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PHYTOINDICATION OF CLIMATIC CONDITIONS AT THE UPPER FOREST LIMIT

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The concept of ecological and physiognomic types of the upper forest limit is formulated. Theoretical and methodological principles of assessment of climatic differentiation of habitats, climatic fluctuations in the past, thermal regime of the vegetational period, and eolian conditions at the upper forest limit are discussed in terms of plant communities and individual plants.

Data from long-term meteorological observations at special stations are required to assess the climate of some particular region. The network of meteorological stations is usually thinly spread in high-mountain regions, however; many of them have been established relatively recently and thus the dynamics of meteorological factors they provide is valid for brief periods only. But even in those alpine regions about which reliable climatological information is available, the data furnished by standard meteorological observations are usually insufficient to determine the actual climatic situation, as it arises at different points of the mountains, on slopes of different exposures, and at different altitudes. This is especially true of major mountainous massifs with highly dissected relief and a wide spectrum of altitudes. The methods of phytoindication represent a valuable adjunct to the results of conventional meteorological observations, enabling us to expand and deepen our ideas about the climatic characteristics of high-mountain regions, and to assess climatic fluctuations in the past, over a period much longer than the existence of even the oldest meteorological stations.

The upper limit (upper boundary) of forest is to be thought of as a zone of degradation of forest vegetation, where more or less continuous though undersized, forests, (low-growing thickets of varying density) grade into woodless communities, which occasionally form complexes with small groups of trees, individual trees, or creeping forms.

Ecologists, phytogeographers, and geobotanists (Krebs, 1911, 1912; Brockmann-Jerosch, 1919; Sokolowski, 1928; Gams, 1937; Galazii, 1954; Kolishchuk, 1958; Gorchakovskii, 1966; Holtmeier, 1967; Plesnik, 1971, 1972; and others) have established the significance of the upper forest limit as an important botanical–geographical boundary. This is at the same time a climatic boundary as well, between the region of forest mesoclimate and that of the mesoclimate of treeless mountain summits.

The climate of the upper forest limit possesses a number of specific features. Snow usually accumulates in large amounts in the temperate zone of the northern hemisphere and in the Subarctic during winter, at least in places (more so than at the relatively high and low mountain levels); this snow is blown by the wind off treeless summits and slopes. This great thickness of snow melts slowly until the beginning or end of July. Soil surface is freed from snow cover quite late, thus limiting the period of plant growth. The mass of snow that stays unmelted for a long time exerts a certain humidifying and moderating influence on the meso- and microclimate of the upper forest limit, creating conditions for successful competition, on the part of herbaceous plants, with woody plants.

The dependency of the structure, composition, and distribution of vegetation on climatic conditions is particularly evident near the upper forest limit. This opens up broad possibilities for using phytoindication with the aim of elucidating local characteristics of meso- and microclimate.

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In any mountainous region, the upper forest limit can usually be subdivided into several ecological and physiognomic types. The ecological types are determined by the limiting factors of the environment. The main types are thermal, eolian, and edaphic.

The level of the thermal type of the upper forest limit is determined above all by temperature conditions; the main limiting factor is heat deficiency. The trees are undersized, often with dead tops and frostcracks in their trunks. Young shoots are damaged periodically by late frosts. The soil cover is developed fairly well above this type of forest limit and is potentially suitable for colonization by forest. The transition from forest communities to treeless communities (shrubs, tundra, meadow, etc.) is gradual. The deterioration of climatic conditions as the absolute altitude increases while the edaphic factors remain the same, affects, first of all, the tree layer, the underlying shrubby, shrubby-grassy, and mossy-lichenose layers being affected to a lesser degree. In the zone of contact between forest and nonforest communities one may, therefore, not infrequently find an incumbent series of communities (Sochava, 1930) progressively simpler in structure (owing to the drop-out of the upper layers), which nevertheless retain the composition and structure of the connective layers.

The eolian type is pronounced in mountain passes and on ledges open to the winds. The major limiting factor is the withering effect of winds on young shoots, especially in winter time. As in the case of the thermal forest limit, fine-grained soils suitable for the settling of woody plants are present above the forest margin; hence there are no obstacles to the advance of vegetation into the mountains. The trees are even more undersized here than in the previous type, they are squat and their trunks are strongly decurrent and twisted. The crowns of trees are asymmetrical, flag-shaped (especially on the edges of forest), with numerous dead branches on the weather side. The trunks show distinct signs of snow polish. Dark coniferous trees (spruce and fir) frequently form dense, interlaced, almost impassable thickets on the eolian-type forest limit. Transition from forest to nonforest communities is sudden, some trees often assuming shrubby or creeping forms with their branches giving the impression of having been cut to conform to the snow level.

The edaphic type is typical of steep slopes, where thickets of low-grown trees come into direct contact with alluvial deposits. The leading limiting factor in relation to these thickets is the removal of fine earth by erosion, absence of developed soil, and widespread alluvial deposits. The trees inhabiting this type of forest limit are taller than in the two preceding types, the annual shoot increment is higher, and the crowns are symmetrical. The line of the edaphic limit of forest vegetation is tortuous, the thickets of low-grown trees being often interrupted by fields of alluvial deposits.

The first two types are of greater significance for the purposes of climatic phytoindication.

The physiognomic types of the upper forest limit are dependent on the composition and structure of forest communities at their upper limit. Low-growth thickets, which are similar in species composition of their components, in structure, biomorph ratio, appearance, tree size, and a number of other features may lie within a single physiognomic type. Examples of such varieties are given below.

Methods of phytoindication permit to determine the following climatic characteristics of the upper forest limit: 1) climatic differentiation of habitats; 2) fluctuations of climate in the past; 3) thermal regime of the vegetative period; 4) eolian regime (predominant direction and force of prevailing winds).*

Phytoindication of Climatic Differentiation of Habitats

In order to get an idea of the diversity of climatic conditions at the vertical limit of forest vegetation and in its vicinity, it is necessary to find out what ecological and physiognomic types of upper forest limit are encountered in the area under study. In the course of field work, local altitutde (with the aid of an aneroid barometer or altimeter), slope steepness, orientation of flag-shaped tree crowns, composition of low-growth thickets, their structure, crown closure, average tree height and diameter (according to species) are recorded for this purpose at reference points sited along the forest limit, in its typical areas. The plant communities encountered at the upper forest limit are mapped at the same time. In processing the data obtained, the forest limit is broken down into segments which are uniform with respect to composition and structure of low-growth thickets and other indicators (Fig. 1), ecological and physiognomic types of the upper forest limit are singled out, and the range, altitude, and relations of individual types are determined. This kind of work is made much easier if aerial photographs are available.

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* Methods of phytoindication for snow cover in high-mountain regions and for the dynamics of alpine glaciers have been described elsewhere (Gorchakovskii and Shiyatov, 1971, 1971a).

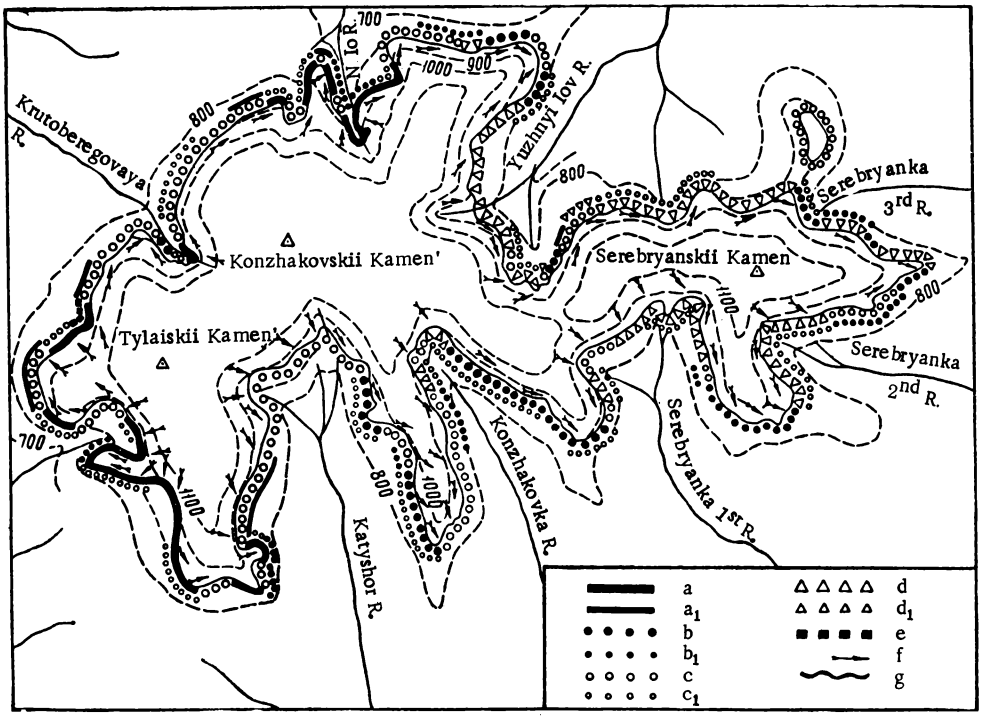

Fig. 1. Physiognomic differentiation (Gorchakovskii and Shiyatov, 1970) of upper forest limit in the Tylaisko–Konzhakovsko–Serebryanskii massif: a–d) dominants; a_1–d_1 codominants; a and a_1 Picea obovata; b and b_1) Pinus sibiricus; c and c_1 Betula tortuosa; d and d_1 Larix sukaczewii; e_1 Abies sibirica; f) direction in which flag-shaped crowns are oriented; g) upper forest limit.

The physiognomic types of upper forest limit range in extent from a few hundred meters to tens of kilometers; each type is characterized by a set of meteorological factors and conditions which are strictly defined for a distincly circumscribed area and which follow regularly recurrent patterns in space. Each physiognomic type of upper forest limit usually has a corresponding type or subtype of mesoclimate. The physiognomic types alternate with each other and recur regularly in localities with similar climatic conditions. Thus, the physiognomic types of upper forest limit reflect the diversity of mesoclimates and their spatial distribution. A greater diversity of mesoclimates in some mountainous region or other is attended by a more pronounced physiognomic differentiation of upper forest limit.

For example, four physiognomic types of upper forest limit can be distinguished in the Northern Urals, in the vicinity of the Tylaisko–Konzhakovsko–Serebryanskii massif (Gorchakovskii and Shiyatov, 1970): tortuous-birch type (dominated by Betula tortuosa), spruce type (dominated by Picea obovata), larch type (dominated by Larix Sukaczewii), and Siberian pine type (dominated by Pinus sibirica). The tortuous-birch and spruce types are peculiar largely to the western slopes of the larger mountain masses, where the climate is relatively mild, with abundant precipitation and a thick blanket of snow, the spruce type being more pronounced on gentle slopes and the birch type on steep rocky slopes or at sites of particularly heavy accumulations of snow, where the vegetative period is of shorter duration. The larch type is typical of the eastern slopes of major massifs, where the climate is relatively harsh and continental and where the snow blown off the bald mountain peaks accumulates in large amounts, which shortens the vegetative period. The siberian pine type is associated with lower mountains or with the rocky eastern slopes of major massifs, where the climate is also continental but the snow blanket is thin.

In the Crimean Mountains, three physiognomic types of upper forest limit may be singled out: northern beech type, formed by crowded low-growth thickets of beech with occasional twisted trunks (Fagus silvatica); southern beech type, consisting of thinly spaced, not infrequently parklike, copses of the same beech species; and pine type, dominated by Pinus silvestris var. hamata. The first type is characteristic of the cool and humid northern slopes of western mountain pastures (annual precipitation amounts to 780–1000 mm); the second type is characteristic of the eastern, less humid pastures (annual precipitation about 500 mm); and the third type is characteristic of the southern slopes of western partures, which receive large amounts of heat from the sun (Krylova, 1953).

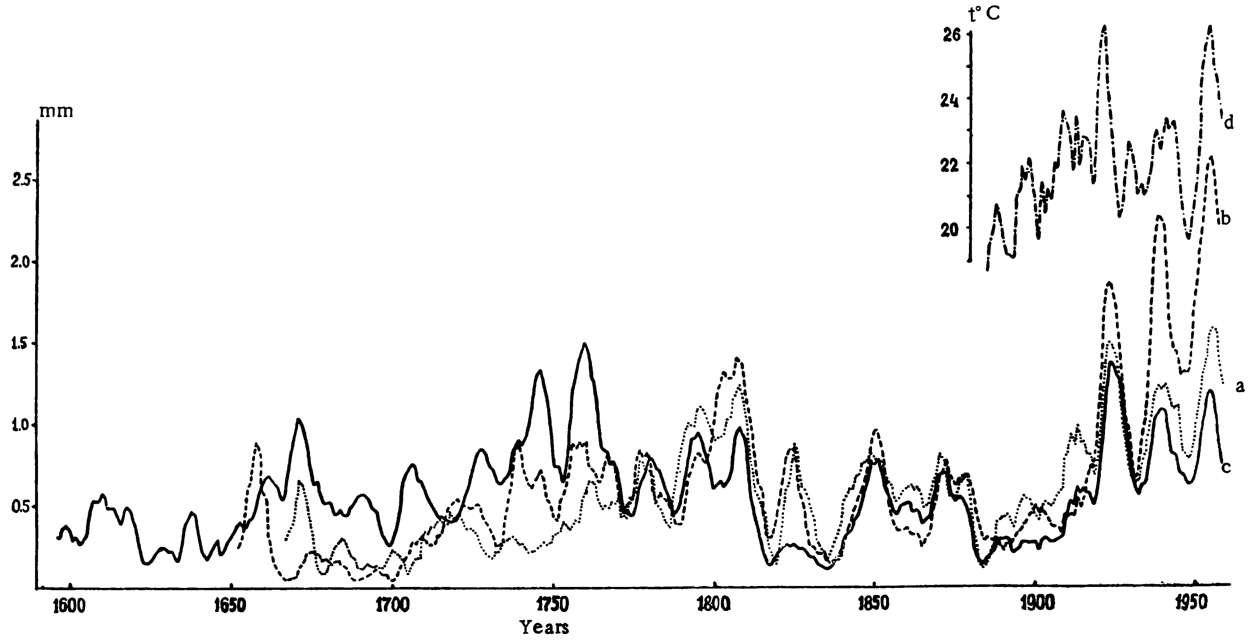

Fig. 2. Fluctuations in growth increment (sliding-scale values of annual rings averaged over a five-year period) of Larix sibirica trees growing in dry (a), humid (b), and marshy (c) habitats in the Sob' River basin (Polar Urals). Each curve has been plotted after analyzing ten model trees. In the upper right corner, fluctuations of summed mean monthly air temperatures during June and July in Salekhard (d) during the 1883-1960 period (mean five-year sliding values).

In the Austrian Alps (Glockner massif), European spruce (Picea excelsa) forms the upper forest limit in localities with more abundant precipitation (Bohm, 1969).

Phytoindication of Climatic Fluctuations in the Past

The upper forest limit is rather dynamic and its migration, when not caused by man's activities reflects climatic changes in high-mountain regions (Griggs, 1937; Glock, 1941; Tikhomirov, 1941; Galazii, 1954; Fritts, 1969; Lamarche and Mooney, 1967; and others). When the climate gets colder (and in arid regions, drier) the upper forest limit is lowered, tree stands thin out and die, massive bodies and islets of forests are reduced in area and the viability of the trees is attenuated; there is mass death of young trees and deterioration or complete cessation of forest regeneration both beneath the superior stratum of tree crowns and above the upper forest limit. In contrast, during warm periods (humid in arid regions), active colonization of previously treeless areas by forest, appearance of viable young plants, and increase in stand density and viability are observed.

The period during which the upper forest limit had been going down or up in the past can be determined on the basis of dendrochronological data in conjunction with material on the age structure of tree stands and with the results of carbon-14 dating.

Dendrochronological methods are based on studies of the variability of annual growth increment of trees and shrubs. At the upper forest limit, in the humid regions of the temperate and subarctic zones, the magnitude of annual growth increment is affected most by the thermal conditions during the vegetative period, particularly during the warmest month – July (Erlandsson, 1936; Hustich, 1945; Schove, 1950; Eklund, 1957, 1958; Mikola, 1962; Kolishchuk, 1958; Shiyatov, 1965). By analyzing the variability in width of annual tree rings one can form judgments about annual fluctuations in thermal regime during a period equal to the maximal life span of woody plants. Conifers are used most frequently in dendrochronological analyses, since they have a longer life span and readily discernible annual layers; they are also very sensitive to climatic changes and their wood is more resistant to decay. In order to eliminate the possible effects of other factors on the magnitude of annual increment, the model trees should be chosen in habitats where the effect of the thermal factor is most pronounced (where there are no signs of deficient or excess moisture, fires, or anthropogenic effects). Sections or drill samples are usually taken from the lower part of the trunk (at a height of 0.3 to 1.3 m). Wood samples should be taken from at least 10-30 of the oldest trees growing under similar environmental conditions in order to construct a dendrochronological scale of climatic conditions in the past.

The dating and determination of false and missing annual rings is done in the laboratory. The width of each ring is then measured and ring-width indices are calculated. These indices represent deviations (percent) from the mean or maximally possible increment norm (Antevs, 1925; Schulman, 1956; Rudakov, 1951; Komin, 1970; Shiyatov, 1970), reflecting the essential changes in climatic conditions during the life of the tree.

A generalized dendrochronological scale is built by averaging the indices obtained for each model. By comparing the scale with the data provided by the nearest meteorological stations (Fig. 2) one may establish the relationship between the ring-width indices and individual indices for temperature and moisture conditions. If such a correlation has been found and if it is reliable statistically, quantitative indices may be obtained, characterizing changes in temperature and moisture regime that had occurred during the period covered by the scale.

The fluctuations of ring-width indices in time are, as a rule, of a cyclic nature, being determined by cyclic fluctuations of climate and solar activity. Numerous studies have been devoted to the cyclic nature of tree growth. The great interest in this problem is due to the possibility of obtaining long-term, uniform tree-ring chronologies. These would enable one to form definite judgments concerning the existence of some cycles or other and thus make more substantiated long-term prognoses. Unfortunately, the cyclicity of growth increment has been little studied in high-mountain regions. Kolishchuk (1966) has noted an 11-12 year cycle of growth increment in Pinus mugo in the Carpathians. Lovelius (1966, 1970) has analyzed the increment cycles in trees growing at the upper forest limit in many mountainous regions of the Soviet Union. He believes these regions to be characterized by 20-30-year cycles. Cycles lasting 11.6 and 34.8 years have been noted for the Khibiny Mountains (Vozovik, Luk'yanova, and Myagkov, 1968). In the mountains of the Polar Urals and Central Caucasus (Tagunova, Troshkina, and Turmanina, 1970), 160-180-year cycles have been traced.

While studying the cyclicity of tree-growth increment, researchers encounter difficulties of a methodological nature. The point is that, as a rule, there is no strict periodicity in the fluctuations of ring-width indices. Each tree-ring series usually consists of several overlapping cycles of varying lengths and amplitudes (Douglass, 1936; Sirén, 1963; Komin, 1970a).

Many methods have been suggested for bringing out such cyclicity. Some of those methods reveal only those fluctuations which are close to periodical. The methods employ periodogram and harmonic analyses (Douglass, 1936; Brooks and Carruthers, 1963). These approaches are of limited use, however, since periodic fluctuations are rarely found in tree-ring series. Methods based on the theory of stochastic processes, which allows for fluctuations of cycle parameters within certain limits, have been finding increasing application in recent years. Methods of sliding n-year curve and of differential integral curve (Afanas'ev, 1967) are often employed. Autocorrelation function and spectral analysis (Bryson and Dutton, 1961; Drozdov and Grigor'eva, 1971) belong to the more complex and time-consuming methods. Komin (1970a) has suggested a procedure for breaking down a tree-ring series into simple harmonics by using sliding n-year curves. The procedure consists essentially in gradual elimination of the longest cycles present from further consideration.

By comparing increment charts for trees growing at the upper forest limit in different mountainous countries, one can assess the migration of the upper forest limit and climatic fluctuations in time and space. Adamenko (1963) has found, for instance, that the cyclicity of tree-growth increment and hence of climatic fluctuations is roughly the same for the upper forest limits of Scandinavia and the Polar Urals, with the difference that the onset of corresponding cycles in the Polar Urals lags behind Scandinavia by 25 years.

Judging by the dendrochronological scales, the dynamics of the upper forest limit in the mountains of the Polar Urals is essentially affected by cyclic fluctuations in temperature conditions, which are 160-180 years in duration (see Fig. 2). During the colder periods, lasting 70-80 years, the upper forest limit either stays at the same level or is lowered slightly, whereas during warmer periods, also lasting 70-80 years, it goes up (Shiyatov, 1965).

In contrast to humid regions, in arid mountainous regions, where moisture deficiency is the limiting factor rather than heat deficiency, the rate of annual growth increment at the upper limit is determined largely by the amount of precipitation. For example, in the White Mountains, on the eastern slope of the

Sierra Nevada (south-western USA), the tree-ring chronologies of bristlecone pine, Pinus aristata, reflect annual fluctuations in the amount of precipitation during the winter–spring period (Fritts, 1969; Ferguson, 1969). In such cases, the dendrochronological analysis proceeds according to the procedure described above; however, trees growing in drier habitats, where moisture deficiency is especially marked, must be selected for ring-width measurements.

The age structure of the forest communities at their upper limit may serve as an indicator of a shift in the upper forest limit and, therefore, in climate. To study age structure, special sampling plots are laid out and all the trees growing on them are counted in terms of species and degree of thickness, and model trees are selected. By comparing the ages of model trees one can estimate the degree of uniformity of forest regeneration. If a tree stand consists of several generations with obvious age gaps, it is indicative of alternatively favorable and unfavorable periods for forest regeneration in the past warm and cold periods).

Dead trees and their remains may be dated by the carbon-14 method, based on the ability of plants to incorporate the natural radioactive isotope of carbon, C^{14}, from the surrounding medium. After plants die their C^{14} content decreases gradually because of decay. The time of a tree death is determined by comparing the radioactivity of carbon in its trunk with that in live trees or in the atmosphere.

In order to reconstruct the dynamics of the upper forest limit, it is desirable to employ all the three methods mentioned above: dendrochronology, age-structure analysis, and carbon-14 method. There are so far, unfortunately, very few examples of the combined use of different procedures. Lamarche and Mooney (1967) employed simultaneously the dendrochronological and radioactivity methods. They have found a large number of dead trees and their remains in the White Mountains (Sierra Nevada) and in the Snake Range (Nevada, USA) above the present upper forest limit. Wood samples were first dated by the carbon-14 method. Then a count was made of the annual rings in each sample, and this yielded the calendar times at which individual trees started to grow and died. The migration of the upper forest limit over the past few thousand years was reconstructed on the basis of data indicating the location of model trees with respect to the present-day forest limit and on the basis of their times of establishment and death.

Phytoindication of Thermal Regime

The absolute level of the thermal upper forest limit depends on general thermal conditions and hence on the zonal location of a given mountainous country. The upper forest limit is lowered gradually as we move from the equator toward the poles and as the corresponding amount of solar radiation grows smaller (Hermes, 1955). In the northern hemisphere the gradient of change in the location of the upper forest limit is about 100 m per 1° of latitude. Another important factor determining the upper-limit level is the degree of continentality of the climate. Given the same geographical latitude, the upper forest limit is higher in regions with a continental climate than in regions with an oceanic climate (Brockmann-Jerosch, 1919). This relationship can be traced not only for mountain systems sufficiently remote from each other but also for the same system by comparing the levels of the upper forest limit on macroslopes differing in degree of continentalness of the climate (e.g., western and eastern slopes of the Urals). Thus, a deviation of the thermal upper forest limit on a particular slope from the mean level established for this particular latitude, serves as an indicator of the degree to which a given climate is oceanic or continental.

Interesting relationships have been found to exist between the upper forest limit level and the thermal conditions during the vegetative period. In the Alps, the mean temperature at the upper forest limit varies from 7.8 to 10.8° in July (Brockmann-Jerosch, 1919); moreover, its values are higher at the periphery than in the central part. Schroter (1928) believed that the mean noon temperatures during July exercise decisive influence on the position of the upper forest limit; in the Alps these range from 10.9 to 14.8°. In the Carpathians the upper forest limit coincides with the July isotherm for +10.5° and the line connecting the points at which the temperature of the air is above 10° during the 60 days of the vegetative period (Vincent, 1933). Davitaya and Mel'nik (1962) have demonstrated that summated active temperatures (above 10°) reflect more accurately the dependency of the position of the upper forest limit on thermal regime; they are rather stable in different mountain systems and do not exceed 200-300°.

Thus, the level of the thermal upper forest limit may serve as an indicator of thermal regime during the vegetative period (July isotherm of about 10°, mean noon temperature in July, close to 12°, and the sum of active temperatures which is roughly 200-300°).

Also, the species composition of trees and shrubs growing at the upper forest limit may be indicative of thermal conditions. Different species of woody plants are known to have different cold resistances. For example, Larix sibirica and L. sukaczewii reach the upper limit in regions with a harsh continental climate, low precipitation, and frequent spring and autumn frosts, while Abies sibirica reaches this line in regions with a more humid and warmer climate.

Present-day trends in thermal conditions at the upper forest limit in the temperate zone of the northern hemisphere and in the Subarctic may be assessed on the basis of viability of the woody and herbaceous plants growing here, as well as on the basis of the rhythm of their seasonal development. Those plants should be selected for observations which are most typical of a given altitude zone (subzone, belt), termed "key zonal indicators." In the course of such studies, systematic mass observations are done on the form of growth and other anatomomorphological characteristics of plants, their annual cycles of growth and development, changes of growth increment in different organs, flowering, fruiting, and propagation both vegetative and by seedage. An attenuated viability of key zonal indicators (stunted growth, loss of the flowering and fruit-bearing stages, absence of reproduction by seedage, etc.) indicates deteriorating thermal conditions in a given region, an impending lowering of the upper forest limit. High viability, intensive expansion beyond the boundaries of the present habitat, on the contrary, indicate an improving climatic situation, a trend toward an upward migration of the forest limit.

The recurrence of late spring and early autumn frosts can also be estimated by studying annual-ring structure in tree cross sections. The rings fix only those frosts which had occurred from the onset of tree growth in thickness till the termination of growth and the lignification of cells. A frost ring differs from the normal one in having a more or less distinct area of injury, where tissue structure is disturbed (there are hollows and intercellular gaps) and the cells themselves are often ruptured and elongated; in conifers the cells are strongly resinous as a result of the abnormal development of a large number of resin ducts (Ivanov, 1961; Glock and Agerter, 1963). To this we may add that the area of injury may lie within both early and late wood, depending on the time of frosts. It is readily determined by examining the rings in transverse sections or in wood drill samples under the microscope. Unfortunately, no one has yet carried out frost indication studies on tree rings under alpine conditions. Our wood samples from the upper forest limit in the Urals indicate that rings affected by frost are very frequent. It seems feasible to be able to establish also from tree rings the recurrence of particularly severe years in high-mountain regions, when meteorological conditions had been unfavorable during both the vegetative period and in winter, as evidenced by injured cambium and by formation of endogenous-alburnum areas in tree trunks.

Phytoindication of Eolian Regime

Winds often change in force and direction in mountains with a strongly dissected relief, depending on local topography. Wind, especially if it is very strong and steady, exerts substantial influence on the appearance of not only aerial but also subsurface parts of plants, as well as their wood structure. The trees growing near the upper forest limit may, therefore, serve as indicators of eolian conditions.

Phytoindication is useful in assessing the direction and relative force of prevailing winds in separate areas of upper forest limit.

The predominant wind direction at the upper forest limit is established by the orientation of the flag-shaped crowns of trees and shrubs, by the orientation of the best polished trunk surface, by that of the trees blown down by winds, asymmetric root systems, and the orientation of eccentric annual rings. Due to the desiccative effect of wind, buds and sprouts die on the windward side of trees, with the result that lopsided, flag-shaped crowns are formed, oriented in the direction of wind. Windblown snowflakes and ice crystals polish tree bark on the windward side slightly above the snow-cover level (for details concerning tree crowns formed under the influence of wind and snow polishing see Gorchakovskii and Shiyatov, 1971). The polishing is more in evidence on the trunks of large trees, particularly conifers. The best polished part of bark surface faces the direction from which the prevailing winds blow. Overturned (uprooted) or wind-broken tree trunks are for the most part oriented with their crowns in the direction of prevailing winds.

Due to the constant swaying and wind load applied mainly in one direction, the root systems are developed unevenly. Our observations in the Polar Urals have shown that a symmetrical root system with first-order laterals branching in all directions are to be found only in young trees of Larix sibirica. As the trees grow the wind load increases; moreover, as the trunk is swayed by wind, the root branches lying on the windward side first break off and then die. At the same time, the branches running in other directions, especially leeward, are preserved and become thicker as the tree grows. The resulting root system

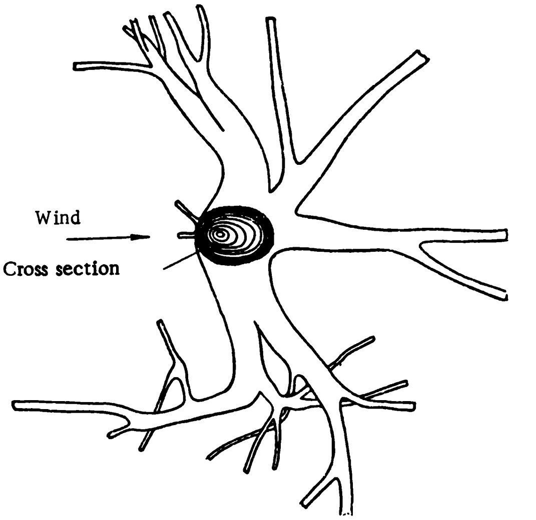

Fig. 3. Asymmetrical root system of Larix sibirica, formed as a result of uneven wind load (indicator of the direction of prevailing winds). Cross section through the base of trunk shows eccentric rings.

is lopsided and bifurcate, with two or three first-order laterals, more adapted to maintaining the trunk in the vertical position (Fig. 3). Such deformation of the root systems under the influence of wind load has been noted previously (Fritsche, cited after Razdorskii, 1955). Asymmetrical root systems are orientated in the direction of prevailing winds; they may serve as indicators of that direction.

The trunks of wind-swayed trees are eccentric in cross section. This seems to be due to the retarded flow of plastic substances through the phloem and uneven development of cambium because of the strains and stresses arising in the trunk. The rings are wider on the leeward side in conifers and on the windward side in deciduous trees. The eccentricity is more marked at the base of the trunk. In a cross section of a growing tree, the line running along the longest radius from the central ring in conifers or along the smallest radius in deciduous trees indicates the direction of prevailing winds.

The flag-like shape of crowns, degree of trunk polishing by snow, the dominant forms of woody plants (straight-trunk form, creeping form, or shrub), coefficient of leaning, and expressiveness of the eolian type of the upper forest limit all may be used as wind-force indicators in a given area of the forest limit.

The flag-like shape of the crowns and the squatness of trees growing at the upper forest limit are proportional to wind force. Where the trees are protected from the wind they have symmetrical crowns. A scale expressing the degree to which the flag shape is developed can be worked out for each plant species and used as a relative wind-force indicator (Yoshimura, 1971). Creeping and shrub-like forms of tree growth develop under harsher wind conditions as a result of recurrent death of apical shoots. The predominance of the creeping and shrubby forms is an indication of harsh wind conditions, and that of trunk forms indicates favorable conditions. The force of wind in some particular area may be estimated indirectly by calculating the leaning coefficient C_L (ratio of ring thicknesses along leaning radius r_L and tractional radius r_T). For conifers $C_L = r_T/r_L$ (Turmanina, 1968). The higher the values of the leaning coefficient the harsher are the wind conditions. It may be that comparing the leaning coefficients for different periods of the life of a tree we might be able to draw inferences about changing eolian conditions in a given area.

In addition, wind force on some particular slope may be estimated according to the degree to which the eolian type of upper forest limit is expressed, since it marks off the areas where permanent winds are strongest.

Using the direction in which the flag-shaped crowns are orientated as the main indicator, Yoshino (1967) has compiled a map of local wind situation for the upper levels of Mt. Neko and Mt. Adzuma in Central Japan. The same author (Yoshino, 1964) and Holtmeier (1971) provide analogous data for some regions of the Swiss Alps.

Our studies in the vicinity of the Konzhakovskii Kamen' massif in the North Urals (Gorchakovskii and Shiyatov, 1970) enabled us to determine the characteristics of wind situation on the slopes of major bald peaks and in mountain passes (Fig. 4). It turned out that, on steep windward (western) slopes of major massifs with pronounced treeless areas, the flag-shaped crowns were orientated, contrary to our expectations, westward instead of eastward. This indicates that when air masses coming from the west collide with the treeless bald peaks, a countercurrent of air is set up at this altitude (see also Sokolowski, 1928), so that easterly winds prevail here. Westerly winds prevail on the western slopes of low passes that do not present an appreciable obstacle to air masses. The same wind direction prevails on the eastern slopes of the passes as well. Near the passes, on both western and eastern sides, the flags of the tree crowns are oriented at right angles to the upper-limit line, that is, eastward in vertical projection. On the northern, southern, and – in terms of exposure – related slopes of major massifs the flags are aligned parallel or at acute angles to the upper-limit line (see Fig. 4). This indicates that air masses

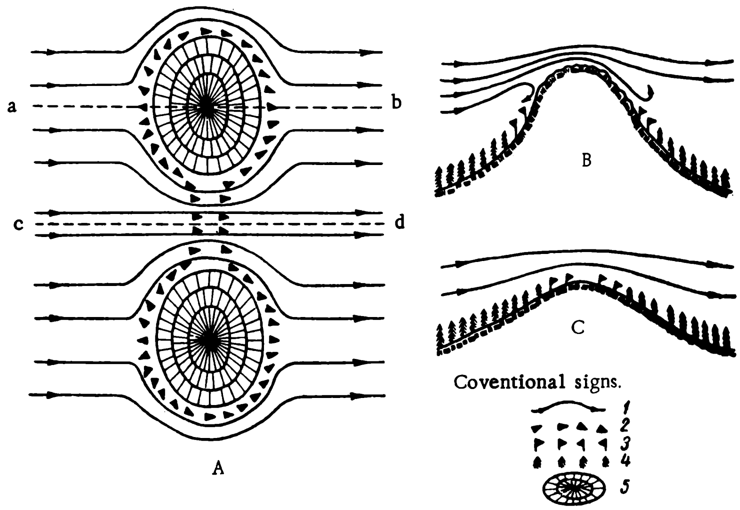

Fig. 4. Typical wind situation near the upper forest limit in the North Urals as revealed by phytoindication: A) Massif with two treeless major peaks and a pass between them (plan); B) vertical profile of the treeless peak along a–b; C) vertical profile of the pass along c–d; (1) direction of wind; (2) trees with flag-shaped crowns at the upper forest limit (plan); (3) the same in profile; (4) trees with symmetrical crowns; (5) treeless peak (plan).

circumvent the massifs from north to south at the level of the upper forest limit. In the North Urals, small mounds up to 1000 m in height with not too pronounced bald tops do not affect the direction of winds to any appreciable extent. The flags are oriented eastward on their slopes everywhere.

CONCLUSIONS

1. Phytoindication of climatic conditions at the upper forest limit is based on the assessment of the effect of climate as a whole or of the individual climatic factors resulting in a given situation (thermal regime, conditions of humidity, winds) on the composition and structure of forest communities inhabiting the upper forest limit, on the shape of aerial and subsurface parts of woody plants, rate of annual growth increment, and wood structure, as well as the viability and seasonal rhythmicity of plant growth and development.

2. The standard procedures involved in phytoindication studies under alpine conditons include mapping the upper forest limit, breaking it down into ecological types, which are determined on the basis of limiting ecological factors (thermal regime, winds, rock content in the substratum, etc.) and into physiognomic types, which reflect the diversity of the species composition and structure of forest communities at their upper limit.

3. The use of phytoindication as an adjunct to the data obtained by climatic studies of particular territories by conventional means makes it possible to assess the climatic differentiation of habitats at the upper forest limit, the chronology of types of mesoclimate, climatic fluctuations in the past over a period far in excess of the period of existence of the oldest meteorological stations, the thermal regime of the vegetative period, and the wind situation (prevailing direction and force of winds in discrete ecotopes).

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