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Artikel: Ecological conditions limiting the distribution of Fagus silvatica L. and Abies alba Mill. near Schwarzenberg (Lucerne) Switzerland

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5. General discussion

Independent factors:

Amongst the independent factors postulated by JENNY (1942), the nature of parent material and slope play a major role, the other factors being of less importance in the area of investigation. Therefore, all the differences between the investigated fir and beech sites are finally due to the fundamental differences between the two types of parent materials namely practically non-calcareous sandstone on less steep slopes and calcareous morainic material on steep slopes.

Importance of the nature of parent material

KUOCH (1954) states that non-calcareous parent material favours conifers ("Nadelbaumfördernde Unterlagen") and calcareous parent material favours broad leaved trees ("Laubbaumfördernde Unterlagen"). This statement is endorsed particularly well in the Guberwald and was partly clarified by the present investigations on various site factors and regeneration problems. These problems are specifically dependent on the nature of parent material which plays a major role in the development of the soil types and thereby also the vegetation types.

In the Guberwald, the parent material of the podsol which occurs under the fir stands is a practically non-calcareous sandstone whereas that of the brown-earth which occurs under the mixed fir-beech stands is a calcareous and loamy morainic material. Because of these basic differences in the nature of the parent materials, the processes of soil formation also differ.

The processes of soil formation:

In regions of high precipitation and high humidity, the permeability which in some respects very much depends on particle size distribution plays an overriding role in the formation of the soils. Parent material with greater percentage of silt and clay particles are not so easily percolated by water. Thus leaching of the nutrients is not so pronounced, all other factors being constant as in the soils derived from more sandy parent material. At the same time, in the Guberwald because of greater biological activity, quick humification and mineralization of litter takes place on the calcareous parent material whereas on biologically less acitve non-calcareous sandstone, humus tends to accumulate. Therefore, (1) on morainic parent material with $CaCO_3$ and remarcable amount of clay and high biological activity we have soil formation of brown-earth-types (2) on practically non-calcareous, sandy and highly permeable parent material, there is a very pronounced leaching of organic-inorganic colloidal complexes and nutrients respectively and thus a formation of podsol-type soils with significant A_{oo} - A_o - A_1-horizons.

Soil and vegetation:

As the process of podsolization proceeds, more and more humus tends to accumulate, accompanied with increasing acidity. In such a situation, species which do not tolerate markedly acidic soils are expected to be relegated to soils with increasing contents of clay which resist to acidification (KØIE 1959). That is why more specialised plants such as Vaccinium myrtillus and other calcifuge plants and mosses succeed in totally occupying the ground forming the Bazzanio-Abietetum typicum on podsol and pseudogley-podsol On the other hand, on base-rich brown-earth and on clay-silt-rich A_1-pseudogley there is the Abieti-Fagetum typicum with species of "A", "B" group (refer to table 2) which avoid extreme acidic soils and a few mosses dominate.

Competition:

In the present investigation, it was recognised that the species having the greatest competitive influence on the establishment of beech is Vaccinium myrtillus which is found to spread an elaborate root system in the humus layer of podsol thereby making the humus compactly interwoven by roots.

Climatically, the middle and upper montane belt of the area is most suitable for the growth of fir and its competitive ability is thus increased. In the same belt, the competitive ability of beech is decreased but it still remains vital enough to form mixed fir-beech forests (Abieti-Fagetum) but only on base-rich soil. However, as the soil becomes poorer in nutrients, the percentage of beech in the Guberwald gets reduced, ultimately giving ground to fir on podsol. Therefore, it seems that in this climatic zone, the competitive ability of beech is so much reduced on podsol that it can not compete with fir and spruce. On the other hand, judging from the ability of fir to grow well on podsol, it seems that its competitive ability is increased. HARTMANN (1964) states that the occurrence of Vaccinium myrtillus denotes the limit of the occurrence of beech and which also indicates the dominance of fir in the montane belt. Due to humus accumulation on acidic soils of the montane belt, V.myrtillus invades the habitat and thus limits the occurrence of beech. But on base-rich soils in the same belt with favourable water supply, a habitat group is formed which is exceptionally dominant in beech with high vigour.

Ecological adaptation of fir and beech:

Fir (Abies alba): Though fir grows luxuriously on base-rich brown-earth in the Guberwald and many other regions of the Alps (KUOCH 1954), it also grows well on podsol.Therefore, KUOCH states that silicate parent material favours conifer forests. MUSTAFA (1932), on the other hand, expresses that the assumption of fir as a tree of silicate parent material is misleading because fir has been found to absorb a greater quantity of calcium than beech on similar habitats. His investigations also show that as fir becomes older, the calcium content of its branches increases and it absorbs a greater quantity of calcium on calcareous soils than on silicate soils. Therefore,the conclusion could be drawn that fir requires a large quantity of calcium for its optimum growth. The question how fir grows well on podsol when it requires a large quantity of calcium could be solved by the following observations:

1. By spreading its extensive root system in horizontal and deeper layers of podsol, fir is able to absorb a large quantity of calcium.
2. Secondly, it seems probable that fir develops an increased ion uptake capacity to compensate a low concentration of an ion in the root medium.

First observation has been confirmed in the Guberwald and also in many other locations by several authors (consult KOESTLER et al, 1968). But the second is a hypothesis and remains to be confirmed experimentally. However this hypotheses has been proved in the case of Vaccinium spp. (a calcifuge), the associate of fir on acidic soils by INGESTAD (1974). Vaccinium having a requirement of calcium as high as that of cucumber (Cucumis sativa, a calcicole) can absorb an even greater quantity of calcium at low availability in acidic soils by selective uptake. A similar type of adaptation to develop an increased ion uptake capacity seems to be possible in fir particularly at an early age when roots have not yet grown into deeper horizons of the podsol. MUSTAFA's readings show that on silicate soils fir has an even higher content of calcium than beech. In the present investigations also it was noted that the leaching of nutrients from the fir crowns on podsol was higher than that from the beech crowns on brown-earth. These evidences favour the second observation. It has also been proved in the case of Betula verrucosa Ehrh. (INGESTAD 1974). Experiments to prove or disapprove such an adaption in fir would give a better understanding of its ecological amplitude.

Beech (Fagus silvatica): It has been shown that beech has a high requirement particularly for calcium. As a result, it grows well on base-rich soil in the Guberwald. Its failure to perform well on highly acidic soils as podsol particularly in an early age is on account of its root system which concentrates mainly in the humus layer where free nutrients are in low concentration. Secondly, it seems that beech roots are unable to absorb enough calcium from a low nutrient salt concentration in its rooting medium from where fir can absorb effectively. However, this presumption remains to be confirmed. But it receives further support from fertilizer treatment experiments. It has been shown that beech seedlings growing on podsol humus grow well after fertilizer treatment (MEYER 1961). This proves that in a medium with low nutrient concentration, beech does not receive enough nutrients and hence it remains underdeveloped. Further it seems that in podsol, the ionic equilibrium is not balanced (BARSHAD 1960) and this too may affect nutrient uptake by beech roots, particularly in the upper montane zone where the competitive ability of beech is reduced.

Natural regeneration:

Primarily, the rare occurrence of beech on podsol in the Guberwald, is on account of lack of natural regeneration. Even in the submontane zone, where the competitive ability of beech is maximum, beech regeneration has been found lacking on acidic soils. Such sites are common in Germany and therefore, numerous workers have carried out experiments to sponsor beech regeneration particularly on those sites where old beech trees are present. A review of these works has been given by BURSCHELL et al. (1964). Soil preparation e.g. removal of litter and humus and fertilizer treatment have been most strongly recommended to sponsor beech regeneration. Also the present investigations in the Guberwald have proved that litter accumulation is the first barrier for beech nut germination. Even when beech nuts germinate on a mass of fine humus, the low nutrient content in the rooting medium and competition reduce the chances of survival of beech seedlings.

In many areas, beech seedlings die on account of drought (WATT 1923, SCHMITT 1936, BURSCHELL et al. 1964). But in the Guberwald, drought do not occur and hence failure of beech regeneration can not be attributed to this factor.

Conclusions:

Thus the parent material sponsoring conifers or deciduous trees proves its influence on the composition of a given stand by building up a specific humus layer, directly interfering with germination and seedling establishment. Various factors controlling the distribution of beech and fir in the Guberwald are expressed in the table 14.

Table 14, Characterization of the factors limiting the occurence of beech on podsol and sponsoring it on bown-earth in the Guberwald (Schwarzenberg).

Factors	Podsol	Brown-earth
Independent factor (nature of parent material	Practically non-calcareous sandstone	Calcareous morainic material
Process of soil formation	Podsolization	Brown-earth formation
Nature of soil surface	Accumulation of raw humus fir litter covers surface	Mineral-mull surface soil crumbe-like
Plant community	Bazzanio-Abietetum typicum fir dominates, no beech trees	Abieti-Fagetum typicum Beech dominates, many fir trees
Quantity of seedfall	A few beech nuts and large number of fir seeds	Large number of beech nuts and fir seeds.
Resting conditions of seeds	Nuts and seeds not covered by litter or soil	Nuts and seeds get covered by beech litter or burried into soil on account of: 1. Earthworm activity 2. Heavy rainfall 3. Surface run-off 4. Frosts
Damage to seeds by animals	Nearly complete loss of beech nuts	Losses very small because nuts get burried or covered
Germination	Not enough water for germination as the nuts lie on fir litter	Enough water for germination as nuts are in good contact with the soil
Duration of resting	Beech nuts rest on litter for long period but not fir seeds	Both nuts and seeds germinate quickly
Damage caused by Fungi	Since beech nuts rest for longer period, fungi render beech nuts non-viable	Beech nuts do not rest for long period and thus fungus damage is small
Number of beech seedlings	Very few	Many
Seedlings establishment	Seedlings form an intensive root system in the humus layer	Seedlings spread their roots evenly in different horizons
Availability of nutrients	Intense competition for nutrients particularly in humus layer with Vaccinium myrtillus	Less competition
Growth of seedlings	Grow slowly	Vigourous growth
Species dominating	Fir dominates over beech	Beech dominating