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**SYSTEM OF TIMBERLINES ON THE EARTH**

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Dans l'article nous résolvons surtout la conception des limites de la forêt et d'arbre du Globe, leur système. Nous distinguons les limites de la forêt horizontales et verticales. Le cours des limites par rapport aux facteurs limitants, les questions terminologiques, les définitions d'après les critères exacts avec la possibilité de tracer la limite forestière comme la ligne dans une bande de transition de la forêt au bord des zones forestières, sont le sujet de notre attention dans l'article. Nous avons adopté une attitude aux opinions diverses sur la savanne et la steppe, de sorte que nous les voyons du point de vue des limites de la forêt et d'arbre. Nous présentons les grandes différences des limites mentionnées dans l'hémisphère du sud et du nord, notre avis y compris.

The timber and tree lines are an important vegetation and also landscape phenomenon. For regional characterization of the vegetation cover, in order to obtain a picture of spatial arrangement of whatever section of the Earth surface, for physico-geographical regionalisation, for planning in the landscape with the objective to use it optimally it is necessary to give higher precision to, also to unify boundary phenomena in opinions and concepts, including timber- and tree lines. This is our main objective. The information on the altitude and course of timberlines on the Earth which we present is on the whole more of informative, general character just because of not cleared up and not uniform concepts and the individual view as well as not uniform valuation of timber- and tree lines resulting from them.

We understand under the term of tree and timberline phenomena only at transition of forest zones into non-forest zones in horizontal and vertical direction. There is a transition girdle (ecotone), conditioned climatically, in which, however, (more in details) also further, non-climatic factors, limiting development of forest, can be taken into consideration (soil conditions, activity of man and other). Therefore the concept of the upper timberline cannot be used in case when the forest ends at the foot of a rocky summit cap of a mountain deeply below the level of the occurrence of phenomena characteristic (conditioned

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climatically) of the timberline (for instance, in altitudes of 800—1000 m in Central Europe where sometimes incorrectly the term of lower timberline at transition from the forest cover of the mountains into deforested lowlands or depressions is used).

Three forest zones on the Earth are separated by non-forest zones. The tropical forest zone (on both sides of the equator) is separated by dry non-forest zones from forest zones of the temperate zones, which are bordered by cold non-forest zones from the polar side. In mountains the forest area is bordered by the upper timberline from above. In dry non-forest zones with higher altitude humidity increases so that conditions for development of forest are formed in more higher altitudes only. Downward the vertical forest girdle passes into dry non-forest formations so that it is bordered by the lower timberline. The forest zones of the temperate zones are bordered by the polar timberlines, arctic on the northern and antarctic on the southern hemisphere, from the side of dry zones by the northern subtropical (on the northern hemisphere) and southern subtropical timberlines (on the southern hemisphere). The tropical forest zone is bordered by the northern and southern tropical timberlines (Fig. 1). They are horizontal timberlines taking their course outside mountains. We do not include the timberlines in the mountains in the horizontal ones (e. g. the northernmost promontories of the forest in the mountains in the arctic timberline) as we distinguish the lower and upper timber lines in them only.

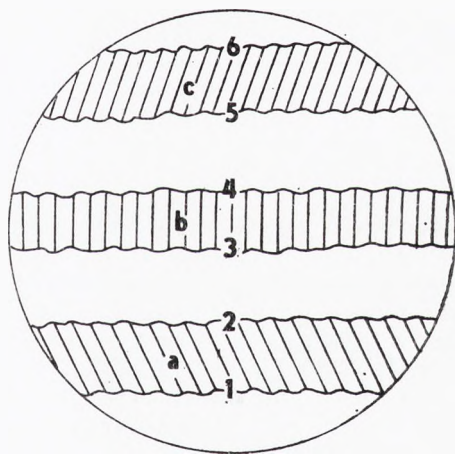


Fig. 1. Scheme of horizontal timberlines on Earth. 1 — Antarctic timberline; 2 — Southern subtropical timberline; 3 — Southern tropical timberline; 4 — Northern tropical timberline; 5 — Northern subtropical timberline; 6 — Arctic timberline; a — forest zone of the southern temperate zone; b — tropical forest zone; c — forest zone of the northern temperate zone.

There is much unclear to chaos in placing of the timberline in the girdle transitional from the forest to non-forest zone. In literature under the term of forest tundra and forest steppe unambiguously the girdle of territory is designated, in which forest associations are alternating with tundra or steppe associations. These transitional girdles are even hundreds of kilometres wide. Where then the timberline has to be placed as a line, for instance, in a map of large scale? For this purpose precise criteria must be established so that the timberline should be measurable and comparable. A landscape, though with

certain vegetation processes phenomena already observed, characteristic of the timberline area, however, where the forest is still overwhelmingly prevailing over non-forest associations, belongs to the transitional boundary girdle of the forest zone. Ecologically, however, it is very different from the territory, hundreds of kilometres far away, where low trees and their groups scattered sporadically in the tundra vegetation only. According to the up to present criterion, which we already mentioned, both types belong to the forest tundra. It is the question of the personal opinion of the author where he will place the timber- and tree line. Then it is no wonder that the differences in the course of the arctic timberline, which is mostly studied from the horizontal timberlines, attain even several degrees of latitude for equal localities some authors (for instance, in the Hudson Bay region).

The timberline is virtually a transition girdle of territory where the forest is passing into non-forest formations. It is the widest, most general definition for the timberline. For its more precise delimitation, so that it could be measured and recorded in the map as a line, we must define it according to precise criteria, which can be established objectively (Jeník, Lokvenc 1962, Plesník 1956, 1971 and elsewhere), mainly differing regionally in what the inhabitants of the given area consider as forest, what is their idea of it. Birch stands (*Betula pubescens* ssp. *tortuosa*), spread along the northern margin of the boreal zone of Northern Europe are considered as forests by inhabitants of northern Scandinavia whereas a Central European would range a great part of them to bushes.

In the transition girdle between the forest and non-forest zone the part adjacent to the forest zone is usually more of the character of forest than of non-forest stands. We consider as a criterion for main division of the transitional girdle the prevalence of the fundamental associations: we range the part of the girdle with areal prevalence of forest stands (where the forest takes up at least 50 % of the surface) to the forest zone, the second part to the non-forest zone. The line separating these two parts is the timberline. It is necessary to separate the forest part of the transition girdle from the forest body where there are already no phenomena characteristic of the transition boundary girdle and to express it also by a term. We designate the part of the transition girdle with prevalence of forest at its transition to the tundra as the tundra forest, the part on the other side of the timberline as the forest tundra (Fig. 2). We propose to apply an analogous principle also at transition of the forest to dry non-forest zones. The timberline divides the transitional girdle into the steppe forest adjacent to the forest zone and forest steppe lying beyond the timberline. The term of steppe forest cannot be used for the xerophilous forest with steppe elements in the undergrowth, as is also indicated by Walter (1968). More complicated is the situation of division of the transitional girdle at the margin of the tropical forest zone for disagreement of the views on the savanna (see next).

*The arctic timber- and tree line* essentially depends on the temperature conditions and duration of the vegetation processes (growing) season. Its ecological parameters have much in common with other timberlines, limited by lacking heat. Its course and character are influenced by permafrost as a particular factor. The thawing depth of the surface layer influences the root system of trees. The permafrost, however, by more cooling of the soil from below slows

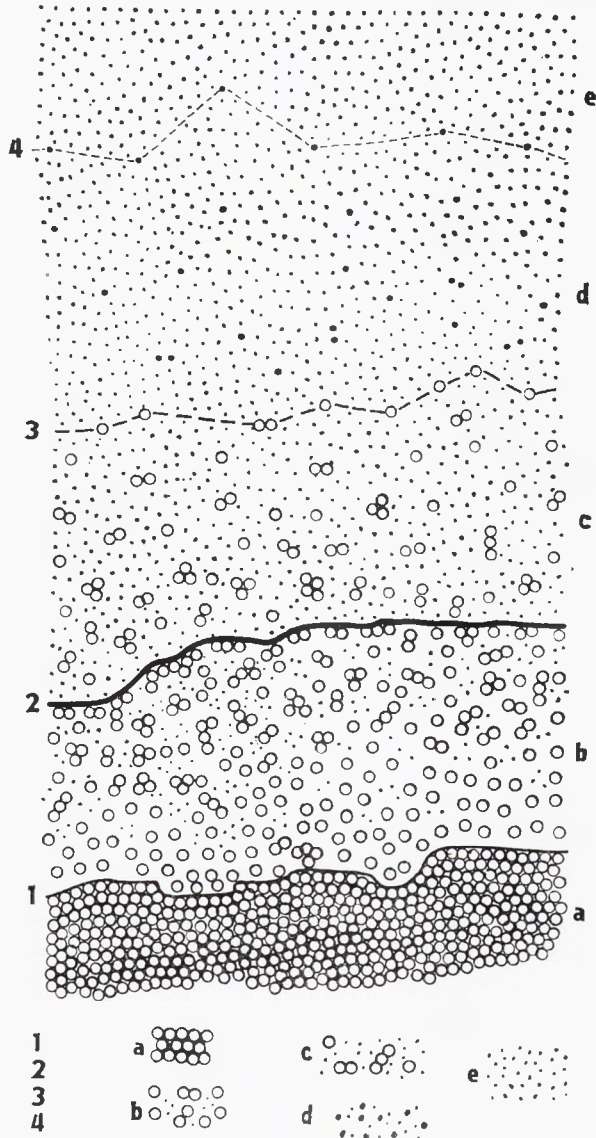


Fig. 2. Transitional girdle of forest to tundra. 1 — Limit of closed forest; 2 — Timber line [canopy of crowns 0,5—0,9]; 3 — Tree line; 4 — Stunted tree line; a — completely closed forest; b — incompletely closed forest with enclaves of tundra associations [tundra forest]; c — tundra with individual trees and their groups; d — tundra with stunted forest trees; e — tundra without stunted trees.

down growth processes of trees, mainly in spring. It shortens the vegetation processes season and, moreover, has an unfavourable effect on wood species

due to loss of water by evaporation in a time when already the sun is heating the bark and the roots still cannot draw it from soil.

The course of the arctic timberline roughly coincides with the July isotherm  $+10^{\circ}\text{C}$  (Fries 1913, Pohle 1917 and other). The data of Prozorovski (1956, 295) that the average July air temperatures at the southern tundra zone boundary attain  $+13$  to  $+14^{\circ}\text{C}$  are surprisingly high and can be hardly put into connection with the arctic timberline. As the course of the arctic timber line is essentially decided by temperature conditions in the growing season, fundamental differences in the position of the arctic timberline are in continental and oceanic regions. Very low winter temperatures in the vegetation inactivity season are also not decisive (Oimjakon with record temperatures even below  $-70^{\circ}\text{C}$  is lying in the taiga). In extreme continental areas of northern Siberia (in the area of Dolna Chatanga) the arctic timberline or tree line reaches  $72^{\circ}40'$  N. In North America it reaches farthest to the north  $68^{\circ}13'$  in northwestern Alaska. In areas with oceanic climate it comes down to lower latitudes, warm and cold sea currents have a significant influence. At the coast of Kamchatka the arctic timberline reaches nearly  $59^{\circ}30'$  N. At the eastern coast of the Labrador Peninsula, mainly owing to the cold Labrador current, it comes down even to nearly  $53^{\circ}\text{N}$ , similarly as on the Alaska Peninsula, in the Hudson Bay different data are mentioned (from  $55^{\circ}30'$  to  $50^{\circ}\text{N}$ ).

*The antarctic tree and timberline*, influenced by extreme oceanic climate and strong western winds, essentially differs from the arctic one. It takes its course in essentially smaller latitudes than the arctic one. To the south it reaches as far as the south of South America,  $56^{\circ}\text{S}$ , at the islands in the South Atlantic around  $40^{\circ}\text{S}$  and in the Indian Ocean about  $38^{\circ}\text{S}$  only. Not only the position in lower latitudes, wood species composition, but also ecological parameters and the total character are quite different at the antarctic timber- and tree line than at the arctic one. Whereas the course of the latter roughly coincides with the July isotherm  $10^{\circ}\text{C}$ , similarly as also of the upper timber line, e. g. in the West Carpathians, the climatic factors limiting development of forest and tree in Subantarctica have not been sufficiently known so far. At the small Gough Island in the South Atlantic, almost untouched by man (Walter 1968, 585), lying at  $40^{\circ}19'\text{S}$ , there is no tree vegetation although the average annual temperature of the air attains  $11,7^{\circ}\text{C}$  and month temperatures are varying from  $10^{\circ}$  to  $14^{\circ}\text{C}$  (Biro 1965, 362) and the average month minima and maxima are between  $2^{\circ}$  and  $24^{\circ}$ .

These very different limiting climatic values are obviously connected with different ecological pretensions of wood species at the arctic and antarctic timber lines. Mutual territorial isolatedness and extreme oceanity of the climate in Subantarctica have influenced development of vegetation very much. In the time of great climatic changes since the Pliocene, when compared with the northern hemisphere, they had more a conservational effect. They have made possible to preserve the species from older warmer periods. Small differences in temperature as well as territorial isolatedness and lacking larger dry Earth mass areas with rich landscape differentiation in Subantarctica restrict vegetation development differentiation. This is also testified by high representation of paleoendemics at the Subantarctic islands, also by climatic parameters of wood species at the timberline. There are probably wood species older in development, already more torpid, ecological relations of which were



fixed in earlier, warmer periods and present-day changed climatic conditions are already more limiting them. The differences in limiting climatic parameters at the arctic and antarctic timber- and tree line lie in different development of vegetation, resulting from distribution of dry land and water and in the final effect in different representation of ecologically plastic, adaptable species.

*On horizontal timberlines*, caused by lacking humidity, is very little information. Therefore we were concentrated on problems, which are connected with them. The *northern subtropical timberline* borders on the southern side the forest zone of the northern temperate zone. At the Eurasian continent oceanity and continentality of the climate have great influence on its latitudinal extension. The distinct monsoon climate in southeastern Asia where the largest continent encounters the largest ocean surface reaches far to the north. The tropical rain forests are passing without interruption at the margin of the continent and at islands into evergreen forests of the subtropical and warm part of the temperate zone, which are connected with the boreal zone of the taiga in northern direction. The continuous girdle of forests in longitudinal direction from the equator to the arctic timberline is not providing space for the northern subtropical timberline.

In the oceanic region at the west of the continent the forest area of the Mediterranean evergreen vegetation extends to the south to Africa and penetrates deeply to the Eurasian continent. There are essentially mountain areas (thus vertical timberlines), in places (mainly in the Sahara) it forms also the northern subtropical timberline. In eastern and southeastern direction (deeper into the continent) continentality increases. Winter frosts are stronger, gradually limiting the area of evergreen hard-leaf vegetation. Instead of it in continental drier areas (also in the Mediterranean region with more intense winter in upward direction) deciduous, in summer green leafy forests set in. With growing continentality to the interior of the continent summer temperatures and evaporation increase very much so that the annual precipitation total is not sufficient for development of tree vegetation. Steppes set in, passing into semideserts and deserts with cold winter at higher drought. In the temperate zone steppes and cold deserts form an extensive forestless zone from the East Asian oceanic to the Mediterranean region. At their contact (including the boreal zone) with the forest zone of the temperate zone the northern subtropical tree and timberline takes its course.

The transition of Mediterranean evergreen wood species vegetation to the zone of subtropical-tropical semideserts and deserts is quite sudden. The transitional girdle with grass formations is indistinct and even disappears. It highly contrasts with the wide zone of steppes between deserts with cold winter and broadleaved (nemoral) deciduous forest. The cause of this phenomenon lies in different resistance to drought in the vegetation processes season. Evergreen hard-leaf wood species are better adapted to it by their xeromorphic structure, however, do not endure stronger frosts. The transition of forest to semideserts is quite slow and gradual (in accordance with gradual decrease in moisture), what may be observed well at the evergreen hard-leaf wood species vegetation in California where the vegetation cover is more preserved than in the Mediterranean region. Deciduous broadleaved wood species are less resistant to drought. For instance, in the time of acute lack of moisture in early

autumn the leaves fall prematurely. Resistance to drought is revealed by precipitation and temperatures in the timberline areas. The northern subtropical timber- or tree line ends in Africa at the coast of the Mediterranean area between Benghazi and Alexandria. The average annual precipitation total in Benghazi is 266 mm, the average temperatures of July are 28—30 °C in the area of the northern subtropical timberline in North Africa (orientation data according to Fiziko-geografičeskij atlas mira 1964). On the contrary, in the northern part of steppes in Europe south of Kiev the average July air temperature is only around 18 °C and the annual total of precipitation 450—500 mm. The differences are too great also when we have objections against ranging of the last mentioned area to the steppe zone.

The zone of steppes reaches (Atlas of the USSR 1969 and other sources) from the mouth of the Danube almost to Kiev (nearly to 50 °N) and from there through the Southern Ural and southern Siberia to Central Asia where it passes into mountains so that the northern subtropical timberline (also in the Southern Ural) is replaced by vertical timberlines. In North America the steppe zone is of longitudinal direction owing to the Cordilliers and rain shadow behind them and extends 54°—56 °N as far as Mexico (Walter 1968, p. 623).

Several pieces of information on transition of forest to steppes, generally used in up to present literature, do not appear to us in full accordance with the regularities of tree vegetation differentiation at timberlines.

The tree and its groups size replace non-forest associations, if they have conditions suitable to development forest formations are winning by their height, space over non-forest ones. If living conditions for the forest deteriorate so much that its very existence is endangered, the forest reacts as one whole by certain measures. It gives information to its constituents, suggestions in the frame of the autoregulation system so that they could resist unfavourable conditions most effectively within the reach of their possibilities. The trees as the lower constituent of the system are subordinate to the forest as a whole. If, for instance, soil conditions are getting worse severely by lacking fine particles soil, the trees reduce their growth to height and in extreme cases are passing into bushes without interruption of crown canopy. Thus the forest is not reacting to lacking nutriments or other constituent of the life-giving complex (water, heat) in a way that as a result of their gradual decrease the trees fall out an the forest as one whole desintegrates so that the strongest individuals could draw nutriments from a larger volume of soil mass and keep by enlarging the root system in the released space. So the trees rather prefer „sharing“ with a small portion of nutriments to disintegration of the forest into individual trees, because the canopy of crowns is the fundamental constituent of forest integrity, protecting the phytoclimate, immensely important for preservation of the forest mainly in dry areas. The canopy of forest prevents from excessive loss of water from soil, keeps higher moisture of air in the stand, makes its better regeneration possible, what is the fundamental prerequisite for the existence of the forest. Grouping of individuals in the struggle for survival, mainly at the boundary of its existence, is thus a general phenomenon (also when in different degree according to light-loving, e. g. other at beech and other at larch (*Larix decidua*)).

Transition of forest to steppe is sudden. Walter (1968, 594—595) also affirms that forest and herb stands in the forest steppe are separated only by a narrow

strip of bushes at the forest margin, what is also valid for the American prairies, which were changed into fields in the last 100 years only. According to Walter (1968) soil conditions are of great importance for representation and distribution of forest and non-forest associations. Deeper, loamy soils usually occupy grass stands. By their dense stoked and continuous stands, rich root system they hinder rejuvenation of trees, because their seeds have not enough moisture here, consumed by grass, for germination. More moisture in soil is below the overrooted layer of grasses only. According to Walter (1968, 595) the trees are able also to grow in steppes for climatic reasons. On shallower, more skeletal soils grass stands are not so dense and compact so that the seedlings of trees get a footing more easily. Beside that wood species roots can also use waters in rock joints here so that such surfaces are usually occupied by forest. An analogous principle of competition and distribution of grass and tree stands is mentioned by Walter (1962) also for savannas.

How to value, however, the occurrence of isolated trees and their groups or forest islands (without influence of groundwater), deep in the steppe territory, hundreds of km far away from the timberline, which we observed in the European part of the USSR, but also in American prairies? Is the great (even more than 100 km) distance of the tree line from the timberline a normal natural phenomenon? If in the steppe the tree is able of normal development, weakens competition ability of grasses by overshadowing (also on deeper loamy soils), reduces evaporation from soil and makes possible to get a better footing for seedlings below tree crowns. Anomalous years with extreme dry growing season affect more isolated trees in the steppe than forest islands, diminishing mutual distance of the timber- and tree line. Climax associations in the warmest parts of Slovakia, neighbouring on extensive warm lowland areas of Hungary, are forest associations. This territory is far away from the forest steppe zone. The pusztas in Hungary are not climatic steppes. There are no essential differences in temperatures of the warmest month and in precipitation in the vegetation processes season as well as in representation of tree species between lowlands of southern Slovakia and territories designated as steppe ones not far away from Kiev. I even do not speak about the prairies where annual rainfall is 600—1000 mm, with precipitation prevailing in summer, in spite of that in North America wood species with different ecological pretensions can be concerned when compared with European forest steppes. Our considerations and objections set out from doubts about the extent of steppes, fixed in literature. Steppe areas in Eurasia belong to old cultural territories. Far from the steppe zone boundaries the steppe plants and animals are being spread by forest removal and extension of secondary steppes. Large territories, designated as steppes in literature, are former forest areas without climax steppes. The steppe zone requires conceptual revaluation on a wide ecological basis. It is necessary to take into account the climatic parameters and existence limit pretensions of woody species, to trace biometrically the life processes and their external manifestations under concrete situations in the vegetation processes season, the capability of reproduction and competition of wood species with herb species, mainly grass groupings, in relation mainly to substrate-soil conditions (this was already partly investigated). Phytocenological methods are important, however, not sufficient alone, as practised mode often. It is also necessary to apply historical, onomastic and other auxiliary methods. There-



fore we also consider our estimation that in central and eastern Europe territories with an annual total of precipitation more than 450 mm and average temperature of July less than 20 °C cannot be taken into consideration as climax steppe territories as informative only and suppose that for development of forest still less favourable climatic parameters are sufficient.

*The southern subtropical timber- and tree line* is less extended when compared with the northern. It is the consequence of the great prevalence of the ocean over dry Earth-mass, high oceanity of the climate and lack of extensive areas with distinct continental climate. In Chile it is formed by evergreen hard-leaf wood species vegetation nearly at 31 °S, in Patagonia in the rain shadow of the Andes the forest passes into the Patagonian steppes. The opinions of the Argentinian pampas are not uniform, Walter [1968] considers them as steppes. In South Africa the continuous forest zone of the temperate belt is missing. The subtropical timberline can be taken into account at transition of the subtropical forest evergreen vegetation to the Namib coastal desert as well as to further forestless areas, mainly caused by rain shadow (in the Cape area, in the Karoo). In Australia the subtropical timberline is formed by evergreen forest vegetation in the southwestern part of the continent with winter precipitation at transition to bush formations (to the north and east) as well as in Victoria where evergreen rain forests of the temperate zone are passing (to the north and west) to open eucalyptus bushes (Mallee).

*The tropical timberline* is of a very idealized course in the scheme (Fig. 1). In any case the section from the Sahara to the Thar desert corresponds to it. Here the trade winds are coming from the continent and are dry. On the contrary, the monsoons blowing from the sea, but also the trade winds passing above the sea suck in much moisture, which they mainly leave at slopes of mountains in the way. Beside that humidity conditions in the tropics are influenced by shift of sun culmination throughout the year and so also the shifts of the whole thermic and hydric system. In the time when the sun is in zenith above the most distant tropic, the system of cyclone circulation of the competent temperate zone and precipitation connected with it shift in direction to the equator and in half a year conversely. Distribution of precipitation in the tropics is much influenced by mountains. Therefore the course of the zone of tropical forests and its boundaries is uncommonly complicated. Owing to the mentioned factors the tropical rain forests push on as far as the tropic area and continuously pass into subtropical forests or to the forest zone of the temperate belt. They take up Central America and reach northerly of the tropic of Cancer. The tropical rain forest passes without interruption from the island world between Australia and Asia to the mainland.

In the southern, more oceanic hemisphere, tropical forests reach still farther beyond the tropic. In South America along the eastern side the girdle of rain and alternating rain forests reaches almost to 30 °S, also along the eastern hillside of the Andes the forest zone surpasses the tropic. Along the eastern margin of Australia the tropical forests are passing continuously into subtropical forests in the southeast of the continent. The timber- and tree line in Africa is much complicated by the so far unsolved problem of savannas, which surround the vast region of tropical (essentially rain) forests of the Congo Basin and coastal girdle of the Gulf of Guinea with adjacent territory.

Is the *savanna* a plant association or transitional territory where forest and

non-forest associations alternate? The opinions of this fundamental question are not uniform. Walter (1962, 247) unambiguously affirms that the natural savanna as grass stand with scattered trees, at a distance 5—10 times their height, is a homogeneous plant association. He designates the grass stand with larger groups of trees to forest islands as park landscape („Parklandschaft“). A considerable part of the authors do not speak explicitly what the concept of savanna includes, however, it results from the sense of the text that they also consider grass stands with groups to small islands of forest (termite, flooded and other savannas) as savannas.

Let us consider the situation in the savanna where a tree can grow for climatic reasons. If somewhere one tree can grow, why also several of them cannot exist together? Is it the lack of water in soil that will sustain one tree, but is not sufficient for several of them? In Serengeti (in the area of Fort Lami), but also elsewhere in Tansania besides isolated trees we have found also groups of trees in grass stands. Walter (1962) attributes a great importance to competition. Mainly on deeper loamy soils grasses form continuous dense stands, in which it is difficult for tree seeds to take a footing. Trees can carry through more easily on shallower, more gravelous soils, in which grass stands are not so compact so that at these places even small islands of forest may originate (on elevations, disintegrated structures of termites etc.). Bushes and trees may get a footing on strongly pastured savannas, because by intense pasturage, trampling compact grass stands are destroyed and weakened by competition. Degradation of pastures takes place. They become overgrown with bushes (Walter 1962) or low trees. In grass stands we have also found (in the vicinity of Serengeti) dense xerophilous bush stands with low tree acacias and xerophilous herbs, with modest representation to lack of grasses.

When such a wood stand could have formed on the degraded pasture and also have developed under the given climatic conditions, the grasses do not push it away so that it becomes a permanent association. In case that man also removed bushes and trees taking a footing on the degraded pasture and then suddenly abandons it, there will be overgrowing with bushes and low trees. If in this or similar form (changed ratio of representation of trees and bushes) they are able to renew and form into a climax association, then their ecological relations are in accordance with the given conditions, also on deeper loamy soils. A definitive withdrawal (irreversible change) of the association can be taken into consideration in relic associations, which are not in full harmony with present living conditions so that when man disturbs them they are not renewed and are replaced by other potential natural vegetation.

The main weapon of wood species in their definitive victory over heliophylliz grasses is shadowing. If it works on degraded pastures, it should also work on undegraded ones. By shadowing of tree vegetation could carry through in competition with grass stands whether an isolated tree (if it casts sufficient shadow) or a group of trees in concerned, also when the extent and position of the overshadowed area with regard to the tree stand is different in the tropics and different outside the tropics. It is necessary to look for further factors in solving the problem of savannas. The classical form of savannas as grass stands with scattered trees fits well for the effect of frequent fires. Dry grass catches fire quickly, not causing serious damage to its regeneration organs.

Even trees with a thick layer of cork are not suffering in their existence by fire passing rapidly from burning grasses. Small bushes and seedlings are destroyed by fire only. The question remains to answer, to what an extent also natural fires (from lightning) are effective here, because the savannas are a cultural territory since long ago, where the shepherd removed undesirable bushes and dry remnants of grasses by fire.

A particular feature on the southern hemisphere are coastal deserts, conditioned by cold sea currents (Atacama, Namib). They reach small latitudes so that the tropical timberline and tree line comes to proximity of the equator, in South America it runs about 4°S and in Africa about 15°S.

In the frame of vertical landscape differentiation in mountains the forest complexes can be bordered by *vertical timberlines*, from above by upper and from below by lower timberlines. In dry zones where the lowermost, warmest parts are without forest because of lacking moisture, the forest can develop in higher parts only as with higher altitude usually moisture increases. Therefore at the margin of forest zones, at transition to non-forest zones, the forest pushes on into dry zones in form of variously wide vertical girdles, bordered by the lower from below and upper timberline from above. The vertical forest girdles are narrowing to wedging out towards the interior of non-forest zones with increasing drought, the lower timberline comes usually distinctly to higher position.

The lower timberlines and tree lines are unambiguously caused by lacking moisture. The question of the limiting factor for the forest at its upper timberline is more complicated. In the depth of dry zones where the vertical forest girdles are already narrow or wedging out the limiting factor for development of forest and tree are the humidity conditions. In mountains situated deep in dry zones (Ahaggar, Tibesti and other) precipitation and total humidity do not display linear increase with higher altitude (Messerli 1973). The occurrence of trees in highest altitude is also running deeply below the level of temperature parameters limiting tree growth.

In temperate zones (besides the marginal parts in neighbourhood of dry zones) the forest is in upward direction generally limited by temperature conditions (in details also other), including the effect of winter conditions. The question of the limiting factor at the upper timberline in *humid tropics* has not been solved satisfactorily. Troll (1960, p. 185) unambiguously considers the drop of temperature and decrease in heat sum as the main factor influencing the upper timberline in mountains of the humid tropics. Some phenomena mentioned by him (e. g. the higher altitude of the upper timberline in valleys than at slopes) may also be a manifestation of the decisive influence of humidity conditions. Small annual temperature amplitudes cause a monotonous course of temperatures throughout the year so that there are no seasons of the year. The temperatures oscillate more during 24 hours, however, roughly equally throughout the year. The growth of wood species at the upper timberline is not interrupted seasonally, however, very slow. Hedberg (1969) has found out at *Dendrosenecio* (*Senecio keniodendron*) at Mt. Kenya (in about 4200 m altitude) that in 19 years it was growing by 45 cm.

At *Dendrosenecio* in east Africa, bound to groundwater, temperature conditions are the limiting factor in high altitudes. They ascend conspicuously above the upper timberline in places with sufficient water in soil. At Kiliman-

jaro we have found in highest position the group of *Erica arborea*, or *Philippia* up to 4,1 m high at the altitude of 3515 m. An isolated individual of *Senecio cottonii* of height 4,6 m is growing only several tens of metres below the saddle between Kibo and Mawenzi, lying at 4350 m. The question arises, what is the cause of such a big difference in altitude, whether only temperature differences or also humidity pretensions of the compared wood species. The broadleaved evergreen rain forest rises to an altitude of about 3000—3100 m in the section Mandara-Horombo. It shows distinct features of the cloud forest. Higher up the ericaceous belt extends, which have a wider ecological amplitude, endure more the drop of temperature and humidity. The features of cloud forest decrease in upward direction in the ericaceous belt and bush, mainly, however, herb vegetation above the bush belt is already of distinct xerophilous character. Above the broadleaved evergreen rain forest belt precipitation rapidly decreases, so that at 4350 m it is 150 mm annually only (Lind, Morison 1974, p. 153).

The moist air in cold high belts of the tropics usually forms vertical fog banks in the timberline area, in which also cold air takes part, moving down from forestless parts above the upper timberline at night. The fogs enlarge the length of diffused radiation to the detriment of direct radiation, still reducing already small temperature amplitudes. They provide precipitation by condensation at contact with the stand (in dry areas they may also exceed the annual precipitation total several times). Owing to them the cloud forest girdle is formed in high positions of tropical mountains with its particular characteristic features.

In high extensive plateau mountains there can be doubling of vertical forest girdles. For instance, moist air driven by winds at the eastern hillside of the Andean plateaus provides sufficient precipitation for the tropical rain forests, usually reaching the eastern plateau margins in form of cloud forest. After transition to the Andean plateaus the currents of concentrated moist air masses are scattered, overheated at day so that reduced humidity often is not sufficient for forest development. The latter gets a footing only higher up, at slopes of high mountains rising from the plateaus.

If we regard the general altitude course of the upper timberlines and tree lines on Earth, we are finding several regular relations. In the humid tropics the highest timberline (climatic) reaches up to 3500—3600 m, rarely also higher (if we do not take *Dendrosenecious*, bound to water or other wood species which are not forming a continuous forest belt into account). The upper timberline and tree line occurs still higher up in the *drier tropics* as well as *subtropics*, however, where is enough humidity. Small groups of trees 4—7 m high, *Polylepis* in the Cordillera de los Andes (in Bolivia) reach the altitude of 4900 m (Koepeke 1961), the highest altitude of the upper timberline on Earth.

In the area of the tropic of Cancer the upper timberline and tree line is found in conspicuously high altitude, however, within the reach of humidity-carrying winds only. At high mountains, rising from the Mexican plateaus, the tree stands of *Pinus hartwegii* reach the altitude of 4150 m (Lauer 1973). In southeastern Asia, within the reach of the monsoons in the Himalaya and in mountains of the warm part of the temperate zone (in China) the timberline surpasses 4000 m altitude. In the mountains of Sikiang it reaches 4500 m



(Hermes 1955). It is to be seen, the upper timberline and tree line is not reaching highest generally in the zone in the equator region, probably due to great cloudiness, which is limiting radiation. In drier zones, with less cloudiness and a greater influence of direct radiation, however, provided that humidity-carrying winds secure sufficient humidity, thermic conditions more suitable to the altitude course of the upper timberline are formed. This is also testified by the fact that in the Himalaya as well as mountains of the warm part of the temperate zone, thus already outside the tropics, the upper timberline altitude is positively influenced by elevated land mass.

In *temperate zones* the upper timberline is generally sinking with higher latitude, roughly proportionally with heat decreasing in the 3—4 warmest months. The temperature conditions in the growing season are, however, much influenced by climate continentality.

In continental regions, owing to higher summer temperatures, the upper timberline is running essentially higher than in oceanic regions. For instance, in the area of Oimjakon in Siberia nearly at 63°N the forest occurs up to 1300—1400 m (Weinert 1966) whereas at the Pacific coast are tundras in the mentioned latitude. The mentioned altitude of the upper timberline differs only very little from the altitude situation of the timberline in lower mountains of Czechoslovakia although these are lying by about 12 to 14 degrees of latitude more southerly.

The great elevated land mass in the temperate zone increases certain continentality features, uncluding rising temperatures in the vegetation processes season, having favourable influence on the upper timberline altitude. In Marmot Creek Basin (nearly 51°N) in the eastern part of the Canadian Rocky Mountains we have found out the upper timberline at altitudes of 2100—2200 m, Hermes (1955) quotes the upper timberline altitude in the area of Mt. Robson (nearly 53°N), which is distinct by elevated land mass up to 2300 m. In the lower marginal parts of the Alps the timberline attains roughly up to 1700—1800 m, however, in the inner parts it reaches almost 2500 m.

The upper timberline and tree line altitude is also depending on ecological properties of the species, which are forming it. There is a big difference in species composition and vertical forest differentiation between the southern hemisphere, including the humid tropics (also their part to the north of the equator), and the northern hemisphere. The main cause of this phenomenon is different oceanity and continentality in combination with arrangement of mountain systems. In Mexico as well as in Southeast Asia mountains of longitudinal direction form bridges for migration of taxa. They have made penetration of development plastic boreal species into the tropics possible. There is, however, not an invasion only, but also species differentiation under new conditions. The tropical landscape with very diverse climatic conditions in horizontal as well as vertical direction, with a rich scale of landscape types from hot humid to warm and dry and in high altitudes even to cold landscapes with richly differentiated soils, changing in the time of great climatic changes as a complex provided conditions suitable to formation of new varieties and species. For instance, Martinez (in Troll 1959, p. 66) distinguishes in Mexico 39 species and 18 varieties of *Pinus* from the total number of about 100 species on the whole Earth. The number of *Quercus* species exceeds the value of more than 200 here. A considerable number of *Quercus*, but also other bo-



real wood species are represented in the tropics of the monsoon region whereas in tropical Africa is a lack of boreal tree species, because there are no connecting mountains with the northern temperate zone.

Quite a different situation is at the southern hemisphere where isolatedness and extreme oceanity of the climate played a significant role in forest vegetation development and cause a great specificity of present vegetation processes conditions. The upper timberline is running much lower here if we compare mountains in equal latitudes on both hemispheres, what may be partly explained by distinct oceanic climate. In Australia at Mt. Kosciusko (about 37°S) the upper timberline rises to 1700—1800 m (Hermes 1955), in Tasmania (to about 42°S) to 1200 m (Schweinfurth 1962). In New Zealand (at about 41°S) in near-ocean mountains the upper tree line rises to nearly 1200 m, to the north at Mt. Ruapehu to about 1500 m and to the south in the southern fiord area it sinks to 900 m (Wardle 1973, A128). In New Zealand the upper timberline and tree line is essentially different in beech (*Nothofagus*) and non-beech areas. Wardle considers as a tree an individual of height 1—2 m (1964, 1965), in further work (1973, 372) 2 m only. *Nothofagus* usually forms monolithic stands, with small admixture of other wood species or without them, which are suddenly ending at the upper timberline. In areas in which *Nothofagus* could not extend in post-glacial time, the forest stands composed of numerous species are gradually passing into subalpine bushes. They are rich floristically (they belong to about 15 genera). With the exception of deciduous *Hoheria* all are evergreen. Their vertical differentiation (division into vegetation belts) is weak. They end suddenly at the upper timberline and tree line, so that Wardle (1973, A134) speaks: „The fact that so many wood species drop out at the same altitude in New Zealand indicates the existence of the fundamental biological limit“.

How to value this exceptionality of the upper timberline in New Zealand? Certain features of forest vegetation point to an analogy with humid tropics (great representation of tree species, little differentiation of woody species into vegetation belts, many lianas and epiphytes). One of the causes of their common appearance are obviously small temperature amplitudes, climate oceanity, including its function in development of vegetation also in the time of great climatic changes. Isolation of islands also played a significant role, as confirmed by considerable representation of paleoendemics. Little differentiation of vertical arrangement of woody species into vegetation belts with higher altitude, the lack of deciduous as well as frost-proof conifers, analogous to boreal woody species, thus lacking ecological differentiation with regard to great temperature amplitudes indicates less ecological plasticity of woody species. Present-day winter conditions, onset of more severe frosts wipe out evergreen species at certain altitude level. Ecological relations of present-day woody species were probably fixed in long past times with warmer, however, oceanic-type climate, which has helped to preserve many species till now. The lack of differentiation, but also further mentioned phenomena point to certain conservatism, antiquity of species, which is connected with their advanced development. *Nothofagus* appears to be a partial exception. This is also indicated by the ability of some species of *Nothofagus* (in South America) to shed leaves for winter. These our considerations are also in accordance with the character and course of the antarctic timberline and tree line.

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## SYSTÉM LESNÝCH HRANÍC NA ZEMI

Otázka lesných a stromových hraníc v doterajšej literatúre je veľmi nejasná, nejednotná, neraz až chaotická. Preto aj údaje o ich priebehu považujeme len za orientačné, opierajúce sa o individuálne názory a posúdenie pozorovateľa. Z uvedených dôvodov nekladíme dôraz na informatívnu stránku ich priebehu a obmedzíme sa len na niektoré základné údaje. V snahe položiť základ pre logické usporiadanie a postupné vykrýšľovanie problémov, predkladáme viaceré otázky do diskusie. Dôraz kladieme na koncepčné otázky lesných hraníc, na ich vzťah k limitujúcim činiteľom, na pojmové problémy, definície podľa presných kritérií, aby sa údaje dali meraním, nie iba odhadom porovnávať, kontrolovať. Zaujímame aj stanovisko k nejednotným názorom na niektoré nelesné formácie (najmä savany) tak, ako sa nám javia z hľadiska zákonitostí diferenciácie lesných a stromových hraníc.

Pod pojmom lesná hranica rozumieme hranicu len v klimaticky podmienenom pre-

chodnom páse [ekoton], v ktorom lesné zóny prechádzajú do nelesných. V tomto ponímaní chápeme doterajší pojem lesotundra a lesostep podľa obr. 2. Lesné a stromové hranice na horizontálne (obr. 1) a vertikálne (v pohoriach).

Arktická hranica lesa a stromu vybieha v kontinentálnych oblastiach Sibíre do 72° 40' s. š., na Aljaške do 68°13', na pobreží Tichého oceána do asi 59°30' na Kamčatke, asi do 53° s. š. na Aljaške, pri Hudsonovom zálive a na atlantickom pobreží Labradoru. Na južnej pologuli následkom extrémne oceánickej klímy prebieha v menších šírkach [56° v Južnej Amerike, asi na 40° na ostrovoch Atlantického oceána a asi na 38° Indického oceána].

V pohoriach vlhkých trópov horná hranica lesa dosahuje zhruba 3500—3600 m. Ešte vyššie vystupuje v suchších trópoch, kde je ešte dosť vlhkosti, v porovnaní s vlhkými však menej oblačnosti. Najvyššie (asi do 4900 m) horná hranica stromu vystupuje v Bolívijských Andách. Vysoko siaha aj v oblasti obratníka raka, avšak len tam, kde vetry prinášajú dostatok vlhky. V Sikiangu dosahuje 4500 m, v Mexiku 4150 m. V suchých pásmach les sa vysúva do vyšších polôh, kde je viac vlhkosti. Vytvára vertikálny pás, ohraničený zdola dolnou a zhora hornou hranicou lesa. S narastajúcou suchosťou do hĺbky suchých pásiem dolná hranica lesa stúpa, horná klesá, takže lesný pás sa zužuje až vyklíňuje.

V mimotropických pohoriach, najmä v nie vysokých zemepisných šírkach, horná hranica lesa sa výrazne dvíha vo vysokých, predovšetkým plošinatých pohoriach. V mierom pásme kontinentalita podnebia (zásluhou teplého leta) veľmi zvyšuje hornú hranicu lesa. Napríklad v oblasti Oimjakon [63° s. š.] horná hranica lesa dosahuje 1300—1400 m, teda takmer takú výšku ako v niektorých pohoriach ČSFR, ležiacich o 12—14° južnejšie. Výšku ako aj celkový charakter lesných hraníc ovplyvňujú aj dreviny, ktoré ich budujú, pretože majú rozdielne ekologické nároky. Najmarkantnejšie rozdiely vystupujú medzi lesnými hranicami v mimotropických oblastiach severnej a južnej pologule. Extrémna oceanita južných častí južnej pologule, izolovanosť, nedostatok väčších súšových oblastí a tým aj nedostatok pestrej palety krajinných typov poznačili vývoj vegetácie aj v obdobiach veľkých klimatických zmien na Zemi. Pôsobili konzervačne a pomohli udržať sa mnohým vývojove starším, ustrnulejším taxónom, čo priam bije do očí pri porovnaní hornej hranice lesa napríklad na Novom Zeelande a v strednej Európe ako aj arktickej a antarktickej lesnej a stromovej hranice.

Obr. 1. Schéma horizontálnych lesných hraníc na Zemi. 1 — Antarktická hranica lesa; 2 — Južná subtropická hranica lesa; 3 — Južná tropická hranica lesa; 4 — Severná tropická hranica lesa; 5 — Severná subtropická hranica lesa; 6 — Arktická hranica lesa.

Obr. 2. Prechodný pás lesa do tundry. 1 — Hranica zapojeného lesa; 2 — Hranica lesa [zápoj korún 0,5—0,9]; 3 — Hranica stromu; 4 — Hranica zákrpkov; a — plne zapojený les, b — neúplne zapojený les s enklávami tundrových spoločenstiev [tundro les], c — tundra s jednotlivými strommi a ich skupinami, d — tundra so zákrpkami lesných stromov, e — tundra bez stromových zákrpkov.