations of intra- and interpopulation variability of characteristics and productivity indexes of trees and plantations and, in the second, developing specialized plantations based on the principles of an optimum combination of the leading and ancillary factors.

In other words, management of pine forests should proceed on a differentiated basis, be integrated in form and specialized in content. The principle of differential approach to management in pine forests should consider all the organizational levels of exploitation commencing from an individual tree or a stand to the intra- and interregional relations. Such a system of management should form the basis of comprehensive utilization of pine forests and due consideration of techno-economic conditions of their exploitation.

The realization of these theoretical principles and the corresponding recommendations on various aspects of the problem under consideration will, according to the author, essentially solve the problems of pine forests in the contemporary taiga forests as also in future. Further, understandably, the various aspects of organizational management to ensure its techno-economic implementation will also have to be tackled.

References

Citations shown in the original text in two parts, i.e. the Russian and non-Russian sources, have been consolidated into a single alphabetically arranged list.

This list also includes a large number of sources (120 to be precise) referred in the text but not cited in the References. The numbers in parenthesis appended to these "missing" entries refer to the page number of the translation on which they occur.

The author may like to complete these citations or deal with them suitably—Translator.

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