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ACTA FORESTALIA FENNICA

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ECOLOGICAL CHARACTER OF TREE SPECIES AND ITS RELATION TO SILVICULTURE

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Introduction

Those parts of the globe in which true virgin forests are still encountered diminish year by year, constituting an irreplaceable loss to silviculture and its closely related sciences, and so to forestry as a whole. The disappearance of virgin forests puts an end to our chances of utilising the results of many hundreds of years of experiment carried out by Nature. These results reveal in a fairly easily readable form the main features of the development of forests as they appear, at their most natural, in each district. With virgin forests disappearing, we lose, to some extent, the essential means to developing the most profitable silvicultural systems of management, and are forced along the road of troublesome experiments which, in view of the slow development of forests, require tens of years before the results — positive or negative — become available. However carefully planned our experiments are, without the natural basis and course of development provided by virgin forests, they easily become a matter of chance, detached and onesided, and they cannot afford that magnificent all-embracing view of nature and its development that can be given by virgin forests only. Nor can they reveal those great lines of direction to be seen in primeval forests only, which whether we wish it or not, we have to follow to a certain extent if our objective is to carry out a forestry policy far-sighted and producing a high yield.

Preservation of the remaining virgin forests, and a thorough understanding of their succession and structure may still, to a great extent, widen and deepen our views on forest nature, and thus provide irreplaceable guidance to silviculture, guidance that might otherwise remain lost or only be obtained perhaps by experiments of long duration. The ecology of tree species, and the closely attached natural development of forests are, among others, problems to which sufficiently convincing and clear answers may be provided by primeval forests only.

Plant Competition in Tree Stands

Nowhere, perhaps, has the significance of plant competition as a factor of plant sociology been emphasized as strongly as in the Finnish theory of forest site types (C a j a n d e r). One of the most essential features of this theory is that the tree stand is understood merely as part of the vegetation, as a competing member, which in its early stages of growth, however, may rank practically equal with the other members, but later on, being the strongest, may become in fact superior. It always has, nevertheless, a most important influence on the course of the competition; particularly in the competition for nutrients in the soil does it continuously interfere with the others. This view — that a tree stand is part of the plant community only, and thus subject to the same laws as the other members of the plant community — is what, from the viewpoint of plant sociology, brings the most essential features and the broad lines of development of tree stands into the foreground, and facilitates their understanding.

Plant competition is present in nature wherever climate and soil are so favourable that vegetation may grow dense enough, that is so dense that individual plants come into contact with each other. Always and everywhere in nature, the disseminules produced are infinitely more abundant than is the space available for the growth of mature individual plants, and as no plant individual is prepared to step aside voluntarily, the plants are engaged in a competition in which some of them must be destroyed. Plant competition, naturally, is entirely blind, but, over a long period, the course it takes and the final result are unfailingly characterised by the region and habitat in question.

Plant competition always implies the elimination of a part of the plant population. If a free habitat, e.g. a burnt area, is in question, the first vegetation on it may consist of all the plant species and biotypes the disseminules of which can reach the place, and the minimum requirements of which this habitat satisfies. When the vegetation gradually becomes so dense that competition commences, the biotypes and species of the population that disappear first are those which find it hardest to thrive on the particular habitat. In the succeeding phases, with competition becoming

more and more fierce, the species most foreign to the habitat are eliminated until finally those remaining consist of the species and of the biotypes strongest of all on the habitat concerned and mutually so equal in strength that they are unable to eliminate each other. The habitat thus acquires a vegetation characteristic of it in every respect, one in which no further changes of note take place, or in which the changes are very slow and gradual. *The tendency of this development, present everywhere, is thus from a vegetation often consisting of a great number of species and, above all, of very haphazard composition, to a regular plant community of characteristic features, in which one species, or in any case as few species as possible, mutually equal in strength, with biotypes best suited to their habitat, predominate.*

Plant competition, similar to that taking place in the field layer of vegetation, also goes on in a tree stand between individual trees and tree species. In the same way as in the field layer, if continued long enough undisturbed, it leads to final regular plant communities, as simple as possible particularly as regards the species present. It similarly leads to an exactly corresponding result in the development of a tree stand, independent of whether the most barren lichenous woodlands of the farthest North, or the most luxuriant conditions of tropical rain forest are concerned. Outwardly, these extremes seem to have nothing in common, but before they reached the final stage they passed through a process of development on the very same lines.

As a final stage of this successional development a stand characteristic of each habitat is produced, either a pure stand formed by one tree species, or a permanent mixed stand. The succession of species and the development of the inner structure of a forest has then reached a stage fairly permanent on the habitat in question, a climax stage, which in its essential characteristics remains stable as long as climatic and edaphic conditions remain, in general, unchanged, and as long as no catastrophe disturbs the development of the stand.

Consequently, if the competition is allowed to continue undisturbed the strongest tree species, biotypes and individuals only will remain. This is most distinctly seen in poor external conditions, in which the flora of tree species is relatively scarce. There the stands, with undisturbed development, would develop, primarily, into pure or fairly pure stands, in the extreme case to one-étage stands formed by a single aggressive tree species. In favourable external conditions, on the other hand, in which the tree flora is rich in species and in which, consequently, there are numerous tree species of equal strength competing with each other, the final stage is much more heterogenous, in the extreme case a veritable tropical rain forest, a permanent, multiétage mixed stand (Cajander 1909). Different as these extreme cases are, a feature common to them is, however, that in both development has resulted in the greatest possible simplicity and regularity, and in each case the final stage represents the stage of greatest simplicity and regularity in the conditions of the region in question.

It is seldom, however, even in natural conditions, that forests reach this final stage of climax, the attainment of which requires 100—500 years. In most cases succession is interrupted by forest fires, hurricanes, etc., and returned to its initial stage again. In forests under human management, again, development is in the majority of cases interrupted by cuttings, and for this reason such forests as a rule remain more heterogenous in structure than primeval forests. It is of the greatest importance, however, to ascertain that, from its earliest origins, the stand of each habitat starts developing towards a given goal, characteristic of it. This development may, by various silvicultural methods, be either expedited or retarded, but its course cannot be changed. Particularly from a silvicultural point of view is this of considerable significance.

Succession of Tree Species in Finnish Forests

The present composition of tree species in the Finnish forests is a result, primarily, of forest fires that have raged through all time, and of the primitive method of agriculture in general practice until the beginning of the 20th century — cultivation by burning-over — even if, more recently, cuttings in particular have added many new features to their character.

On dry gravel, sand and fine sand soils the influence of forest fires on the composition of tree species has been fairly slight because of the fact that in Finland Scots pine only, *Pinus silvestris*, is capable of growth and regeneration on these soils. On fresh moraine gravel soils the case is different. When a forest fire destroyed a forest of this kind, or when a burnt-over field was abandoned, the area was rapidly re-occupied by the forest. But the first set of tree species invading the area was not,

as a rule, identical with the original forest. The dominant tree species to appear after a fire were alder, *Alnus incana*, aspen, *Populus tremula*, species of birch, *Betula verrucosa* and *pubescens*, and sometimes, more rarely, pine, either with one of them alone forming pure stands, or with all of them together in mixed stands of most varied compositions. The Norway spruce, *Picea excelsa*, which spreads more slowly and when young is of slow growth, on the other hand, had to give way to burn-beating and forest fires, and even disappeared from extensive areas. The forests acquired, as a consequence of burn-beating and forest fires, an artificial and unnatural composition of tree species, which could not, of course, remain stable when burn-beating started to decrease and finally came to an end at the beginning of the 20th century and when forest fires were got under control.

Upon this a new phase commenced in the development of the composition of tree species. The spruce, aggressive, but compelled to give way to forest fires and burn-beating, now began, more and more actively, to re-occupy its former habitats, and the area of forests dominated by broadleaf trees began to decrease. This phenomenon, the spreading of spruce stands at the expense of hardwoods, is in fact the most typical feature of the present succession of tree species in Finnish forests. It is a tendency to return to the original composition of tree species, towards the greatest possible simplicity and regularity, i. e. to the final stage, pure stands of the strongest tree species. In due course the forests would no doubt attain this stage, provided their development were not interrupted by natural catastrophes and by cuttings.

In consequence of burn-beating and forest fires, as mentioned above, different kinds of mixed forests primarily of broadleaf trees, were formed, and later on the penetration of spruce into these forests dominated by broadleaf trees further increased the number of mixed forests. By far the greatest part of Finnish forests now consist of mixed stands. In the relatively barren Finnish conditions, these mixed stands have to be understood, as set out above, as vegetation composed of a number of species, and exposed to chance factors, and not as complete and final plant associations of permanent composition. They are only more or less developed transition stages, subject to continual changes, in the development towards the climax stage, a pure or nearly pure spruce stand on fresh, or pine stand on dry soils.

Fully comparable in their development with these mixed stands, are the pure stands (birch, aspen, alder and pine stands on fresh soils) resulting from burn-beating and forest fires. They, too, are transition stages gradually changing in the course of their further development, provided that development may go on in peace, into stands dominated by spruce, or into pure spruce stands. The succession thus may be on the following lines:

pioneer stand				climax stand
alder → birch	birch →	birch → spruce	spruce → birch	spruce

The rapidity of this development depends essentially on the tree species present in the mixed stand, on their age and abundance. As a rule, the final stage is reached sooner the more different are the ecological qualities of the tree species; and it is arrived at more slowly the more closely their qualities resemble each other. Further, the mixed stand stage will last longer the less abundant is the presence of the strong tree species and the younger it is compared with the weaker tree species. All factors of this kind may expedite or retard the development, but its course towards the final stage cannot be altered by them.

As an example may be mentioned that, since a mixed stand in Finland is formed by ecologically fairly similar tree species, birch and pine, it takes well over a hundred years before the stand develops into a pure pine stand (Lappi-Seppälä 1930), and 300 to 400 years before a mixed stand of spruce and pine develops into a pure spruce stand. If, instead, the mixed stand consists of tree species very dissimilar ecologically, e. g. the strong spruce and the weak alder, the stand becomes a pure spruce stand in as short a space of time as 40 years. If the spruce is very abundant in the stand, the alder will disappear in 30 years' time; in a reverse case the alder may be able to defend itself for several decades longer (Kalela 1936).

In the succession of tree species in Finnish forests the same tendency can be observed as in the development of vegetation in general. The vegetation invading a free habitat is of a very haphazard and heterogenous composition (as a rule a mixed stand dominated by broadleaf trees) which later on, due to plant competition, develops towards ever greater simplicity and regularity, and finally leads to a permanent and fairly unchangeable plant community, a climax stand (depending on the habitat, either a spruce or a pine stand).

Ecological Groups of Tree Species

As the tendency of successional development described above, from a young vegetation, rich in species and exposed to chance factors, towards regular plant communities, is to be found everywhere, the features described above of the succession of tree species are not characteristic of the Finnish and North-European forests alone: development on the same principle occurs everywhere. It is true that the more favourable the conditions in which a stand grows, the richer in species and the more complicated in structure is the final climax stand, but the tendency of development towards a climax stand, in its main features, is identical in both cases.

In general, the following types of climax stands, as conditions become more and more favourable, may be discerned.

1. Stand consisting of one crown-layer and one tree species.
2. Stand consisting of one distinctly dominating crown-layer but of two or three tree species.
3. Mixed stand consisting of two or three crown-layers each of which is formed by one dominating tree species.
4. Mixed stand consisting of several crown-layers, in which each crown-layer is formed by several tree species.

The simplest, to conform with Group 1, is the climax stand of the entire Northern coniferous forest zone (e. g. Cajander 1916, Högbom 1934, Kalela 1945, 1946 etc.), on the edges of dry deserts (Cajander 1916, Morosow 1928, Kalela 1942 etc.), and in the upper mountain regions (Kalela 1942, Etter 1943, Auer 1947, Sigmont 1948 etc.). Climax stands of Group 2 and 3 are encountered in considerably more favourable conditions, e. g. in Central European valleys and on low and mid-slopes of mountains (Mayr 1909, Koch 1944, Etter 1943, 1947 etc.), in a great part of the Canadian and United States forest areas (Kujala 1945 and cf. later), excluding high slopes of mountains, and on the low rain slopes of the Patagonian Andes and New Zealand mountains (Rothkugel 1916, Cockaye 1928, Kalela 1942 etc.). Climax stands of Group IV are present in the most favourable conditions only, on the low slopes of mountains and in valleys of rainy, tropical regions, in the form of abundantly luxurious mixed stands, rich in species (cf. below).

As a climax stand is a result of lengthy and fierce competition of plant species, plant individuals, and biotypes, it is always composed of those tree species only which, on the region and habitat in question, are stronger than the other tree species. As this obviously is the case it is no wonder that these climax tree species seem mutually to form a group quite homogenous ecologically, although taken systematically they are very remote and foreign to each other.

It seems to be characteristic of these tree species (cf. Morosow 1928) that their seeds are fairly heavy and difficult to disperse, that their seed years are repeated at long intervals, that their sprouting capacity is often weak or non-existent, that their speed of growth in the early years is slow, that in their early stages they are sensitive to frost, sun-scorch and excessive transpiration, that their shade tolerance is fairly good, their ability to recover good, that they die hard and are long-lived, and that their growth continues until late in age; thus, as a rule, they develop into big trees and form the largest-sized forests in the area. In short, they are tree species slow in spreading but strong in competition. A further characteristic, often, is that their wood is of considerable hardness and resistance, and of high value, and forests consisting of these species are, as a rule, the most valuable and serviceable economically. Furthermore, it is typical of these tree species that they are usually not the first to spring up in a new opening in the original forest, but only come together with other trees or even after other tree species have formed a stand or a seedling stand.

Other tree species again, those that are to give way in the course of competition and succession and are never present as the dominating species of climax stands, also resemble each other remarkably in many respects, and can almost be contrasted with the climax tree species. These so-called pioneer tree species generally produce an abundance of seeds annually, their seeds are light and easily dispersed by the wind, their sprouting capacity is good, often remarkably intense, they grow speedily while young, are not sensitive to frost, sun-scorch or excessive transpiration — on the contrary they require a lot of light and growing space; but they are short-lived and stop growing fairly early, and thus, as a rule, they are smaller in size than the former and incapable of producing forests nearly so large in volume. Typical, therefore, of this species is that the trees increase and spread readily and easily, but are weak in the struggle against other tree species. Their wood is often rather soft and easily decayed.

Between these extreme ecological groups there are, in addition, a great number of tree species which, at least in their ecological qualities, represent intermediate stages. Some of them are closer to pioneer tree species, others again to climax tree species, and this is reflected in their presence in the forest picture of a region.

On the Occurrence of Ecological Groups of Tree Species

These three ecological groups of tree species seem to be present in all forest regions of the globe, but their mutual abundance is greatly dependent on the way in which the forests have been treated and the frequency of the various natural catastrophes. Where the forests have been able to retain their character of virgin forests, climax tree species dominate completely, while pioneer and ecologically related tree species have had to assume quite an insignificant position and are present merely as slight admixtures in the most favourable spots. The composition of tree stands in virgin forests is therefore, in most cases, of great economic value and worth preserving. On catastrophe areas again of virgin forests, e. g. on fire-devastated areas, pioneer tree species hold the dominant position and often form extensive forests, frequently of not too great an economic value.

The effect of cuttings is on the same lines. Particularly where forest has been destroyed or reduced to a very poor condition by irrational exploitation, climax tree species are perceptibly reduced in number or may be totally absent over extensive areas, pioneer tree species having replaced them. Extensive areas of former virgin forests are thus, due to cuttings, at present occupied by tree species of the pioneer type, and reduced in value. It is true that the composition of tree species on such exploited cutting areas gradually begins, more and more, to approach the original climax stage, for which reason only the most recently devastated forest areas are occupied by typical pioneer tree species while, on older cutting areas, tree species of pre-climax or even climax groups are already present among the pioneer tree species; the development is naturally fairly gradual and takes a long time.

The influence of civilisation on the composition of tree species in forests is thus fairly remarkable, and generally tends to increase the proportion of pioneer and similar tree species in the forest area at the expense of climax tree species. This trend of development is naturally stronger and speedier the less rationally and the less in conformity with nature the forests are treated. Only where really rational silviculture, conforming with natural methods, is practised can the proportion and position of forests composed of climax tree species be retained at full yield, and the pioneer tree species, often inferior in their qualities and economic value, be prevented from gaining dominance and considerably reducing the value of the forests.

Examples of the mutual fluctuations of pioneer tree species and climax tree species, of new areas occupied by them, and of the development of forests towards the climax stand are already fairly numerous in the international literature on forestry, although it is only recently that these problems have started to attract more attention. In the following, the results of certain investigations in different parts of the globe and under various climatical conditions are given.

The most typical example available from Northern Europe is the influence, described above, of forest fires and burn-beating on the composition of tree species in Finnish forests. An exceptionally typical pioneer tree species of these conditions is alder, *Alnus incana*, while spruce, *Picea excelsa*, is an equally typical climax tree species. Fairly typical pioneer tree species also are the species of birch, *Betula*. As shown by Sarvas (1948), a feature typical of birch is, e. g., that, characteristic of the pioneer species, it regenerates almost entirely on new catastrophe areas only, and hardly ever under a mother stand. Their former habitat is taken possession of by other tree species, and the birches move to afforestate new catastrophe areas. The same applies to aspen (*Populus tremula*) and pine (*Pinus silvestris*) on fresh habitats. — A similar development may be encountered in Siberian Taigá areas as well (Morosow 1928).

On investigating mixed stands of Cembran pine (*Pinus cembra*) and European larch (*Larix europæa*) in the Swiss Alps, Auer (1947) found that larch is a typical pioneer species inasmuch as its preservation in the Alps is entirely dependent on falls of rocks, avalanches, moraines freed from their ice cover, and other habitats offering no competition, always to be found in the Alps. It is, however, hardly ever able to regenerate on these habitats invaded by it as the habitat is unfailingly and rapidly taken possession of by either the Cembran pine or spruce, which compel the larch to retreat, or else a new natural catastrophe destroys the wood, and the development returns to its initial stage again.

In the United States a number of interesting investigations into changes of tree species in the forests there are carried out. Larsen (1929) has described the influence of forest fires on the composition of tree species in the Bitterroot Mountains, Northern Idaho. On the destruction of a *Tsuga-Thuya-Abies grandis* stand e. g. by forest fire, the first group of tree species to invade the extensive burnt areas is produced by *Pinus contorta var. latifolia* and *Larix occidentalis*. Next to appear in the stands of these tree species, as the strongest species of undergrowth, are *Pinus monticola* and *Pseudotsuga taxifolia* which, it is true, may also be the first tree species to grow on burnt areas. As a rule, however, the former tree species are the most frequent, particularly on extensive areas which have suffered from several fires. When these tree species reach maturity and the stands begin to get thinner, *Tsuga heterophylla*, *Thuya plicata*, and *Abies grandis* make their appearance underneath them, eventually taking possession of the habitat and forming once again a climax stand.

Lutz (1929) has studied the succession of tree species in Southern New England. As a rule, *Juniperus virginiana* and *Betula populifolia*, in varying abundance, are the first dominant species to appear on an open area. Scattered in the stands there are, in addition, e. g. *Acer rubrum* and *B. lenta*. This phase of development usually takes 40 to 80 years, depending on the quality of the habitat. As these pioneer tree species get older, new hardwood species in great numbers make their appearance among them, starting with inferior species such as *Carpinus caroliana*, *Juglans cinerea*, *Populus grandidentata*, etc. Gradually they are relegated to a more and more subordinate position underneath more valuable and stronger hardwood species penetrating the area later. The most important of these later newcomers are *Quercus borealis maxima*, *Q. alba*, *Q. coccinea*, *Q. montana* and *Q. velutina*, *Betula lenta*, *B. lutea* and *B. papyrifera*, *Fraxinus americana*, *Carya*, *Fagus*, *Ulmus* etc., producing a typical, pure hardwood stage. As development continues, the *Quercus* species gradually obtain a more and more dominant position, and several hardwood species disappear. At the latest at this stage, *Tsuga* also makes its appearance as undergrowth below the hardwoods. Gradually *Tsuga* gains more and more prominence and the result is a Tsuga-hardwood stand, which according to Lutz represents the climax stage.

Very similar to this is the succession of tree species in central New England (New Hampshire) as well (Cline and Spurr 1942). Characteristic pioneer species on this area are *Betula populifolia*, *Prunus pensylvatica*, and *Populus tremuloides*, which always rapidly take possession of areas that have become open, and which retain their dominance for 40 to 50 years. *Betula papyrifera* and *Castanea dentata*, which are also already of quite frequent occurrence in the pioneer stand, are stronger and longer-lived tree species, and remain longer on the habitat. As actual pre-climax species the writers consider, above all, *Pinus strobus, Quercus borealis maxima, Acer rubrum,* and *Picea rubens.* These tree species thus succeed the pioneer species and form a pre-climax stand prior to the climax species proper taking possession of the habitat. On drier habitats these species, and particularly *P. strobus,* may even form climax stands (physiographic climax), in the same way as *Pinus silvestris* does in Northern Europe. Most important of the tree species present in climax stands proper are *Tsuga canadensis, Fagus grandifolia, Betula lenta,* and *Acer saccharum.* Of these particularly the first-mentioned one, hemlock, is a strong and aggressive climax species, while beech is not as aggressive. Further tree species present in climax stands, though in more protected places only, are *Fraxinus americana, Betula lutea* and *Tilia glabra,* as well as, though less regularly and less typically, *Prunus serotina, Quercus alba,* and *Pinus resinosa.* According to the author, it takes about 400 years to reach the climax stage as *Pinus strobus,* being long-lived, does not disappear from the stand until then.

Coile (1940) has also tried to elucidate the causes occasioning the decline of pioneer species and the invasion of climax species. In North Carolina pure, even-aged stands of *Pinus taeda* usually become established on former agricultural land within 10 years of cultivation ceasing. After the establishment of pine there is a gradual invasion of hardwoods consisting of both typical understory trees such as dogwood (*Cornus florida*), and oaks (*Quercus alba, Q. velutina, Q. borealis*) and hickories (*Hicoria carolinae-septentrionalis, H. glabra, H. ovata*) of the climax forest. *P. taeda,* except as scattered individuals, does not successfully reproduce either in old pine stands or in stands dominated by oaks. On studying the causes of this change of tree species Coile comes to the following conclusions: the decline of *P. taeda* dominance at the end of one generation is caused by the failure of *P. taeda* seedlings to compete with established forest vegetation for soil moisture and nutrients. The superficial root system of *P. taeda* does not penetrate below the surface soil zone, which is characterised by a large area of absorbant surface in the form of small roots. Invasion of oaks and hickories, their development to a dominant position and their continued dominance, is caused by the initial rooting habit of their seedlings, which enables them early to penetrate below the surface zone of high root concentration where competition is intense during periods of moisture stress.

Of other investigations into the succession of tree species in the United States forests, the following may be mentioned: Corson, Allison and Cheyney (1929), Larsen (1930), Lutz (1930),

Huberman (1935), Nichols (1935), Hough (1936), Morey (1936) and Wilm (1936). All these investigations, carried out in different parts of the United States, show that the tree species appearing on catastrophe areas are of very different qualities from those present in the original forest, and that the course of development is always towards a given climax stage in each case.

In tropical forests also the main features of succession are known to be the same. In the composition of the tree species of the tropical rain forests all three ecological groups of tree species are represented. The tree species characteristic of each region and at least so far of greatest economic value, are as a rule present in primeval forests, while pioneer species are little seen. On the other hand, the composition of tree species appearing after forest devastation is entirely different from that in primeval forests, and consists primarily of pioneer species easily spread and of rapid growth, but short-lived and often of less economic value. These secondary stands, however, in the tropics, rapidly resume their original character of climax stands if allowed to develop in peace. In general, the rotation and development of tree species in the tropics seems to be much more rapid than in less favourable conditions. It must, however, be borne in mind that in certain cases, in which the present forests, due to climatic changes, are passive and unregenerating, a forest devastation may be succeeded by an entirely different plant formation (shrubby growth, steppe, etc.).

A few examples of investigations into tropical forests may be mentioned. According to Benoist (1924), a devastated forest area in French Guiana first becomes grassland (composed of species of *Solanum, Sida, Miconia,* and other genes), succeeded by vegetation and bushy-forest of *Cecropia-* and *Inga-*genes and numerous shrubs. Only then comes the actual secondary forest of rapidly growing trees with soft light wood, and ultimately a climax forest of more slowly growing trees with hard durable wood. Similarly, Cook (1909) states that cleared areas in Central America were rapidly covered by a temporary vegetation, entirely different from the original stand, and Beard (1944) reports from the Island of Trinidad that, upon clearing, pioneer species, »especies colonizadoras», take possession of the habitats and form on them forests of inferior value which have to be made more valuable by forest cultivation. Kenoyer (1929) describes in great detail the succession of tree species in Barro Colorado Island, Panama. Two years after forest clearing the first pioneer species make their appearance in great abundance of species, dominated by the species of genus *Cecropia.* This vegetation, however, stands a short time only, from 3 to 15 years. Subsequently new pre-climax species, as a rule of small size, gradually appear in ever increasing numbers. The majority of them are of the families *Moraceae*, *Polygonaceae*, *Caesalpniaceae* etc., and a ground vegetation, rich in species, develops underneath them. This stage of vegetation succeeding a clearing is dominant for between 15 and 50 years. After the lapse of 50 years from clearing, the actual climax species, of large size and abundant shade, appear on the habitat and rapidly occupy it.

In tropical Africa the development obviously proceeds on exactly the same lines. Najera (1930) describes from Spanish Guinea how there too the first plant to appear on devastated areas is »bosque secundario», of little value. One of the most typical pioneer tree species of tropical Africa is *Musanga Smithii*, the area of distribution of which covers large districts in the farthest corner of Guinea Bay. It makes its appearance on all tropical forest openings, on devastated forest areas, on the road clearings etc., rapidly forming fairly pure but short-lived stands. Thus it constitutes one of the most pronounced characteristics of secondary forests in this region, whereas, in primary virgin forests, it is inconspicuous and of no significance (Polchau 1941, Willsher 1940). Vermoeren (1922) gives detailed descriptions of the influence of forest devastation, primarily on the Gold Coast. On cleared areas a typical pioneer stand, consisting of species of the genes *Musanga*, *Tucina*, *Harungana*, etc., is the first to appear. This stage lasts from 10 to 30 years, and it is succeeded by stands of entirely different tree species, dominated by species of e. g. the genes *Bosqueia*, *Conopharyngia*, *Alstonia*, *Funtumia*, *Albizzia*, etc. This stage also is of fairly short-lived duration only, 20 to 50 years. In stands formed by these tree species ever greater numbers of climax species gradually make their appearance and, as a rule, in a few decades, take entire possession of the habitat. The forest thus returns to its original composition within a fairly short space of time, 60 to 100 years.[1]

[1] Of the comprehensive literature on the development and treatment of tropical forests mention may be made here of the articles published in the series »Indian Forester», »The Caribbean Forester», »Tropical Woods», and »Kolonialforstliche Mitteilungen».

Ecological Character of Tree Species and its Relation to Silviculture

In the previous chapters the main attention has been directed towards the ecological character of tree species and its forms of appearance in different conditions. The conclusion drawn is that evidently wherever conditions are favourable enough for forests, species of all three ecological groups are encountered. Their undeniable and consistent presence in the forest picture of each region offers an interesting subject for review: the way in which the differing ecological characters of tree species have had to be taken into consideration in silvicultural methods, and the extent to which they, and the natural tendency of forest development primarily determined by them, obviously ought to be taken into consideration in silviculture.

The succession of tree species in a forest always leads to a given final result, to a climax stand, determined by the climate, quality of soil, and the mutual biotical strength of the tree species of the region. The initial forest of even similar climax stands may be widely different in different cases as the effect of chance factors at the initial stages may be considerable. This initial forest, however, through a development now long and multistage, now short and simple, gradually, degree by degree, produces a stand more and more similar to the climax stand of this habitat. It implies a tendency towards complete harmony, a state of equilibrium, in which changes would be as slight as possible. As a rule, the initial development takes place at a fairly rapid rate, but is slowed down the closer to the climax stage the forest develops. One of the ultimate stages is the so-called »Dauergesellschaft», still, it is true, subject to changes which, however, are slow and of little importance in practice. Obviously the climax stands mentioned in literature are very often just »Dauergesellschaften», and have not really reached the climax stage.

Forest fires and other catastrophes, cuttings etc., may interrupt this development or considerably retard it but not change its course. Even if interrupted the development recommences towards the same end, and if retarded its course remains unaltered. This development thus implies an enormous force, which in many respects decisively affects the success of silvicultural measures taken in the forests. Consequently, if for one reason or another attempts are made to lead the development of forests along other than natural lines, the natural tendency of forest development aiming at a certain result will all the time, continuously, oppose and weaken the effect of such measures. In most cases this will jeopardise success, and the more so the greater the conflict with natural development. The case is different when the natural tendency of development of forests is recognised — independent of whether it is the succession of tree species or of the internal structure of a forest that is in question — and silvicultural measures are taken in consideration of and adapted to it. All silvicultural measures will then be assisted and supported by that powerful force included in the development of forests. Every step then means promoting natural development, adding to success and considerably improving results.

It is thus comprehensible that this natural development essentially limits the possibilities of silviculture, but at the same time — provided the measures taken are carried out with due regard for the utilisation of natural development — it increases the prospects of success and of rationalisation, and provides a fairly definite basis for activities. In most cases it necessitates very simple but at the same time natural and effective methods of forest treatment (K a l e l a 1945, 1948). The same idea is reflected in the statement made by B e a r d (1941): »The particular advantage of natural methods for the treatments of degraded woodlands is the absolute certainly of obtaining results of some kind», and in the words of K ö s t l e r (1948): »Die Natur setzt dem Menschen gerade auch im Forstwesen unüberschreitbare Grenzen, je klarer wir diese Grenzen erkennen, desto abwegiger muss uns die Vorstellung einer 'Beherrschung der Natur' erscheinen. Mehr vermögen wir nicht, als unsere Handlungen ihr anzupassen — — —, natürliche Vorgänge zu unserem Vorteil abzuwandeln — — —, und manche Umwelteinwirkungen abzuwähren — — —».

When starting to review the influence of the natural succession of forests and of the ecological character of tree species on the methods of forest treatment, it is necessary to make a short mention of a dendrological feature which at the same time has a bearing on international silviculture. It must be admitted that when reading dendrological and silvicultural literature the reader often finds it difficult, in spite of detailed descriptions of tree species, to form an idea of the occurrence on their distribution areas of the tree species of a region strange to him and of the factors affecting their occurrence. The reader is entirely dependent on how successfully the author has been able to describe the factors affecting, in particular, the distribution ecology of tree species, and this considerably hampers the appreciation and understanding of the silvicultural measures used. If, instead, the ecological character of the tree

species of a region could be described, however simply, for instance by using the ecological types mentioned above, the picture of the composition of forests and the proportions of the different tree species in it would be much more distinct.

Knowing for instance, that in New England *Betula populifolia* is a typical pioneer species and *Tsuga canadensis* again a climax species, on the basis of these given data alone we can form a fairly good idea of their conditions of occurrence. Further, knowing that *Musanga Smithii* of the tropics and *Alnus incana* of the barren North are pioneer species, we can picture to ourselves the prerequisites for their occurrence. We understand that these *Betula*, *Alnus* and *Musanga* species are of very little significance in virgin forests, whereas they are frequent and even dominant (provided the habitat, for edaphic or climatic reasons is appropriate) on fire, clear-cutting, and other devastated areas, etc. Further we shall get an idea of the many ecological qualities of these tree species, e. g. their regenerative capacity, growth rapidity, duration of life, etc., and even of the silvicultural methods suitable for them. On the basis of ecological types we should be able to understand better than before, the composition of forests in strange conditions and the methods found to be best in treating the forests in each district, as well as the difficulties encountered by professionals in each country in their endeavours to arrive at a silviculture of as high a level as possible.

This is of immediate practical importance for instance in c u l t i v a t i o n o f f o r e i g n t r e e s p e c i e s. Very often, when establishing exotic cultures, erroneous or less successful measures are resorted to because of lack of attention to the ecological nature in its natural surroundings of the tree species to be cultivated. Although it must be borne in mind that occasionally, e. g. a climax species in certain conditions, may in character approach a pioneer species (R o b i n s o n, 1942), it is, however, very probable that given approximately similar climatic conditions the cultivations most likely to succeed are those carried out with due consideration for the ecological character of the species; a climax species, for instance, has been grown, in accordance with its character, protected while young by some suitable pioneer species. Whether the cultures could be made more successful still if the shelter trees of the exotic climax species consisted of a pioneer species of its home country remains to be proved, but bearing in mind the close co-operation, often almost resembling symbiosis, in which tree species mutually grow, this would seem fairly probable. O f t e n a v e r y s i m p l e s t a t e m e n t, b a s e d o n f a c t s, r e g a r d i n g t h e e c o l o g i c a l n a t u r e of a tree species in its home country, would greatly facilitate its cultivation in strange conditions.

Further it is particularly necessary to emphasise that the name of the genus of tree species need not in itself reveal much about the ecological character of a species of this genus, as species of one and the same genus may be of entirely different ecological groups. Thus e. g. in the Eastern United States, some species of *Betula* are pioneer trees (e. g. *B. populifolia*), others again species of the transition group (e. g. *B. papyrifera*), and some of them climax species (e. g. *B. lenta* and *B. lutea*). The same applies to the species of genus *Schorea* of the Malayan Peninsula, some of which are contained in each of these groups.

In raising forests several aspects of the ecological qualities of tree species have to be taken into consideration, and from their consideration fairly distinct guidance can be obtained on, for instance, the carrying out of thinnings. In a pure even-aged or fairly even-aged stand competition, as has been mentioned, takes place primarily between tree individuals and biotypes, and the result of the competition is that at each stage primarily the strongest biotypes on the habitat are preserved while the weaker ones, more and more suppressed are forced into decline. This course of development is more pronounced and absolute the more disadvantageous are environmental factors on forest growth (apart from extreme conditions, e. g. at the limits of forest growth), and the more typical the pioneer species forming the stand. This obviously is why, in poorer external conditions as in the Northern Coniferous Forest Zone, that thinning leads to the best results — being truest to nature — which aims at preserving the most valuable part, the dominant part of the stand as uniform as possible, both with a view to the stage of development of the tree individuals, and to their mutual position. The thinning thus affects both dominated crown layers, removed as being without a future, and dominant crown layers to an extent ensuring the greatest possible undisturbed development of the best individuals. In these circumstances silviculture has varied from the outset and continues to aim primarily at raising the same individual trees, and there is no necessity to depend on the recovery of those tree individuals which during the earlier development of the stand remained underneath other trees, condemned by nature and representing an inferior type, their recovery in these conditions always being fairly weak. The unproductive time taken by the recovery of these tree individuals is thus avoided.

Although it is natural that in all even-aged stands, no matter

how favourable the conditions of growth, the strongest biotypes always gain a dominating position and constitute the most valuable part of the stand, it may be possible that in very favourable environmental conditions the prerequisites for the recovery and post-recovery growth of the trees of the dominated crown layer are so good that a greater number of trees of the dominant crown layers may be removed than in poorer conditions, and reliance be placed on the recovery of the trees of the dominated crown layers to replace them. In such conditions perhaps the running counter to natural development involves less of a drawback than is represented in poorer conditions, although on the other hand favouring of the strongest biotypes under favourable conditions might lead to particularly good results. It is natural, however, that in these conditions also the various ecological groups differ mutually. It seems as if the drawback is least in a pure, even-aged stand of climax species, and biggest in a pure stand of pioneer species.

Somewhat different is the case in pure stands not born even-aged and uneven in structure. As the trees in them date from different reproduction years each age class also comprises individuals of strong biotypes, even though in present circumstances, growing underneath older trees, they may appear poorly developed. The utilisation of the individuals genotypically the best, after removal of the older trees, may even lead to good results in favourable conditions, although it is difficult to pick out the best individuals genotypically among undergrowth trees stunted in many different ways. Another difficulty is that the undergrowth trees, generally of the same age as the shelterwood, must be kept separate from younger, genotypically good tree individuals. This naturally hampers the most effective treatment of an uneven-aged stand, and may constitute one of the main reasons why experience gained from selection-cuttings is exceedingly varied. In any case it is obvious that an uneven-aged form of stand and selection-cutting suit only climax species of favourable conditions, as a rule suiting other tree species less the more typical pioneer species they are and the poorer the conditions of growth.

The raising of mixed stands is more complicated, and consideration of the ecological character of their tree species is of greater importance than in pure stands. In raising mixed stands it must as a rule always be borne in mind that each of them tends to develop towards a certain final stage of composition and structure, the climax stage. In most of the cases this implies that in young mixed stands there may always be a number of tree species which, if natural development takes its course, will have to decline in the stand. The more typical pioneer species they are, the more certainly and the more early will they decline. The preservation of these declining tree species particularly, required for one reason or another in a mixed stand, is often very difficult as it conflicts with natural development. Up to a certain limit, of course, it is not impossible, but in such a case it must always be borne in mind that the continued preservation of pioneer species in a stand requires special measures, in the majority of cases continuous aid, which increases silvicultural expenses and may prove unsuccessful. Chr. Auer (1947) e.g. mentions that, in Oberengadin, Switzerland, »ein dauerndes Fortbestehen eines plenterförmigen Arven-Lärchenwaldes in unveränderter Mischungs- und Aufbauform nicht natürlich ist und mit irgendwelchen waldbaulichen Mitteln in der bisher angestrebten Form auch nicht dauernd erhalten werden kann».

On the other hand, the assisting of climax species in a mixed stand occasions hardly any difficulties as, in the course of nature, sooner or later, they would gain dominance in the stand. — Most generally the case may be that the mixed stands easiest to manage are those consisting of tree species of one and the same ecological group; the more varied the groups of which the trees in a mixed stand consist, the more complicated is the management of the mixed stand and the more easily can mistakes occur, provided preservation of the mixed stand form is required.

In regeneration of forests the ecological requirements of the different tree species appear in a still more pronounced form. It is in the regeneration factors (seed quantity, dissemination of seeds, sprouting capacity, initial rapidity of growth, need of shelter growth etc.) that the pioneer and climax species, in particular, differ from each other, and in natural conditions regenerate in different ways: pioneer species are the first tree species on more or less open areas, while climax species in general avoid open areas and regenerate only under shelter growth. Consequently the latter, in most of the cases, have adapted themselves to passing through their initial growth period under a mother growth consisting either of other tree species or of their own mother stand, in order to avoid all the dangers to which they are exposed while young, and gradually to occupying a habitat for themselves by fighting.

Experience as well as investigations and experiments carried out have shown that this course, if followed in regenerating cared for forests as well, usually leads to the best results. In Finland, particularly in regenerating spruce forests the method found best for typical spruce habitats is that in which the seedling stand is secured underneath fairly dense mother growth and gradually released by opening up the mother stand. In these circumstances spruce-seedling growth may spend its first years

sheltered from frost, sun-scorch, excessive transpiration, surface vegetation etc. (Heikinheimo 1944, Lukkala 1946). On the other hand, this method is not at all suitable e.g. for the Finnish *Betula* species, in many respects similar to pioneer species. In compliance with their nature, they require much wider and more open regeneration areas, and in the majority of cases quite special regeneration conditions, such as screefing (burning-over, preparation of the soil spot, etc.) (Sarvas 1948, cf. also Lutz 1929). — In the same way the conclusion arrived at in Central Europe is that such typical climax species as *Fagus silvatica* and *Abies pectinata* are best regenerated naturally underneath a shelter growth. Lutz (1929) also states that to ensure successful regeneration of *Tsuga* stands it is necessary to secure reproduction before the final cutting, i.e. a seedling growth must be provided underneath the mother stand. In their initial stages the reproduction cuttings must be very light so that the seedlings can begin to grow, and only later on may cuttings be intensified. On clear-cutting areas *Tsuga* seedlings, apart from those in advance growth, only make their appearance underneath other tree species. Similar observations have been made by Corson, Allison and Cheyney (1929) regarding the regeneration of *Pinus resinosa* in Minnesota. Seedlings of this tree, there a climax species, appeared in abundance on cutting areas cut after the seed ripened, whereas cutting areas cut before the seed matured came into brush and were invaded by *P. banksiana* or aspen, and burned areas by aspen.

The same applies to forest cultivations in these districts. The planting of typical climax species is most successful when carried out underneath a typical pioneer species. Planting of spruce underneath grey alder has proved very profitable in Finland, provided the shelter growth is removed in time, 5 to 10 years after the planting (Cajander, E. K. 1933, Heikinheimo 1941, etc.). Robinson (1942) has investigated the results of reforestation of waste lands in Scotland and found that spruce plantings on open land were very seriously arrested in growth during their early years, to such an extent even that they were considered to have failed and for this reason were replanted with Scots pine and European larch. As soon as these species had begun to grow and had overtaken the spruce seedlings, the latter recovered rapidly and commenced a virile growth. On the basis of these results Robinson draws the conclusion that successful planting of climax species necessitates a shelter growth of pioneer species.

In the tropics also both experience and investigations have led to similar results. As examples may be mentioned that, according to Brooks

(1941), climax species planted in Trinidad on an open area became chlorotic and grew very slowly, but returned to normal as soon as the understory of pioneer species was established, when growth of the crop improved. Similar experiences were reported by Beard (1944). Attempts were made at immediate reforestation of open areas cleared for cultivation but left unattended, with valuable tree species. The plantings, however, failed completely. Only when the natural development of forests was followed to the greatest possible extent did activities begin to show success. The present tendency is to grow more and more valuable forest using the natural way. The intention is not, however, to use typical pioneer species as the first tree species as they are of no economic value, but preferably some pre-climax species capable of regeneration and development on open areas and at the same time of better economic use than the pioneer species. The results attained have proved very satisfactory. — On the Malayan Peninsula also it has been found that plantings aiming at forests of valuable climax species have turned out better underneath a secondary growth of mostly pioneer species than on open areas (Watson 1935).

In natural regeneration, in the tropics as well, the same lines must be followed. It is quite natural that when attempting to change the present tropical virgin forests into forests of economic value, one of the objectives is to increase the proportion of valuable tree species scattered through these forests. These methods have probably been developed farthest in the virgin forests of the Malayan Peninsula (Durant 1937, Strugnell 1938, and others). As every opening made in the forests is very easily invaded by less desirable, valueless (pioneer) species, a special method has been developed there, the so-called »Regenerations-Improvement--Fellings» system based on the undergrowth, the vines and lianes being removed. Subsequently, every year without a break, but cautiously and gradually, trees of no value are removed from the stand, and in this way the number of valuable tree species in the seedling stand in a few years attains considerable proportions. The valuable mother trees are finally removed only when the new seedling stand has beyond doubt initiated growth and will overcome surface vegetation. This method leads to good results particularly with pre-climax species still capable of fairly easy regeneration, whereas the typical climax species with heavy seeds and good shade tolerance must be regenerated with much greater caution. Of particular interest is the method of regeneration described by Durant (1936) which, with its successive stages, aims at promoting the seedling growth, and in this form reveals a principle very similar to that of the spruce regeneration method of the North recommended by Heikinheimo (1944). Fairly good results have been achieved particularly in districts with poor sales prospects, (Strugnell 1934, 1937, etc.) e.g. by not removing, in the regeneration of stands and adjustment of the composition of tree species, valueless tree species but by girdling them and in this way killing them standing. By the slow, gradual release of space resulting from this procedure the climax species of the kind described have profited most as their regeneration requirements are best satisfied thus. The death of the girdled trees, if necessary, may be expedited by poisoning the trees through the girdling wounds, when the leaf-canopy and degree of shade may be regulated to the development of the seedling growth (Strugnell 1937, Oliphant 1934, and others). By the girdling method close similarity to natural regeneration is achieved, the leaf-canopy gradually thinning with the slow death of the old trees. — A method with the same objective is the one used in tropical Africa, in which a small regeneration gap is formed around each valuable tree individual to allow the seedling of this species to develop. These gaps, however, cannot be cut until the time of year when the fruit of each tree individual ripens, and they have to be formed in accordance with the prevailing wind at that season (Kennedy 1935).

These few references to the methods — arrived at on the basis of experience, observations and investigations — trying to change tropical virgin forests into forests more valuable economically, show that the regeneration of valuable climax species in these favourable conditions must be carried out principally on the same lines as the regeneration of e.g. Norway spruce and hemlock, the Northern climax species.

Seedling stands of climax species must be established underneath a mother stand, and the establishment and first development of the seedling stand must be assisted, more cautiously and with more frequent cuttings the more luxuriant the habitat and the greater the danger that either surface vegetation or less desirable shrub and tree species may develop wild. It is a natural feature of these tree species to pass through their early stage under a shelter growth, and a too great and sudden removal of the shelter growth will retard their regeneration or make it impossible, as is indicated by experience and investigations everywhere.

Furthermore, experience and investigations seem to indicate that, when climax species are regenerated rationally, i.e. under a shelter growth, the greatest success is achieved if in the first phases of regeneration primarily trees of the lower crown layers are removed from the forest canopy and the regular, light and even canopy of the dominants is left, as the lower crown layers are the greatest obstacle to the regeneration of the dominants. Adapted to the circumstances, a cutting method like this seems to yield the best results both in the Northern spruce and pine stands and in the tropical rain forests (Francke 1941, Brooks 1941, Kalela 1945 a, b).

Particularly in the tropics is the preservation of the most valuable tree species ensured in this way, simultaneously with the achievement of their best possible initial development. Any method contrary to this leads to the decrease or even disappearance of the most valuable tree species and to the unchecked growth of pioneer species, as is shown by experience everywhere. In this way it can also be understood how very detrimental a continuous and systematical removal of the dominants always is. It unfailingly leads to laying waste forest areas, deterioration of tree species, decrease in the supply of wood and weakening of the possibilities of silviculture.

Summary

The ecological character of forest forming tree species and its significance in the natural development of forests and for silviculture has been briefly dealt with above. It is natural that the division into three ecological groups cannot be clear-cut. The individual groups cannot be clearly differentiated but in most cases overlap each other with no distinct demarcation line. Particularly the tree species belonging to the extreme groups of species, the pioneer and the climax, differ so distinctly in an ecological respect, and their significance in forest nature is so different that their characteristic features must necessarily be taken into consideration in rational silviculture. This division thus reveals certain features characteristic of the composition of the tree species of each region, which in a remarkable way promotes the understanding of the natural succession of forests and thus facilitates the attainment of as simple, effective, and true-to-nature a silviculture as possible.

This division into ecological groups based on facts, though of indefinite demarcation lines, greatly facilitates choosing among the different methods of treating stands and understanding the silvicultural methods of foreign regions, as well as elucidating the natural tendency of development of the forests of each region. As the species of trees belonging to the same group are very similar in their ecological properties, it is evident, that the stands, formed by species of the same group, must follow the same broad lines in their silvicultural treatment. For instance, it is obvious that a mixed stand consisting of both pioneer and climax species represents a transition stage only, in which the climax species strive for a dominating position, and the preservation of the pioneer species is difficult. This at once gives certain features to the treatment of forests and indicates the broad lines of the plan of management. If, on the other hand, a climax stand, even a young one, consists merely of climax species the conception of the future development of the forest assumes an entirely different aspect, and the prerequisites for the preservation of the mixed stand form are different from those of the former case. Similarly, it is natural that the regeneration of climax species must be effected by methods entirely differ-

ent from those used in regenerating pioneer species. Knowing that the regeneration of e.g. a climax species is in question, leads to a regeneration method following a certain course: establishment of the seedling growth under the mother stand, and its gradual release. Local conditions affect the method in detail only. The regeneration of pioneer and pre-climax species again must be effected by very different methods adapted to their nature, the main features of which, however, independent of the region concerned, are always the same and characteristic of these groups: clear cuttings, strip cutting, seed-tree method, and other methods ensuring space, light, and width; and further the various methods of screefing the soil: burning-over, preparation of soil spots, etc. The general, but most important and essential features are thus considerably clarified by taking into consideration the ecological character of the tree species.

The climax species biotically strong and always striving for a dominating position, however, so far at least are not of particular economic value and use in all regions, and the tendency therefore must be to replace them by other tree species, perhaps foreign to the region, but valuable. It is natural that forest management under such conditions incurs much greater difficulties than in regions where the climax species are valuable and where the natural development of the forests, from the very beginning, leads to this end, a forest of the greatest possible economic value, and in which each appropriate intervention expedites and promotes this development.

A more advantageous position is held by such countries as still have virgin forests to form a framework and main object for forest biological studies. Only where fairly extensive primeval forest regions exist can the main features and details of the natural succession of forests, the ecological value and character of the different tree species and the final climax stage of forest development be ascertained with adequate certainty. In these only can the broad lines of forest development be drawn without laborious experiments, and these forests also supply the most important, simplest, soundest and most effective and natural instructions for forest management. By studying the succession of natural forests and directing it to serve the most profitable economic use of forests, the highest possible silvicultural level may be attained. This is one, perhaps the most important reason why the preservation and study of the virgin forests still in existence is indispensable.

Selostus

Ekologiset puulajiryhmät ja metsänhoito

Kasvien välinen taistelu, joka vallitsee kaikkialla siellä, missä kasvillisuus voi kehittyä riittävän tiheäksi, johtaa aina lopputuloksena tiettyyn tasapainotilaan, jossa muutokset ovat hyvin vähäisiä. Kilpailuvapaalle kasvupaikalle, esim. tuoreelle kuloalalle, voivat ensimmäisen kasvillisuuden muodostaa kaikki ne kasvilajit, joiden diasporit sinne pääsevät leviämään ja joiden edes vähimpiä kasvupaikan vaatimuksia se vastaa. Lajisto on siis hyvin kirjava ja sattumanvarainen. Mutta jatkuvasti kiristyvä kilpailu karsii aste asteelta pois ne lajit, biotyypit ja yksilöt, jotka tällä kasvupaikalla ovat bioottisesti muita heikompia, kunnes jäljelle jäävät vain voimakkaimmat ja keskenään tasaväkiset yksilöt. Loppuaste alkaa silloin syntyä ja muutokset pienenevät ja hidastuvat.

Sama kehityksen kulku voidaan todeta kaikkialla maapallolla ja paitsi pintakasvillisuuden, myös puuston kehityksessä. Kaikkialla aukeitten alueitten ensimmäisen puulajiston muodostavat yleensä kokonaan toiset puulajit kuin ne, jotka olivat vallitsevina alkuperäisessä metsässä. Mutta tämä ns. pioneerilajisto ei ole yleensä pitkäaikaista. Sen tilalle tunkeutuu toinen, voimakkaampien, mutta hitaammin leviävien puulajien muodostama lajisto. Tästä puulajistosta kehittyy monesti jo lopullinen metsikkö, mutta usein ja varsinkin suotuisissa olosuhteissa tämäkin puulajisto saa ainakin suureksi osaksi väistyä vielä voimakkaampien puulajien tieltä ennenkuin tasapainotila saavutetaan, mihin saattaa kulua 100—500 vuotta.

Tämän suuntainen kehitys, joka vastaa täysin kasvisosiologien selvittämiä kasvillisuussuksessioita, on havaittavissa kaikkialla. Jokaisen seudun puulajistossa ovat edustettuina varsin selvät ekologiset puulajiryhmät: pioneeripuulajit, jotka helposti leviävät, kasvavat nopeasti, mutta ovat lyhytikäisiä ja bioottisesti heikkoja, sekä klimaxpuulajit, jotka taas ovat hitaasti leviäviä, nuorina hidaskasvuisia, mutta pitkäikäisiä ja voimakkaita puulajeja. Lisäksi voidaan erottaa kolmas välittävä ryhmä, pre-klimaxlajit, jotka ovat ekologisesti milloin lähempänä pioneerilajeja, milloin klimaxlajeja. Taloudelliselta arvoltaan ovat ainakin toistaiseksi klimaxlajit arvokkaimpia ja pioneerilajit huonoimpia.

On luonnollista, että näiden puulajiryhmien esiintyminen on myös aivan erilaista. Klimaxlajit ovat vallitsevina koskemattomissa luonnonmetsäalueissa sekä järkiperäisen metsänhoidon alaisissa metsissä, pioneerilajit taas katastroofialueilla (paloaloilla, myrskyntuhoalueilla jne.) sekä metsänhävitysalueilla ja ne esiintyvät sitä vallitsevampina, kuta tuoreempi katastroofialue on. Väliastelajit taas esiintyvät etupäässä vanhemmilla katastroofialueilla. Täten jo maininta puulajin ekologisesta luonteesta antaa käsityksen sen esiintymisen edellytyksistä levinneisyysalueellaan. Ajateltakoon vain esim. harmaalepän, pioneerilajin, ja kuusen, klimaxlajin esiintymistä Suomessa.

Aivan vastaavasti esim. tieto, että Pohjois-Amerikassa Betula populifolia on pioneeri- ja Tsuga heterophylla-klimaxlaji antaa meille suuripiirteisen käsityksen näiden puulajien esiintymisen edellytyksistä kotiseudullaan.

Mutta yhtäläisyys samaan ekologiseen ryhmään kuuluvien puulajien kesken ulottuu pitemmällekin. Koska samaan ryhmään kuuluvat puulajit ekologisilta ominaisuuksiltaan ovat varsin samanlaisia, vaikka systemaattisesti olisivat toisilleen hyvinkin vieraita, on ilmeistä, että samaan ryhmään kuuluvien puulajien muodostamien metsiköiden metsänhoidollisen käsittelynkin täytyy kaikkialla seurata samoja suuria linjoja, joiden yksityiskohtiin tosin paikalliset olosuhteet painavat oman leimansa. Kokemukset ja tutkimukset ovat osoittaneet, että metsiköitä uudistettaessa on klimaxlajien taimisto hankittava joko emämetsän tai suojusmetsän alle ja sieltä vähitellen vapautettava, jotta uudistuminen parhaiten onnistuisi. Samaten on näiden puulajien istutukset suoritettava mieluimmin pioneerilajin muodostaman suojusmetsän alle, jotta tulos muodostuisi hyväksi. Aukealla alalla niiden taimet kituvat tai menehtyvät. Pioneerilajien uudistaminen seuraa aivan toisia suuntaviivoja. Ne ovat tilaa, valoa ja väljyyttä vaativia lajeja, jotka sitä paitsi usein vaativat uudistuakseen maanpinnan valmistuksen (polton, laikutuksen tms.). Niitä uudistettaessa tulevat kysymykseen sellaiset hakkaustavat kuin paljaaksihakkaus, siemenpuuhakkaus, kaistalehakkaus jne.

Myös harvennushakkauksissa puulajien ekologinen luonne on otettava huomioon. Yleensä ovat helppohoitoisimpia sellaiset metsiköt, joita muodostavat samaan ekologiseen ryhmään kuuluvat puulajit, joita voidaan riittävän kauan kasvattaa rinnakkain. Sen sijaan pioneerilajien ja klimaxlajien muodostamien sekametsiköiden kasvatus on vaikeampaa ja enemmän ammattitaitoa vaativaa, etenkin jos pioneerilaji halutaan metsikössä säilyttää, koska tällaiset puulajit ovat väistyviä lajeja.

Luodessaan täten luonnollisella pohjalla selväpiirteisyyttä ja yhdenmukaisuutta metsänhoidollisiin käsittelytapoihin, ekologisten puulajiryhmien selvittäminen voi helpottaa kansainvälistä yhteistyötä metsänhoidon alalla.

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