Results and discussion of individual results

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4. Results and discussion of individual results

4.1. Phytosociological results

According to the vegetation table (1), the following vegetation units with beech and fir occur in the Guberwald. (Names of associations and sub-associations are given according to ELLENBERG and KLOETZLI 1972).

Table 2, Sociological characterization of the vegetation units in the Guberwald. (Abieti-Fagetum typicum, Carex alba-variant = AFa; Abieti-Fagetum typicum, Carex remota-variant = AFr; Abieti-Fagetum luzuletosum = AFl; Bazzanio-Abietetum typicum, Leucobryum-variant = BAl and Bazzanio-Abietetum typicum, typical variant = BAt).

	Characteristic species	AFa	AFr	AFl	BAl	BAt
A	Mercuralis perennis	V	-	-	-	-
	Ranunculus lanuginosus	V	-	-	-	-
	Hedera helix	V	-	-	-	-
	Vicia sepium	V	-	-	-	-
	Carex alba	IV	-	-	-	-
	Poa nemoralis	IV	-	-	-	-
	Calamagrostis varia	III	-	-	-	-
	Veronica latifolia	III	-	-	-	-
	Brachythecium velutinum	III	-	-	-	-
	Tortella tortuosa	III	-	-	-	-
	Cardamine pentaphyllos	III	-	-	-	-
	Knautia silvatica	II	-	-	-	-
B	Phyteuma spicatum	V	IV	-	-	-
	Lamium galeobdolon	V	IV	-	-	-
	Galium odoratum	V	IV	-	-	-
	Sanicula europaea	IV	IV	-	-	-

	Petasites albus	II	IV	-	-	-
	Primula elatior	IV	IV	-	-	-
	Elymus europaeus	III	III	-	-	-
	Plagiothecium curvifolium	III	III	-	-	-
	Hookeria lucens	II	III	-	-	-
	Plagiothecium silvaticum	III	III	-	-	-
	Paris quadrifolia	II	III	-	-	-
C	Viola silvestris	V	IV	IV	-	-
	Hieracium murorum	V	IV	IV	-	-
	Geranium robertianum	V	IV	IV	-	-
	Fragaria vesca	V	III	III	-	-
	Carex silvatica	III	IV	III	-	-
	Ajuga reptans	III	IV	III	-	-
	Solidago virgaurea	III	III	III	-	-
	Lysimachia nemorum	II	V	IV	-	-
	Mnium undulatum	III	III	III	-	-
	Mnium punctatum	III	III	III	-	-
	Prenanthes purpurea	III	III	III	-	-
	Catharinea undulata	I	III	II	-	-
	Pellia epiphylla	III	II	II	-	-
	Epilobium montanum	I	II	III	-	-
D	Cicerbita muralis	-	IV	II	-	-
	Circaea lutetiana	-	III	-	-	-
	Carex remota	-	III	I	-	-
E	Athyrium filix-femina	-	V	IV	-	-
	Festuca altissima	-	IV	IV	-	-
	Equisetum silvaticum	-	IV	III	-	-
	Dryopteris filix-mas	-	IV	III	-	-
F	Carex pilulifera	-	III	V	II	-
	Galium rotundifolium	-	III	IV	III	-
	Mnium affine	-	III	III	III	-

	Luzula pilosa	-	II	III	III	-
G	Dryopteris austriaca	-	IV	V	IV	IV
	Thuidium tamariscifolium	-	IV	V	V	V
	Eurhynchium striatum	-	V	V	V	IV
	Vaccinium myrtillus	-	IV	V	V	V
	Polytrichum formosum	-	III	V	V	V
	Dicranum scoparium	-	III	V	V	V
H	Dicran-odontium denudatum	-	-	-	V	IV
	Rhytidiadelphus loreus	-	-	-	V	IV
	Hylocomium splendens	-	-	-	V	V
	Ptilium crista-castrensis	-	-	-	IV	IV
	Pleurozium schreberi	-	-	-	III	III
	Hypnum cupressiforme	-	-	-	IV	IV
I	Leucobryum glaucum	-	-	-	III	-
	Cladonia spp.	-	-	-	III	-
	Vaccinium vitis-idaea	-	-	-	III	-
J	Sphagnum girgensohnii	-	-	-	-	IV
	Plagiothecium undulatum	-	-	-	-	IV
	Lepidozia reptans	-	-	-	-	III
	Bazzania trilobata	-	-	-	-	III

4.1.1.1 Abieti-Fagetum typicum, Carex alba-variant (e.g. ELLENBERG and KLOETZLI 1972, no. 18):

This community occurs on soil without humus accumulation and on steep slopes. It shows a more or less natural composition of species since the forests on steep slopes are preserved to protect the soil from erosion.

Beech is dominant and fir subdominant while spruce is found occasionally. This is the only community in the Guberwald where beech is dominant. There are many large and old beech trees. It is well represented also in seedling and sapling stages. Fir occupies the second place and spruce the third place with regard to natural regeneration. Shrubs as Rubus idaeus, Sorbus aucuparia, Rosa pendulina grow sporadically. Mercurialis perennis etc. of "A" group (for plant groups refer to table 2) are characteristic with 50 - 90 % constancy. Typical species of Abieti-Fagetum typicum ("B") group and of Abieti-Fagetum ("C") group are also very frequent in this community. Among the mosses, Tortella toruosa and Brachythecium velutinum are found only in this community though they occur sporadically. Moss cover is below 5 %.

ELLENBERG and KLOETZLI (1972) divide the Abieti-Fagetum into three sub-associations while KUOCH (1954) into four. This community is related to KUOCH's Abieti-Fagetum festucetosum in having common species and similar habitat, to the submontane community Carici albae- Fagetum caricetosum montanae (ELLENBERG and KLOETZLI 1972) in having Poa nemoralis, Carex alba, C. montana, C. flacca, to Cardamino-Fagetum typicum in having Cardamine pentaphyllos, Ranunculus lanuginosus, Hedera helix and Mercurialis perennis and to Taxo-Fagetum in having Calamagrostis varia, Knautia silvatica and Rosa pendulina on steep slopes. Its relation to submontane communities show a climatic transition. ELLENBERG and KLOETZLI state that Abieti-Fagetum is the climax community in the upper montane zone and is similar to Cardamino-Fagetum typicum in having similar habitat. Typical plants of this community indicate a base-rich nature of the habitat.

4.1.1.2 Abieti-Fagetum typicum, Carex remota-variant (e.g. ELLENBERG and KLOETZLI 1972, no. 18):

This community occurs on gentle slopes and occupies the largest area in the Guberwald. It has been intensely managed timber utilization. Plantations of spruce are made extensively on the habitat of this community. Hence it is not in a natural state.

Fir is dominant where extensive plantation of spruce are not made but spruce dominates at the places of plantations. Beech is found frequently. All the tree species grow well. Fir seedlings and saplings are seen everywhere. Spruce seedlings are found at suitable places. Beech regeneration occurs only under the beech trees and nearby places. Rubus fructicosus, R.Idaeus, Lonicera nigra, Sambucus racemosa and Sorbus aucuparia form the shrub storey. Under 30 -40 % tree cover Rubus spp. cover is 60 - 70 %. Species of "C" group are characteristic of this community. Species of "B" and "C" groups dominate. It differs from Abieti-Fagetum typicum, Carex alba-variant in having species of "E" group and in lacking species of "A" group. The presence of the species of "G" and "F" groups show the acidic nature of the habitat.

This community is related to Abieti-Fagetum elymetosum (MOOR 1952, KUOCH 1954) in having species like Carex remota, Equisetum silvaticum etc. which show wetness of the soil. Both communities are found on clayey soil on gentle slopes. Its true montane character is accentuated by not having submontane species. Beech does not regenerate well. According to MOOR (1952) a good beech regeneration lacks in this community due to suboptimal growth conditions and particularly due to the rareness of the mast years in this zone. Also human interference seems to play an overriding role in controlling the beech regeneration in this community, being easily accessible for forest practices. Plantations of Picea abies have been made extensively for economical reasons. Picea is found to induce deterioration of the soil conditions (GENSSLER 1959, ULRICH et al. 1971) by compacting and increasing acidity of the soils. As a result of changing habitat conditions, indicator plants of acidity tend to dominate the ground. Therefore, Vaccinium myrtillus, Thuidium tamariscifolium, Polytrichum formosum, Dicranum scoparium are found very frequently in this community. ELLENBERG (1963) states that spruce favours the occurence of "confer forest plants". The change in the habitat conditions and the vegetation seems to be in favour of confers, particularly of fir. Ample fir regeneration in the spruce dominant stands is on account of "generation change" (SIMAK 1951). Thus in intensely managed forests in this area beech subsequently gets relegated to other favourable habitats e.g. on steep slopes where there is no human interference. Instead of beech, now fir and spruce come to dominate this community. Because of all these changes induced by human interference, the natural trend is altered.

4.1.1.3 Abieti- Fagetum luzuletosum, Equisetum silvaticum-variant (e.g. ELLENBERG and KLOETZLI 1972, no. 19):

The soil under this community is characterized by humus layer which is 5 - 7 cm thick. It occurs on gentle slopes and is managed.

Fir is dominant and spruce subdominant while beech is found here and there. Regeneration of fir and spruce is observed everywhere but beech regenerates sparsely. Rubus fruticosus is the only shrub that dominates. Species of "F"group are typical of this community. Plants of "C" group are found frequently. But it differs from Abieti-Fagetum typicum in not having species of "A" and "B" groups. Plants from "C" group dominate showing acidic nature of the habitat. Acidophytic mosses attain 50 % cover, the highest in the Abieti-Fagetum in this area.

On one hand this, community is related to Abieti-Fagetum typicum, Carex remota-variant by having the species of "E" group and on the other hand to Bazzanio-Abietetum typicum by having species of "F" and "G" group. Therefore, it shows transition between Abieti-Fagetum typicum and Bazzanio-Abietetum typicum. KUOCH (1954) treats this community also as a transitional between "Luzula silvatica - Fagetum" and fir- and Vaccinium myrtillus-rich Piceetum subalpinum with regard to climate. Preponderance of acidophytic mosses and plants like Vaccinium myrtillus indicate humus accumulation and poor nutrient content of the soil. Beech regeneration lacks on account of humus accumulation.

4.1.1.4 Bazzanio-Abietetum typicum, typical variant (e.g. ELLENBERG and KLOETZLI 1972, no. 46):

This community occurs on plateau soils with periodical stagnation of water. It has also been managed.

Fir is dominant and spruce subdominant while beech occurs rarely. Fir and spruce thrive. Beech, when planted also grows well. Ample fir and spruce regeneration is observed while that of beech rarely. Rubus fruticosus is the only shrub found here. The species of "J" group are characteristic of this community. Characteristic plants of "H" and "G" groups also occur here. Vaccinium myrtillus covers 90 % of the ground and the mosses form a thick carpet.

This community was first described by KUOCH (1954) under the name Myrtillo-Abietetum. Earlier, it was referred to as a Piceetum (BRAUN BLANQUET 1950) since characteristic plants of Vaccinio-Piceeion occur in it. In the Swiss Midlands, submontane plateau fir forests dominated by Abies alba were described as "Mastigobryeto-Piceetum"(="Bazzanio-Piceetum") MEYER (1949). Later this type of plateau fir forest was described in detail by FREHNER (1963) under the name Querco-Abietetum. ELLENBERG and KLOETZLI (1972) treat all these communities under the name Bazzanio-Abietetum. It is the poorest in phaneroganic species. Beech regeneration lacks here on account of the moss carpet.

4.1.1.5 Bazzanio-Abietetum typicum, Leucobryum-variant (e.g. ELLENBERG and KLOETZLI 1972, no. 46):

This community occurs on the slope where thick humus accumulation takes place. It is also managed.

Fir dominates monotonously. Spruce occurs sparsely and beech rarely. Fir regenerates in thickets while spruce under favourable light conditions. Beech regenerates rarely. Fir grows well and big trees are observed. The species of "I" group are typical of it. Plants of "F" group also occur. Plants of "G" and "H" group dominate. Mosses form a carpet on the ground.

This community differs from the above community in having plants of "I" group which indicate dryness of the habitat and in not having "J" group which indicate wetness. It is related to Abieti-Fagetum luzuletosum in having the plants of "F" group. This community is also poor in phanerogamic species.

4.1.1.6 Discussion:

The analysis of plant communities in the Guberwald reveals that Abieti-Fagetum typicum is the richest in phanerogamic species while Bazzanio-Abietetum is poorest. Judging from the occurence of indicator plants, it seems that a community rich in species occurs on base rich soil while a species poor on acidic and degraded soil. Also species rich communities have species flowering in spring and do not have many mosses while species poor ones do not have plants flowering in spring and have many mosses attaining high ground cover. In natural Abieti-Fagetum, beech always attains a high cover percentage but in the Guberwald, its percentage has been reduced to a minimum due to human interference. However, beech dominates in the Abieti-Fagetum typicum, Carex alba-variant on steep slopes rich in $CaCO_3$ and devoid of human interference. In this community beech does not attain a greater height as it is evident by casual observations than fir but fir attains great heigth in all the communities in the Guberwald. In this regard KUOCH (1954) states that in natural pure beech forests, fir does not attain a greater height than beech but grows taller than beech in natural fir-beech forests (Abieti-Fagetum). Fir even attains height of 35 - 40 m in the Bazzanio-Abietetum. In the Abieti-Fagetum, natural beech regeneration occurs in patches. However, it remains much below the percentage it would normally attain under natural conditions. As a result fir regeneration is enhanced. The pattern of occurence and dominance of fir and beech in this area is in support of KUOCH's (1954) theory that non-calcareous parent material sponsors conifers and calcareous parent material sponsors broad leaved trees.

The sociological groups of plants from "A" to "J" (table 2) show a gradual transition in indicator value from base-rich to extremely acidic soils. Increasing acidity is associated with increasing humus accumulation thereby showing poor nutrient content of the soils. On such a soil plants with low nutrient requirements can grow. Therefore, specialised calcifuge plants as Vaccinium myrtillus which spread their intense root system in the humus horizon and attain a high mycorrhizal infection succed in dominating the habitat where raw humus accumulates. On such sites, old beech forests exist outside the area of Abieti-Fagetum e.g. in the colline to submontane belt. But they do not occur on acidic soils in the Guberwald. In this regard ELLENBERG (1963) states that where there is equilibrium between litter fall and mineralization, beech remains vital and forms vital forests even on acidic soils. In the Guberwald humus accumulates and conditions are created for podsolisation. In a climatic area such as the northern Alps humus accumulates even on a calcareous plateau in Rengg (Entlebuch). On this plateau old beech trees are found but no natural regeneration is observed. Therefore, there is a negative trend between beech regeneration and acidification of soils while with fir it is positive. HARTMANN (1964) in this regard states that biological limits for broad leaved trees lie in the community poor in phanerogamic species; particularly the occurence of Vaccinium myrtillus in the upper montane zone sets a boundary for broad leaved species, especially for beech.

KUOCH (1954) and BACH et al. (1954) characterize the site of Bazzanio-Abietetum as plateau, terrace or very gentle slopes where practically there is no effect of slope. But in the Guberwald, a special variant of Bazzanio-Abietetum typicum is found on 40 - 50 % slope. According to KUOCH and BACH et al. on such a slope either Abieti-Fagetum or Equiseto-Abietetum should be present in the northern Swiss Alps. However this slope with base-poor sandstone, carries a well developed podsol which is subsequently well drained and thoroughly leached of nutrients. Under these conditions neither Abieti-Fagetum nor Equiseto-Abietetum can develop, the former because of thick humus accumulation and lack of enough nutrients and the latter because the soil is not clayey and not imperfectly drained. Hence such a habitat is only suitable for specialised plants as Vaccinium myrtillus and acidophytic mosses which are typical for Bazzanio-Abietetum typicum, Leucobryum variant.

According to the above vegetation units, a vegetation map of the Guberwald is prepared. (Fig. 6).

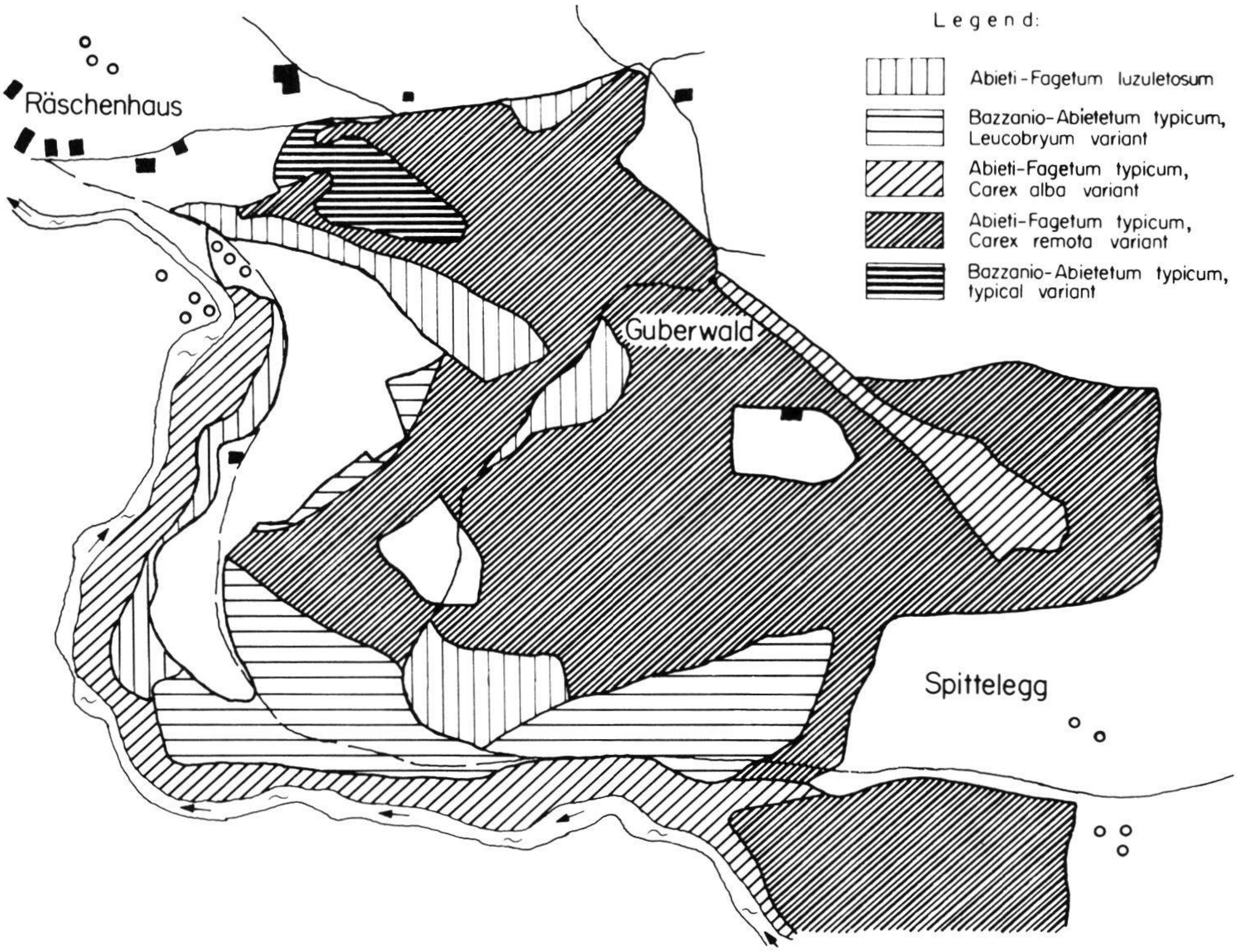


Fig. 6, Vegetation map of Guberwald

4.2 Soil profiles

4.2.1 Soil profile under Abieti-Fagetum typicum, Carex alba-variant (fig. 7A):

It is a nutrient rich brown-earth developed from calcareous morainic material. It is found on steep and also on gentle slopes. It shows the following characteristic horizons:

A_1: 20cm, mull, surface crumb-like in structure, blackish brown in colour presence of earthworms, pH 5.6, loamy in texture, contains calcareous and non-calcareous stones of various sizes, main horizon of root spread, transition from A_1 to B_v not clear.

B_v: 20-60cm, brown in colour, presence of earthworms, pH 6, loamy in texture, contains calcareous and non-calcareous stones of various sizes.

B_v/A_1: 60-80cm, being on steep slope, shows presence of mull and hence blackish brown in colour, presence of earthworms, pH 6.5, loamy in texture, contain calcareous stones of various sizes. Presence of A_1 is because of land slide.

4.2.2 Soil profile under Abieti-Fagetum typicum, Carex remota-variant (fig. 7B):

It is a fine particle rich $A_1/B_{v,g}$-pseudogley developed from marne material. There is formation of a reduction horizon in the deeper layers. It is found on the ridge and also on the gentle slopes. It shows the following horizons:

A_1: 15cm, mineral mull, surface crumb-like in structure, blackish in colour, presence of earthworms, pH 4.5, silty in texture, transition to B_v diffuse.

B_v: 15-30cm, brown in colour, presence of earthworms, pH 5, silty in texture, transition to reduction horizon well marked.

$B_{v,g}$ 30-80cm, brown-gray in colour, no worms, pH 5.5, compact, silty-clayey in texture

4.2.3 Soil profile under Abieti-Fagetum luzuletosum (fig. 7C):

It is an extremely acidic brown-earth with local podsolization developed from non-calcareous parent material. It occurs on gentle slopes. It shows the following characteristic horizons:

A_{00}: litter accumulated mainly from fir and spruce.

A_0: 10cm, partially decomposed mor type humus, blackish brown in colour, fibrous, pH 4.5,

A_1: 10-20cm, blackish in colour, no earthworms, pH 4.5, loamy in texture.

A_2: localised, gray in colour, loamy in texture.

$B_{v/fe}$: 20-80cm, brown in colour, pH 4, loamy in texture, deposition of sesquioxides in 20-50cm horizon.

4.2.4 Soil profile under Bazzanio-Abietetum typicum, typical variant (fig. 8B):

It is a complex of podsolized pseudogley and podsol with reduction in lower horizons. It shows different intensities of podsolization and pseudogley formation. In the following chapters it is referred to as pseudogley podsol. It is situated on gentle slopes and plateau. It shows following characteristic horizons:

A_{00}: litter mainly from fir, spruce and mosses.

A_0: 10cm, brown in colour, fibrous, mor type humus, pH 4.

A_1: 10-20cm, blackish in colour, no earthworms, pH 4, loamy in texture.

A_2: 20-25cm, gray in colour, loamy in texture, pH 4.5.

B_s :25-60cm, reddish brown in colour, pH 4, loamy in texture, marmorization,

Bs/g:60-80cm, gray-brown in colour, pH 4, gray patches of reduction.

4.2.5 Soil profile under Bazzanio-Abietetum typicum, Leucobryum-variant(fig. 8A):

It is an iron-humus podsol developed from sandstone material. It occurs on the slopes of varying inclinations. It shows following characteristic horizons:

A_{00}: litter mainly from fir and Vaccinium myrtillus.

A_0: 15cm, mor type humus, fibrous, brown-black in colour, pH 3.5, compactly interwoven by the roots of Vaccinium myrtillus.

A_1: 15-20cm, black in colour, mineral-humus horizon, pH 3.5, sandy in texture, transition to A_2 well marked

A_2: 20-40cm, gray in colour, extremely sandy in texture, pH 4.5,

B_h : 40-50cm, blackish brown in colour, contents of percolate from A_2 are deposited in this horizon, sandy loamy in texture, pH 4.5.

B_s : 50-120cm, reddish brown in colour, pH 5, loamy in texture, marmorierung,

$B_{s,t}$: deep, blackish brown in colour, pH 5, silty loamy in texture.

Amongst all the soils, brown-earth seems to be the richest in nutrients while podsol the poorest and others in between these two soils.Organic matter tends to accumulate on non-calcareous soils while on steep slopes with lime there is a mull horizon. Earthworms are present only in brown-earth and A_1-pseudogley. Comparison with the results mentioned in chapter 4.1 shows that the plant communities on nutrient rich soils are richest in phanerogamic species while those on poor soils are poorest in phanerogamic species but richest in mosses. beech is found on nutrient rich brown-earth while absent on podsol in the Guberwald.

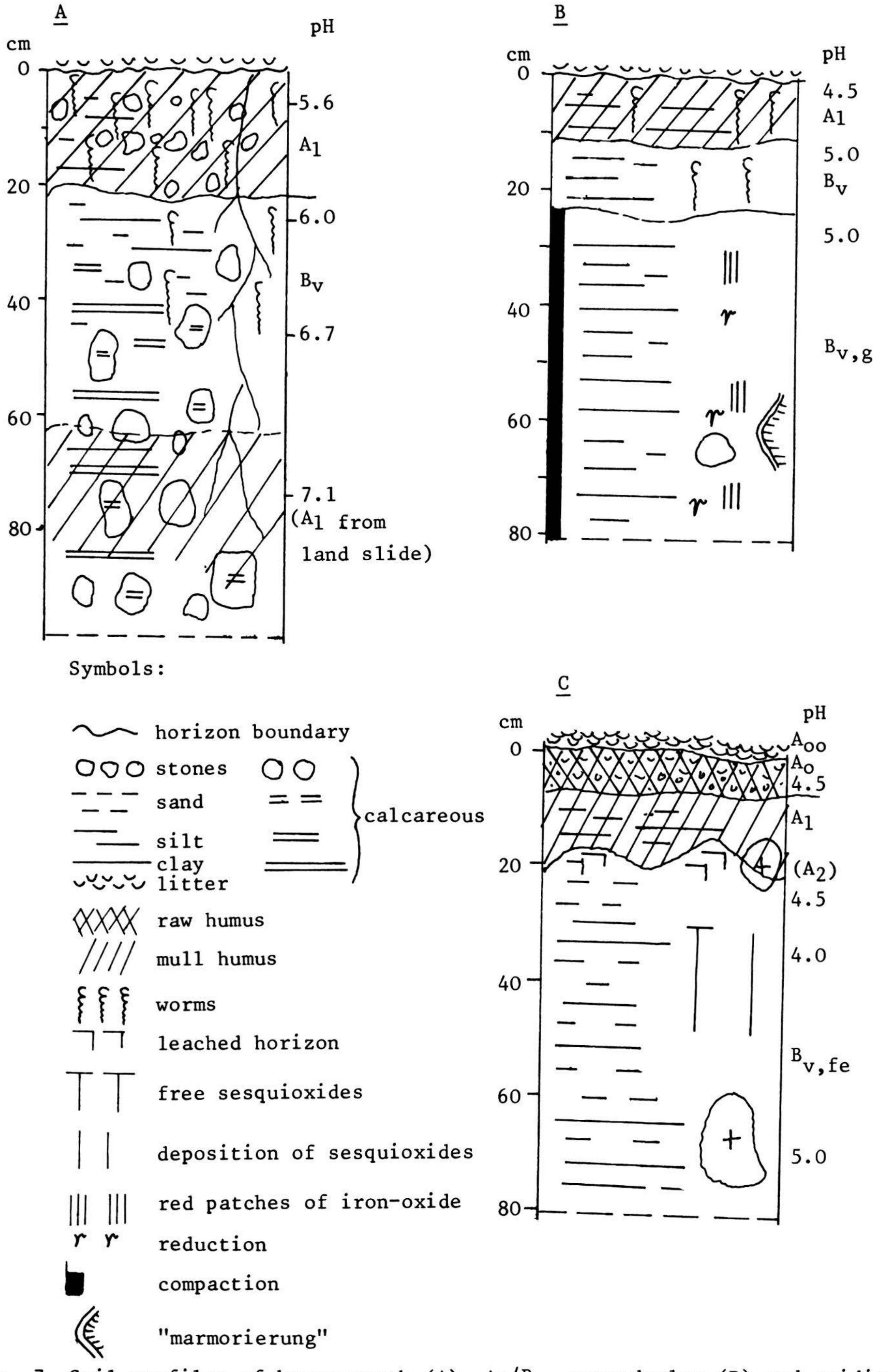


Fig. 7, Soil profiles of brown-earth (A), $A_1/B_{v,g}$-pseudogley (B) and acidic brown-earth (C).

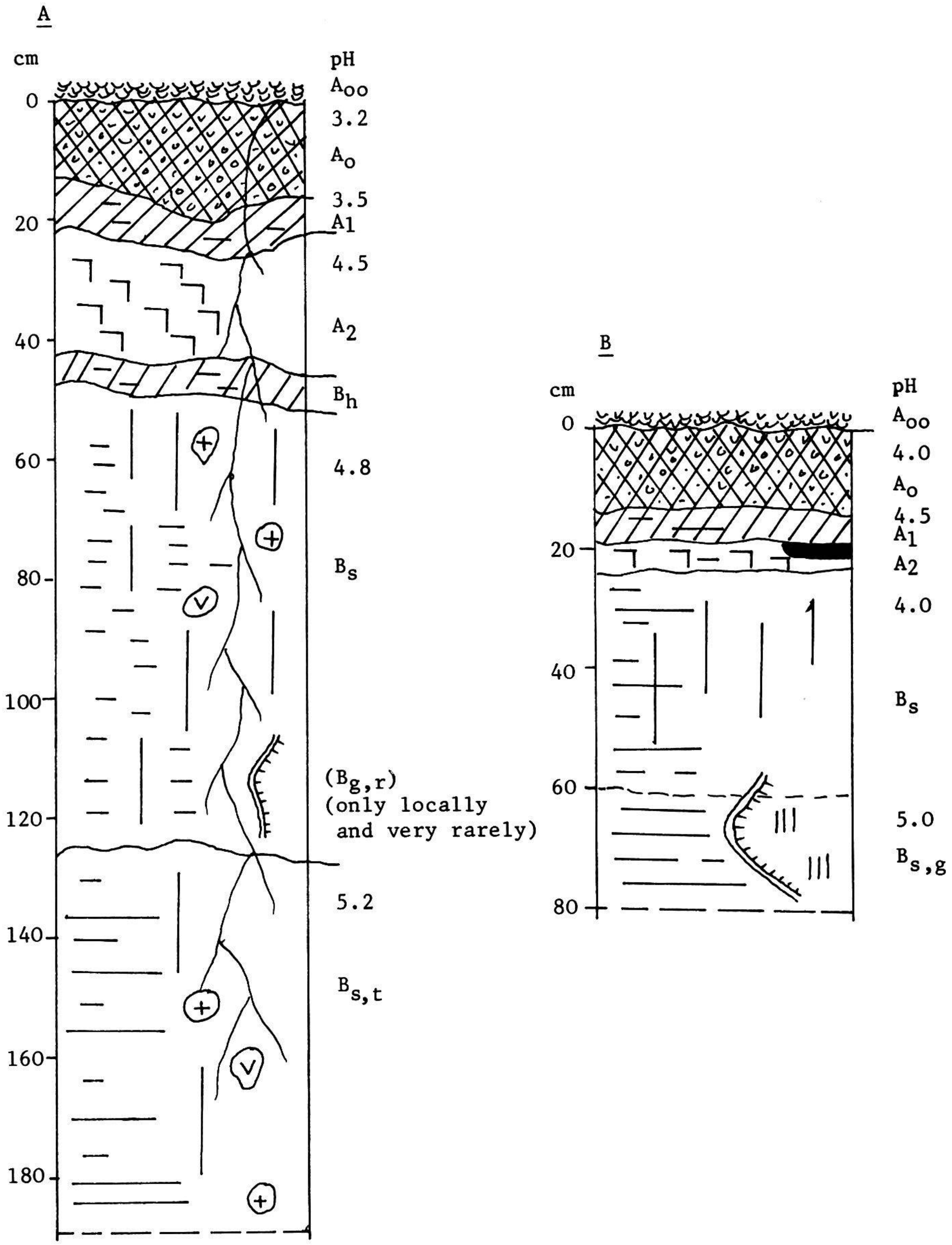


Fig. 8, Soil profiles of podsol (A) and pseudogley-podsol (B).

4.3.1 Particle size

The results of particle size analysis are expressed in table 3. They show that podsol in 10-20cm depth is extremely sandy (89% sand, 8% silt and 3% clay). A_1-pseudogley on the contrary, has a large content of silt and clay particles (65-80%) while a small amount of sand particles (20-35%). Brown-earth is in between these two soils having 50% silt and clay and a rest of sand.

The study of soil texture leads to the understanding of many soil properties. By its extreme sandy nature, podsol contains large pores and as a result has less available water. RICHARD (1955) calculates 5 times less available water in the sandy soils of "chablais" than in the silty soil. Not only availability of water depends on the texture of the soil but also mineral nutrients. It is well known that mineral nutrients are held by clay and colloidal particles while they get leached through the sandy soil. KØIE (1951) states that humus accumulation depends on pH and silt-clay percentage of the soils. The more acidic and sandy the soil is, the greater is the accumulation of humus. This seems to be the case in the Guberwald too. Moverover, the factors (high rainfall, low temperature and humidity)favouring the process of podsolization, augment humus accumulation on acidic sandy soils.

Textural properties of the soil are, therefore, one of the factors limiting the distribution of plants by influencing other properties of soil. KØIE (1950) states that in Denmark, beech hardly forms wood below 8% content of silt-clay and that it becomes increasingly competitive with larger contents of small particles under otherwise unchanged site conditions. His results show that Vaccinium myrtillus can thrive with smaller content of smaller particles. whenever V. myrtillus dominates in the montane zone, it shows unfavourable site conditions for beech. Beech does not occur on the wet soils in the Guberwald. ELLENBERG (1963) and PFADENHAUER (1971) mention that the competitive ability of beech gets reduced on soils becoming periodically wet.

Table 3. Particle size analysis of the soil samples from two depths.

Soil type	depth (cm)	clay (%)	silt (%)	sand (%)
Brown-earth	10-20	23	27	50
	40-50	22	28	50
Podsol	10-20	3	8	89
	40-50	7	12	81
Soil transitional podsol and A_1-pseudogley	10-20	18	42	40
A_1-pseudogley on the ridge	10-20	24	42	34
	40-50	28	39	33
A_1-pseudogley on the slope	10-20	21	49	30
	40-50	20	59	21

4.3.2 Desorption curves

The gravimetric determination of water content in soil does not give ecologically important information whether the soil water is available to the plant or not. Availability of the soil water depends on the tension with which it is retained in soil (RICHARD 1955). Desorption curves give the relationship between the water content (volume percent) and soil water tension with which water is bound in soil, thereby making it possible to estimate the amount of available water in different soils. A desorption curve has two ecologically important points as follows:

1. Field capacity (FC): It is the water content of a normally drained soil after the gravitational water has drained away and capillary water movement has become very slow (VEIHMEYER and HENDRICKSON 1949). Field capacity of a soil is a function of its soil profile. Therefore, pore size distribution in the different horizons of a profile determines the range of field capacity. In the Guberwald, A_1-pseudogley and brown-earth-type are not normally drained. However, for calculating available water in the soil, it is necessary to know a range of field capacity. Therefore, field capacities of the soils in the Guberwald were estimated from the tensiometer readings of 20 and 50cm depths.

2. Permanent wilting percentage (PwP): It is the range of soil water content at which plants remain permanently wilted. For the mesophytes, this percentage is reached at about 15at .

Available water: this is the amount of soil water for plant growth between field capacity and permanent wilting percentage. Available water may be divided into easily available (between field capacity and 0.8at) and not easily available water (between 0.8 and 15at).

Fig. 9 shows the desorption curve for brown-earth. The upper horizon (10-20cm) has larger total pore volume than that in the lower one (40-50cm).

Under relatively smaller pressure, the desorption curve of podsol bends strongly, thereby showing high content of large pores. (information from RICHARD 1971) The total pore volume is larger in the upper horizon (58%) than in the lower one (46%). Available water is also greater in the upper horizon (31%) than in the lower one (22%).

Fig. 10 and 11 show the desorption curves for A_1-pseudogley on the ridge and slope respectively. The upper horizon of A_1-pseudogley on slope has larger total pore volume than in the same horizon of A_1-pseudogley on ridge. Available water in the upper horizons of A_1-pseudogley on slope and also on ridge is nearly the same. Same is the case in the lower horizons.

The comparison of these curves of three soil types shows that in general the upper horizons contain a larger amount of total pore volume than that in the lower horizons. This is on account of the presence of humus and better soil structure. Amongst all the soils, the upper horizon of A_1-pseudogley on ridge has the largest amount of total pore volume while brown-earth has the lowest. The largest amount of rapidly drained water is present in podsol(19%). The amount of available water in the upper horizons of all these soils does not differ greatly. But it differs greatly in the lower horizons being largest in A_1-pseudogley (33%) and lowest in brown-earth (18%) (table 4).

The greater amount of large pores in podsol shows its high permeability and thus a trend to dry out since the largest amount of available water is bound with a smaller tension which leads to luxurious consumption of water by the plants. However, being located in a region of heavy precipitation, podsol rarely dry out. The large amount of fine pores in the lower horizon of A_1-pseudogley presumably leads to the formation of a reduction horizon.

RICHARD (1955) states that periodical saturation of a soil does not have adverse effect on the growth of fir. Fir seems to tolerate the site conditions on A_1-pseudogley which is imperfectly drained and on podsol which is normally drained. This shows wide range of adaptability of fir with regard to soil water. PFADENHAUER (1971) also reported that in the Aargauer Swiss Midlands, fir grows on imperfectly drained soils while beech on comparatively well drained soil.

Table 4, Estimation of total pore volume (V_p), rapid drainage water (W_r), available water (W_e) and not available water (W_n) from the desorption curves of the soils.

soil and depth		V_p %vol.	W_r %vol.	W_e %vol.	W_n %vol.
Brown-earth					
	10-20cm	55	*	*	21
	40-50cm	39	6	18	15
Podsol					
	10-20cm	58	18	31	9
	40-50cm	46	19	22	5
A_1-pseudogley					
ridge	10-20cm	62	16	27	19
	40-50cm	54	5	32	17
A_1-pseudogley					
slope	10-20cm	55	9	29	17
	40-50cm	40	5	33	12

* Desorption curve of this horizon shows a large standard deviation (Fig. 9). Therefore, the values are not utilized in interpretation.

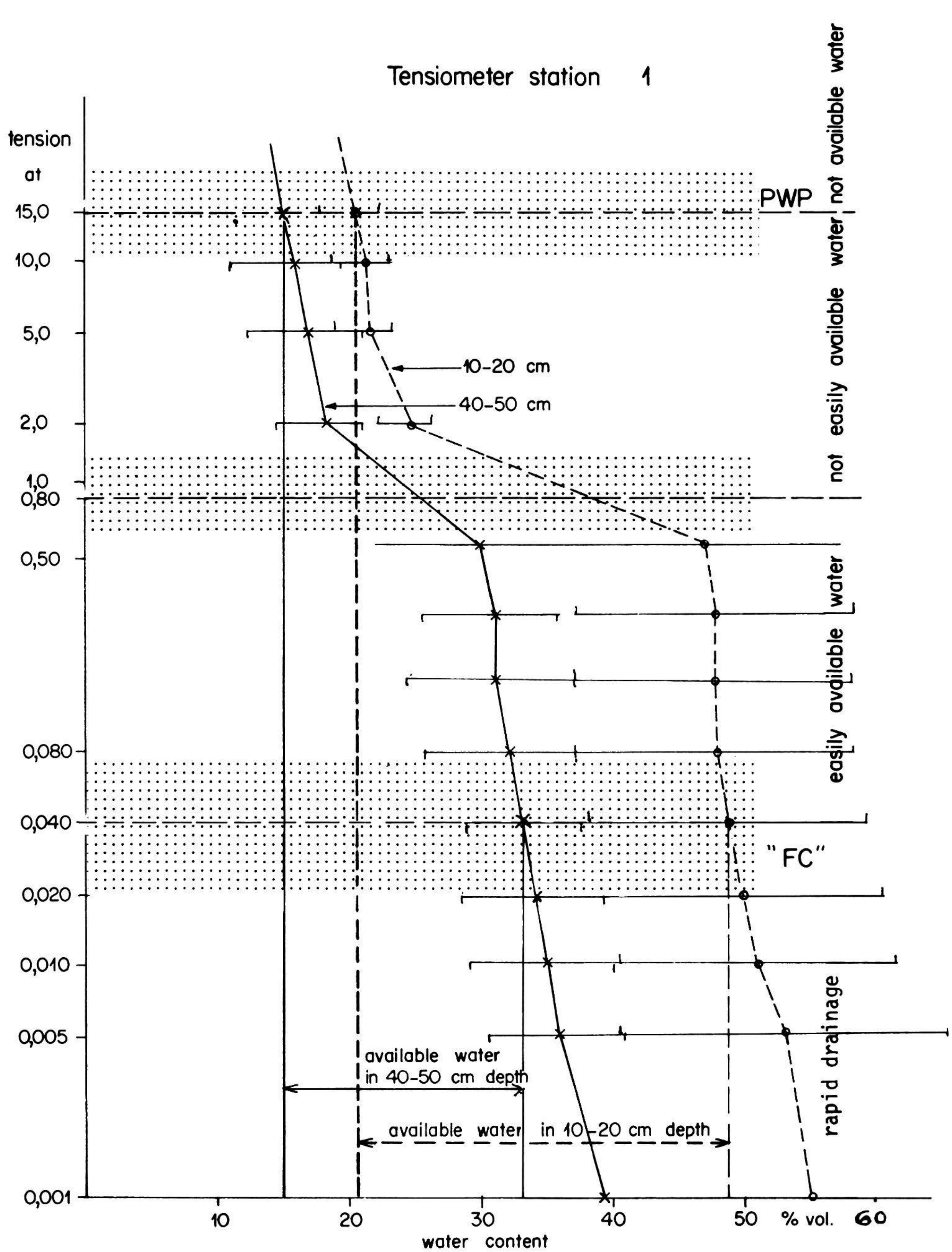


Fig. 9 , Desorption curve for brown-earth under Abieti-Fagetum typicum Carex alba-variant.

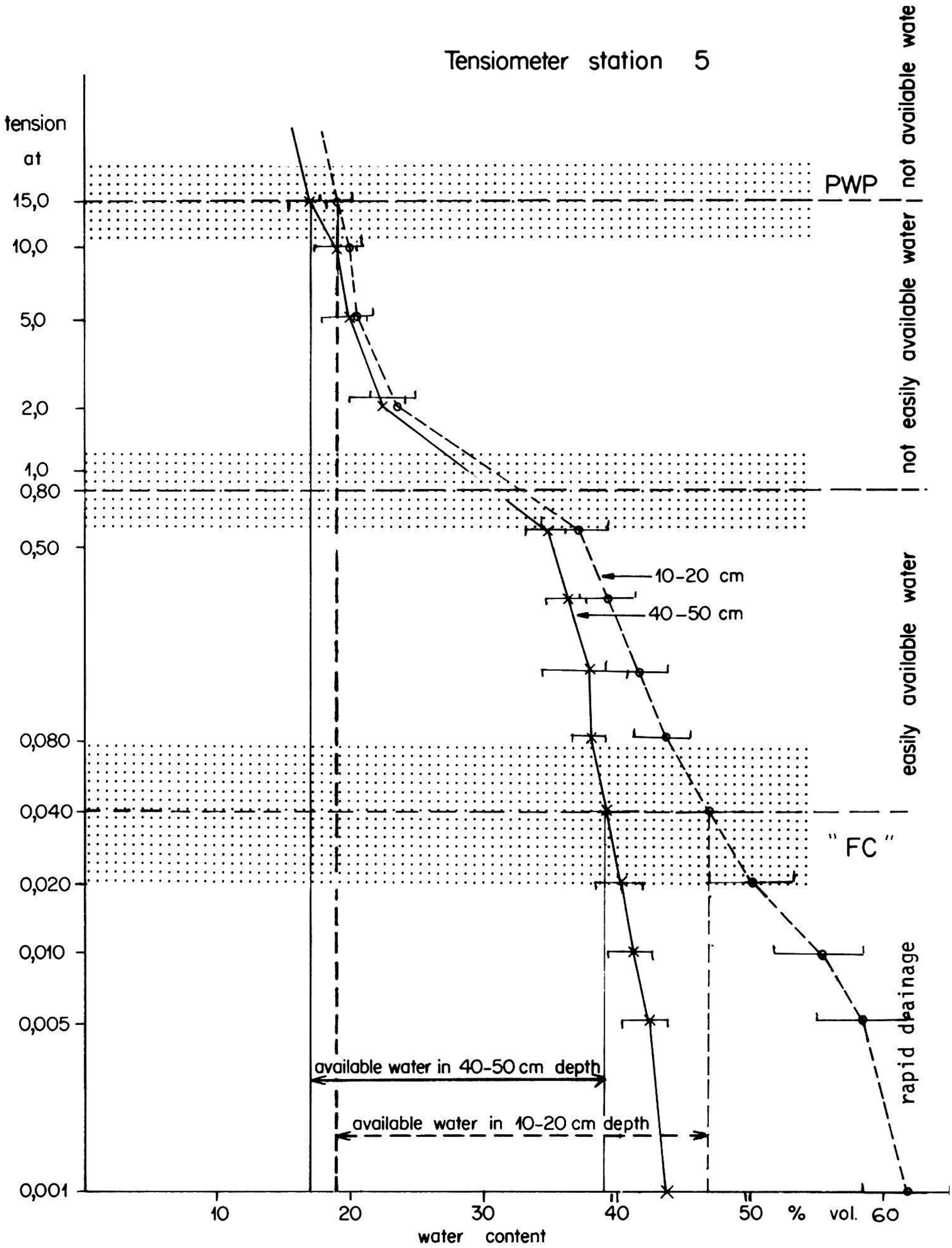


Fig. 10, Desorption curve for A_1-pseudogley under Abieti-Fagetum typicum Carex remota-variant on ridge.

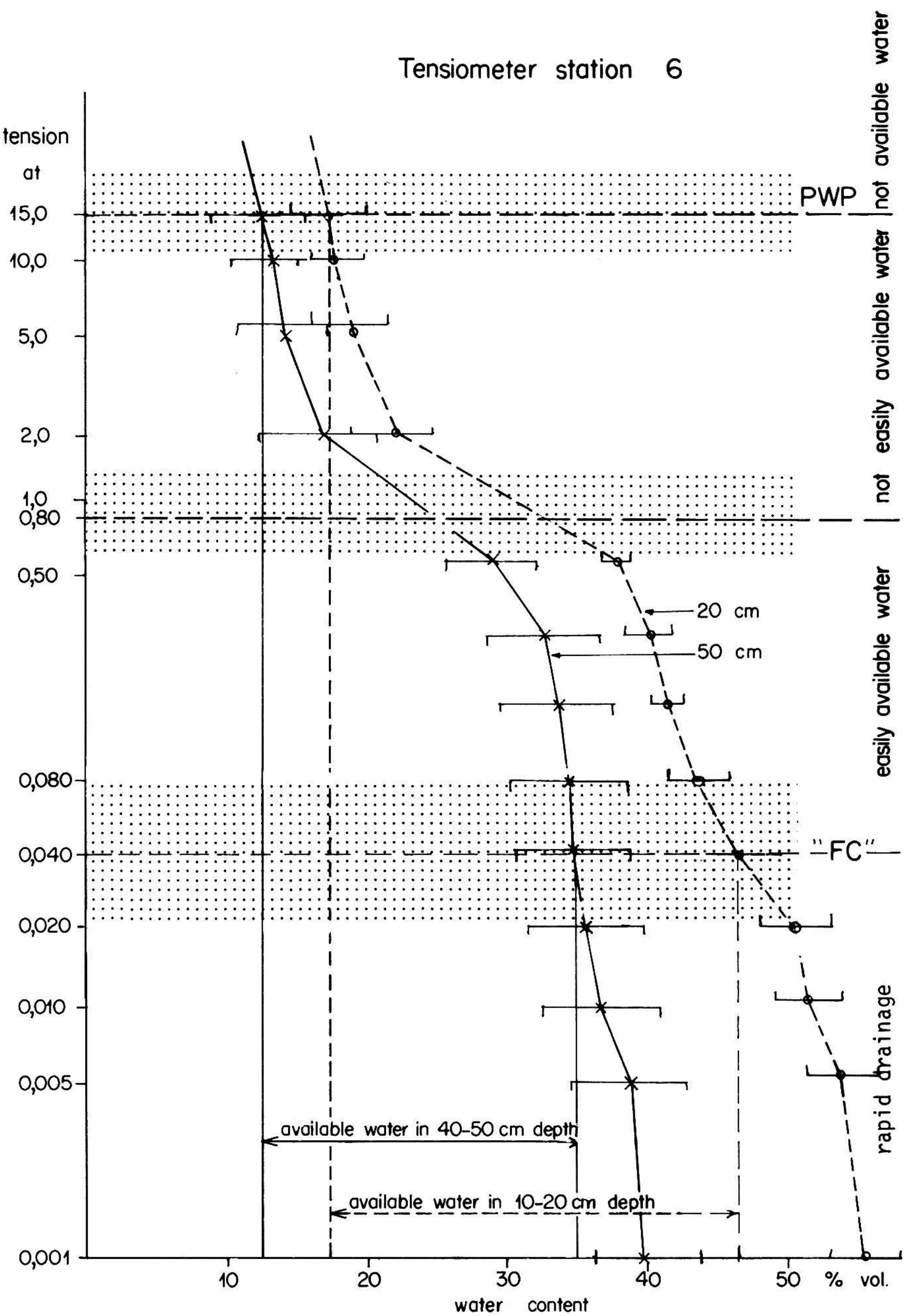


Fig. 11, Desorption curve for A_1-pseudogley under Abieti-Fagetum typicum, Carex remota-variant on slope.

4.3.3 Course of soil water tension

It was assumed that water regime in different soils may affect the regeneration of beech. Therefore, measurements of the course of tension at various places were carried out during the growth periods of 1972 and 1973. The results are expressed in Figs. 12 and 13. (Tensiometer stations are located in Fig. 4)

Tensiometer-
Station 1 : Course of tension in the brown-earth under Abieti-Fagetum typicum, Carex alba-variant reveals that water in the soils remains always easily available in the growth period since the highes recorded value was only 104 cm of water column (0,104 at).

Tensiometer-
Station 2 and 3 : Course of tension in the humus layer as well as deeper layers of podsol under Bazzanio-Abietetum typicum, Leucobryum-variant shows that water remains in the range of easy availability.

Tensiometer-
Station 4 : Course of tension in transitional soil between podsol and A_1-pseudogley under Abieti-Fagetum typicum, Carex remota-variant rises to 678cm of water column (0.678 at). But the water remains in the range of more or less easy availability.

Tensiometer-
Station 5 and 6 : Course of tension in the A_1-pseudogley under Abieti-Fagetum typicum, Carex remota-variant also reveals that water remains in the range of easy availability.

Though podsol is sandy, even then water remains in the range of availability. This could be attributed to ample rainfall in this region (table 5). The rainfall is well distributed throughout the growth period. The longest rainfree period occurs in the month of October when plants start slowing down physiological activities. WATT (1923), SCHMITT (1936) and BURSCHELL et al. (1964) reported that frequently the humus layer dries out and therefore, the beech seedlings growing on humus layer also resultantly die. This is not the case in the Guberwald.

Table 5. Monthly rainfall data from the year 1960 to 1970.

Year	April	May	June	July	August	September	October	Yearly
1970	247	160	299	170	283	77	106	1749
1969	209	117	286	162	294	69	33	1773
1968	163	176	181	175	305	240	35	1891
1967	106	244	244	116	146	216	81	1891
1966	193	131	168	263	326	86	136	2111
1965	269	262	205	275	170	178	21	2205
1964	192	239	154	74	198	113	193	1632
1963	67	130	160	258	154	88	54	1685
1962	130	290	104	138	196	113	47	1697
1961	145	239	213	202	168	50	71	1545
1960	188	214	269	234	258	203	154	2090

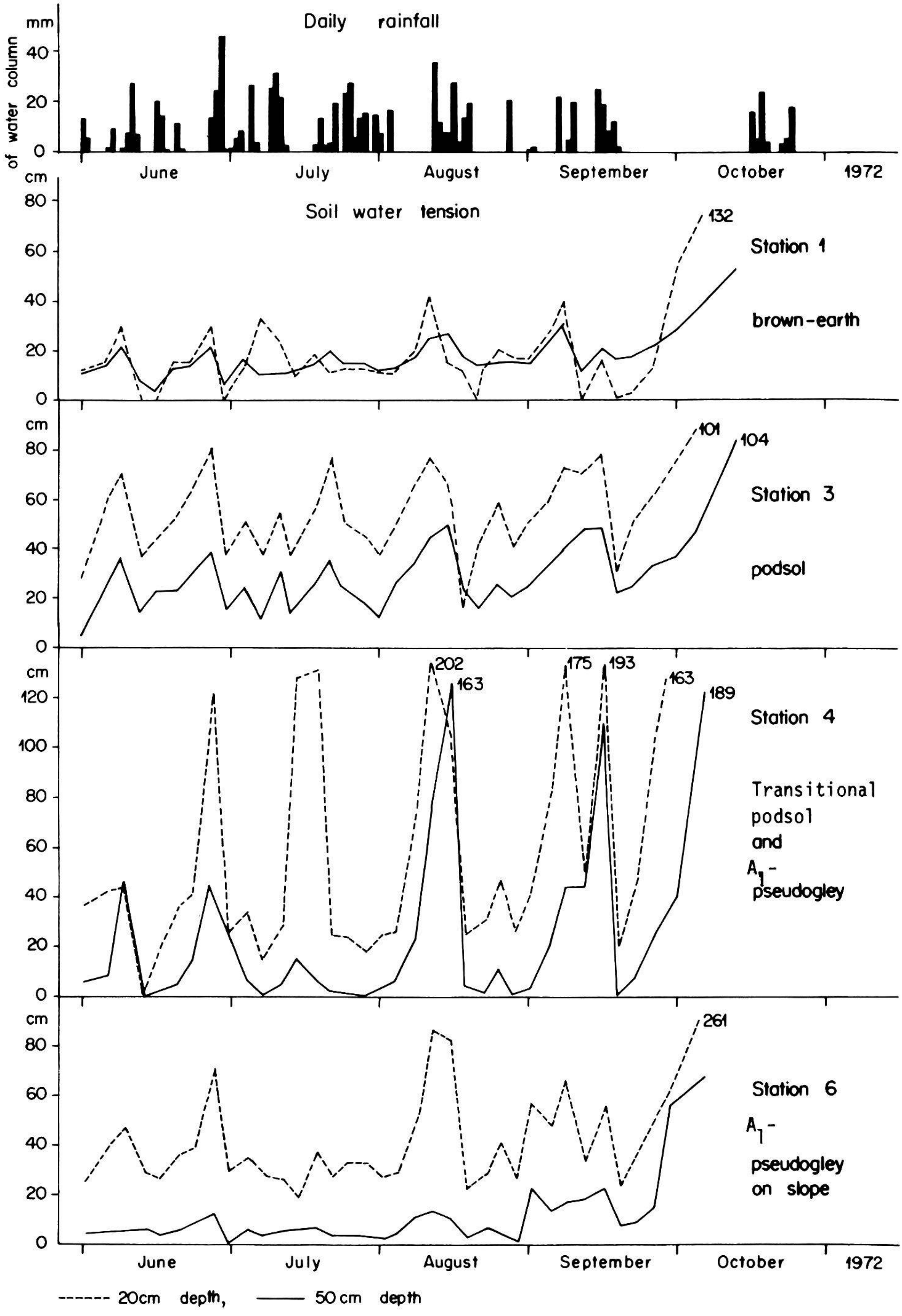


Fig. 12, Course of soil water tension in different soils in 1972.

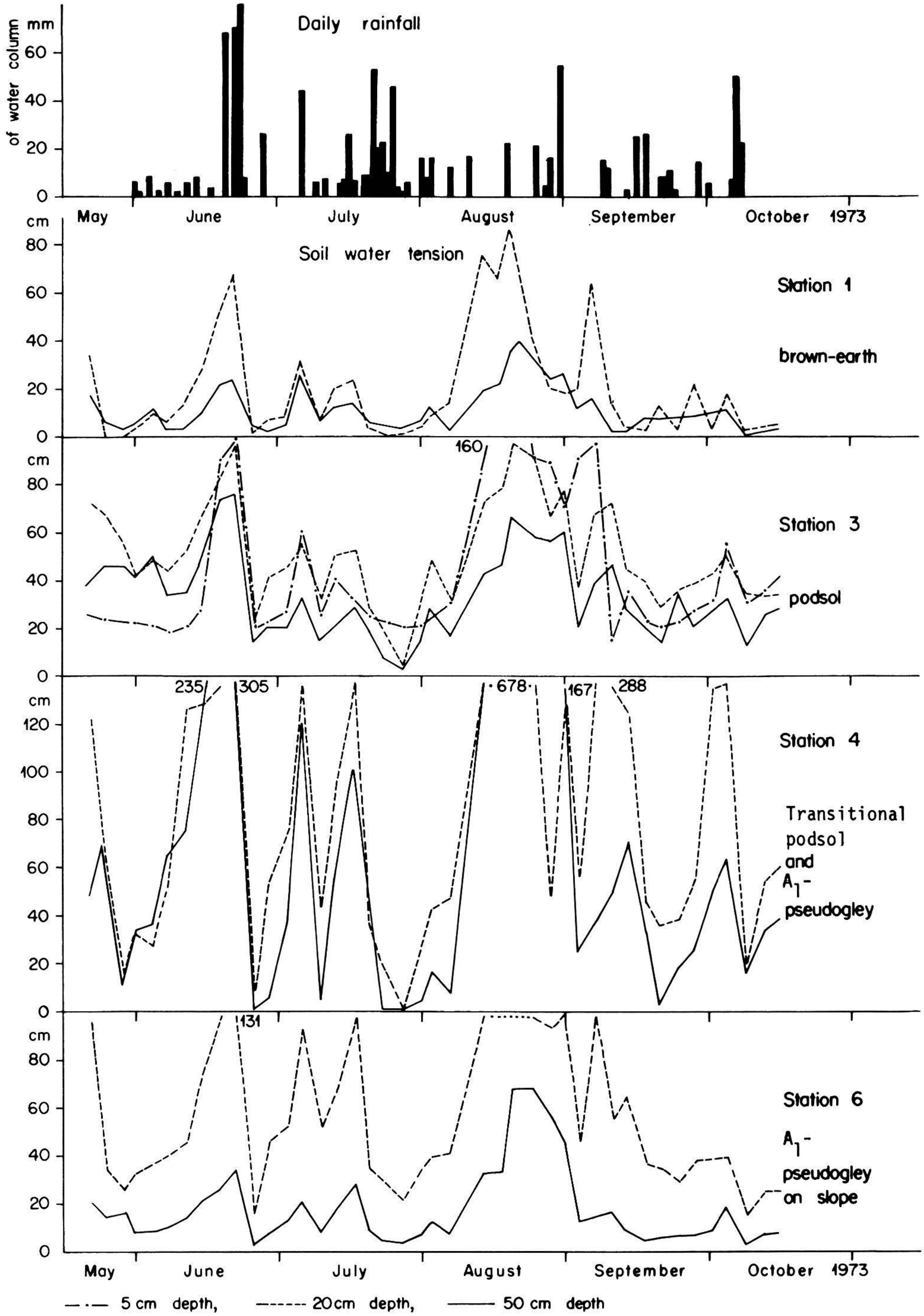


Fig. 13, Course of soil water tension in different soils in 1973.

4.4 Soil chemical results

4.4.1 Soil reaction:

Podsol is the most acidic (pH 3,5) of all the soils investigated while brown-earth is only weakly acidic (pH 6). The pH value increases with increasing depth of soils (fig. 14).

4.4.2 Carbonate content:

Brown-earth does not show the presence of carbonate in 1 - 10 cm depth but with increasing depth, carbonate content also increases amounting to 9,8 % (dry weight) of the soil in 40 - 60 cm depth. Carbonate from the upper horizons is leached into the deeper horizons of brown-earth (see chapter 4.5). Podsol, A_1-pseudogley and soil between podsol and A_1-pseudogley do not show the presence of carbonate in the horizons investigated.

4.4.3 Nitrate and ammonium (fig. 14):

The present investigations show that in brown-earth only nitrification takes place while in podsol only ammonification and in A_1-pseudogley and soils between podsol and A_1-pseudogley both nitrification and ammonification take place. As expected the relatively highest amount of available nitrogen occurs in the upper layers of all the soils and it decreases with the increase in depth. Brown-earth shows 2,6 mg NO_3-N / 100 g dry wt. of soil in 1 - 5 cm depth while podsol 10,8 mg NH_4-N / 100 g dry wt. of soil after six weeks incubation. In soil between podsol and A_1-pseudogley, it amounts to 66,7 mg NH_4-N /100 g and 1,2 NO_3-N / 100 g dry wt. of soil, in A_1-pseudogley on ridge 30,0 mg NH_4-N / 100 g and 0,5 mg NO_3-N / 100 g dry wt. of soil in 1 - 5 cm depth. Thus the relatively largest quantity of available nitrogen is present in soil between podsol and A_1-pseudogley.

JENNY (1958), ZOETTL (1963) and RUNGE (Cf. ELLENBERG 1971) also reported that in podsol only ammonification takes place while in brown-earth nitrification. However ROMELL (1953, Cf. KLOETZLI 1969) reported nitrification in the raw humus horizon of podsol. N-mineralization in the soils of the Guberwald is broadly correlated with pH and the type of humus. In this regard MEYER (1961) states that the biological activity of nitrifying micro-organisms decreases with decreasing pH and increasing raw humus content. In the humus layer of podsol pH is 3,2 and raw humus accumulates up to 20 cm. Therefore, only ammonification takes place. On the other hand, brown-earth has pH 6 and there is no raw humus accumulation. This results in the nitrification in brown-earth. But the amount of nitrate after six weeks incubation is comparatively smaller. Similar results have been reported by LINDQUIST (1932) and PFADENHAUER (1971). This is reported to be on account of slow nitrogen mineralization in mull humus which is stable ("Dauerhumus") (SCHEFFER and SCHACHTSCHABEL 1966). Soil between podsol and A_1-pseudogley show both nitrification and ammonification on account of their crumb-like soil structure and pH range between 3,5 and 4,5.

The amount and form of available nitrogen has a great influence on the distribution of plants. In this regard ELLENBERG (1971) states: "Most of the vascular plants may use NH_4-ions as well as NO_3-ions. However, the so-called calciphytes are not able to absorb NH_4-ions in a very acidic medium whereas the acidophytes are. Therefore, the kind of N-containing ions mainly produced in the soil is important for the composition of the phyto-cenoses." In podsol only ammonification takes place and the amount of NH_4-N is the smallest amongst all the soils. This reflects on the floristic composition of the plant community on podsol. In this community, Vaccinium myrtillus which grows well with NH_4-N (BOGNER 1966, INGESTAD 1974), dominates the ground vegetation. With increasing pH and NO_3-N, vegetation becomes richer in phanerogamic species from podsol —— acidic brown-earth, —— A_1-pseudogley —— to base-rich brown-earth.

Picea abies grows well on A_1-pseudogley where both ammonification as well as nitrification take place. Picea also thrive on podsol where only ammonification takes place. Therefore, it can tolerate a nutrition of only NH_4-N.

Abies alba grows well on podsol in the Guberwald as well as on A_1-pseudogley and brown-earth. Therefore, Abies grows equally well either with NH_4-N or NO_3-N or both.

Fagus silvatica grows well on brown-earth but not well on podsol. Failure of beech regeneration and slow growth on podsol can not be attributed only to the form of N-nutrition though it may be one of the factors.

HARLEY (1949) found that in nature, beech mycorrhiza grow well in soils where ammonification takes place and also according to MELIN (1959) most of the mycorrhizal fungi utilize NH_4-N better than NO_3-N. Therefore, failure of beech regeneration on podsol can not be attributed to the lack of mycorrhiza.

4.4.4 Exchangeable cations:

Exchangeable calcium (Fig. 14): Amongst all the soils,brown-earth shows the largest amount of calcium, having 17,6 meq / 100 g in 1 - 5 cm depth and 45 meq / 100 g in 40 - 60 cm depth. For the other horizons the values range in between. Podsol contains the smallest amount of calcium, having only 5,8 meq /100 g in 1 - 5 cm depth. The amount of calcium in podsol decreases with increasing depth while in brown-earth, it increases with increasing depth. This reflects on the process of soil development and the parent material from which the soils developed. Brown-earth developed from calcareous parent material and hence it has large reserves of calcium in the deeper horizons. A smaller amount in the upper horizons of brown-earth is on account of leaching. Podsol, on the contrary, developed from non-calcareous sandstone. The upper horizons of podsol show a higher amount of calcium on account of the humus accumulation. A_1-pseudogley contains the amount of Ca-ions ranging in between. A_1-pseudogley contains the largest amounts of calcium in the upper horizon (5 meq / 100g) as well as in the deeper horizon (5,4 meq /100 g in 40 - 60 cm depth).

Exchangeable potassium: The amount of potassium in the upper horizons of podsol and A_1-pseudogley is larger than that in same horizon of brown-earth. Podsol contains 0,6 meq / 100 g and brown-earth contains 0,2 meq / 100g in the upper horizon. The higher amount in the upper horizon of podsol seems to be on account of humus accumulation. The smaller amount in the upper horizon of brown-earth seems to be due to reduced cycling of K (DUVIGNEAUD and DENAEYER-DE-SMET 1971).

Table 6 , Chemical characteristics of different horizons of soils in the Guberwald. Samples were collected on 3 July 1972.

For NH_4-N and NO_3-N determinations were made from samples sieved with 4mm sieve and rest with 2mm sieved samples.

Soil type and depth	HOH %weight	pH	Fresh NH_4-N mg/100g	Fresh NO_3-N mg/100g	After incubation NH_4-N mg/100g	After incubation NO_3-N mg/100g	$CaCO_3$ %	Ca meq/100g	K meq/100g	Na meq/100g	Mg meq/100g	H meq/100g	"S" meq/100g	"V" %	Ca/Mg
Brown-earth															
1- 5cm	47	5.8	0.7	0.0	0.0	2.6	0.0	17.60	0.19	0.08	0.59	5.4	18.46	77	29.8
5- 10cm	46	6.0	0.0	0.5	0.0	2.3	0.0	21.70	0.11	0.12	0.58	4.0	22.51	84	37.4
10- 20cm	36	6.2	0.0	0.3	0.0	0.7	0.4	19.70	0.11	0.10	0.68	4.4	20.59	82	29.0
20- 40cm	32	6.7	0.0	0.2	0.0	0.3	2.4	28.10	0.15	0.15	0.50	4.5	28.90	86	56.2
40- 60cm	23	7.1	0.0	0.1	0.0	0.3	9.8	45.00	0.15	0.21	0.59	0.0	45.95	100	76.3
Podsol															
1- 5cm	200	3.2	1.4	0.0	10.8	0.0	0.0	5.85	0.63	0.13	0.99	53.3	7.60	12	5.9
5- 10cm	46	3.3	0.1	0.0	0.0	0.2	0.0	1.35	0.07	0.04	0.34	15.7	1.71	10	4.4
10- 20cm	70	3.2	1.3	0.0	1.6	0.0	0.0	0.65	0.11	0.06	0.23	24.9	0.99	4	2.8
20- 40cm	11	3.5	0.0	0.0	0.2	0.0	0.0	0.60	0.05	0.06	0.17	19.4	0.88	4	3.5
40- 60cm	25	4.5	0.0	0.0	0.2	0.0	0.0	0.37	0.05	0.04	0.16	9.2	0.62	6	2.3
Soil between podsol and A_1-pseudogley															
1- 5cm	133	4.0	3.9	0.0	66.7	0.3	0.0	9.35	0.60	0.10	1.02	31.0	10.07	26	9.2
5- 10cm	38	4.0	0.2	0.0	0.0	0.3	0.0	-	-	-	-	-	-	-	-
10- 20cm	40	4.5	0.0	0.0	0.5	1.2	0.0	2.40	0.19	0.06	0.40	10.8	3.05	14	6.0
20- 40cm	29	4.7	0.0	0.0	0.1	0.1	0.0	2.27	0.11	0.06	0.43	7.7	2.87	27	5.3
40- 60cm	24	5.0	0.0	0.0	0.0	0.0	0.0	2.00	0.09	0.07	0.38	5.2	2.54	33	5.3
A_1-pseudogley on slope															
1- 5cm	100	3.8	3.4	0.0	29.6	0.5	0.0	6.35	0.59	0.10	0.99	31.0	8.03	21	6.4
5- 10cm	45	4.1	0.4	0.4	0.0	1.0	0.0	-	-	-	-	-	-	-	-
10- 20cm	40	4.5	0.0	0.0	7.5	0.0	0.0	3.00	0.28	0.08	0.45	12.9	3.81	23	6.6
20- 40cm	24	4.6	0.0	0.0	0.4	0.0	0.0	5.70	0.15	0.08	0.63	4.7	5.56	54	9.0
40- 60cm	27	5.0	0.0	0.0	3.7	0.0	0.0	5.90	0.11	0.06	0.53	7.9	6.60	45	11.1
A_1-pseudogley on ridge															
1- 5cm	81	3.6	2.2	0.0	15.6	1.2	0.0	4.90	0.42	0.09	0.80	28.6	6.21	18	6.2
5- 10cm	36	4.0	0.1	0.2	0.0	0.8	0.0	-	-	-	-	-	-	-	-
10- 20cm	36	4.5	0.0	0.0	1.1	0.0	0.0	1.75	0.11	0.06	0.36	12.7	2.28	15	4.9
20- 40cm	26	4.6	0.0	0.0	0.5	0.0	0.0	4.10	0.08	0.07	0.52	5.7	4.77	46	7.8
40- 60cm	27	5.0	0.0	0.0	0.6	0.0	0.0	5.35	0.11	0.06	0.42	3.8	5.94	61	12.7

Exchangeable sodium: Sodium shows the same trend as potassium. Podsol and A_1-pseudogley contain the largest amounts in the upper horizons and smaller in the deeper horizons, Brown-earth, on the contrary, shows the smallest amount in the upper horizon (0,08 meq / 100 g) while largest in the deeper horizon (0,2 meq / 100 g).

Exchangeable magnesium: The amount of magnesium in the upper horizons of podsol is the largest (1,0 / 100 g) while smallest in the same horizon of brown-earth (0,6 meq / 100 g). Magnesium content in all the horizons of brown-earth is nearly the same while in podsol it decreases with increasing depths.

4.4.5
Total exchangeable metallic cations: Total exchangeable metallic cations of soil depends upon the amount of calcium present in it, since it is present in greatest quantity. The largest amount of exchangeable cations is present in brown-earth (18,5 meq / 100 g) and the smallest in podsol (7,6 meq / 100 g in 1 - 5 cm depth). In brown-earth, the amount of exchangeable cations increases with increasing depth while in podsol and A_1-pseudogley, it decreases with increasing depth.

4.4.6 Ca/Mg and Ca/K ratios:

Brown-earth shows a greater Ca/Mg (30 in the upper three horizons and 56 and 76 in the deeper horizons) and Ca/K (100 in the upper and 300 in the lowest horizon) ratios. Podsol, on the contrary, shows the smallest Ca/Mg (2 - 6 varying in different horizons) and Ca/K ratios (7 - 19 varying irregularly in the different horizons). A_1-pseudogley shows values in between these two.

High Ca/Mg and Ca/K ratios denote the equilibrium of ion complexes in soils. In acidic soil such as podsol, ionic complexes remain in the state of imbalance on account of smaller Ca/Mg and Ca/K ratios. MANIL et al. (1963) also found a low Ca/mg ratio in acidic soils of Belgium. BARSHAD (1960) states that magnesium intervenes in many ways in the ionic equilibrium of acidic soils. Imbalance of the ionic complexes in soils results in imbalance in the uptake of nutrients by plants. Only some of the plants can stand such a condition. On account of this and other factors Vaccinium dominates the ground vegetation and fir dominates the tree storey monotonously. Therefore, it seems that fir is tolerant to imbalanced nutrition while beech is not. As the condition of ionic complexes improves in the soil, beech occurs in a greater proportion, ultimately dominating on brown-earth.

4.4.7 Exchangeable hydrogen ions (Fig. 14):

Amongst all the soils, brown-earth shows the smallest amount of hydrogen ions (5,4 meq / 100 g in 1 - 5 depth) while podsol shows the highest amount (53,3 meq / 100 g in 1 - 5 cm depth). A_1-pseudogley shows values in between above two soils.

4.4.8 Base saturation (Fig. 14):

Amongst all the soils, brown-earth is the richest in base saturation (77,4 % in 1 - 5 cm depth and 100 % in 40 - 60 cm depth) while podsol is the poorest (12,5 % in 1 - 5 cm and 6,3 % in 40 - 60 cm depth). With increasing depth, brown-earth becomes richer in base saturation while podsol in general becomes poorer. A_1-pseudogley is in between these two soils. With increasing depths, base saturation increases in A_1-pseudogley.

Base saturation is greatest in brown-earth on account of the high amount of calcium ions and small amount of hydrogen ions. Podsol is the poorest in base saturation on account of the small amount of calcium ions and the large amount of hydrogen ions. Of all the horizons of podsol, the humus horizon is the richest in base saturation due to accumulation of nutrient in the humus. ULRICH et al. (1971) state: "especially, for Ca and Mg, the accumulation of mobilizable ion-stores in the 0 horizon causes an unbalanced depth distribution which is characterized by what may be called as noise heaviness. This is especially true for Mg and is indicative of some kind of stress situation, since the mineral soil seems to be more or less exhausted in respect to this element." In the case of podsol in the Guberwald, horizons below the humus show an extremely small amount of Ca, K, Mg and Na (particularly Ca). Therefore, the humus horizon is the store of nutrients in podsol. As a result of this <u>Vaccinium</u> sp. and fir spread their roots intensitively in the humus horizon so as to absorb nutrients which become available in the process of mineralization. This also indicates the intensity of root competition for nutrients. Nutrients unavailed by the roots of plants but in free state get leached into the deeper horizons. This indicates extreme stress situation in podsol. Brown-earth, on the contrary, has large reserves of mineral nutrients. On account of erosion, leaching and utilization by plants, the upper horizon of brown-earth is poorer when compared to the deeper horizons. DUVIGNEAUD and DENAEYER- DE SMET (1971) reported that on Ca-rich soil, cycling of Ca is increased because of luxurious consumption by beech while cycling of K is reduced.

These differences in base saturation of the soils investigated reflect upon the composition of vegetation. Beech grows well on brown-earth and is rarely found on podsol. On the other hand, fir grows well on podsol in the Guberwald. This indicates the ability of fir to withstand nutrient stress conditions in poor soils particularly in the early age since in the later age fir roots reach the deeper horizons of podsol and also draw mineral nutrients from there. Beech, on the contrary, is adversely affected by the nutrient stress conditions on podsol. This results in its slow growth on podsol in the Guberwald.

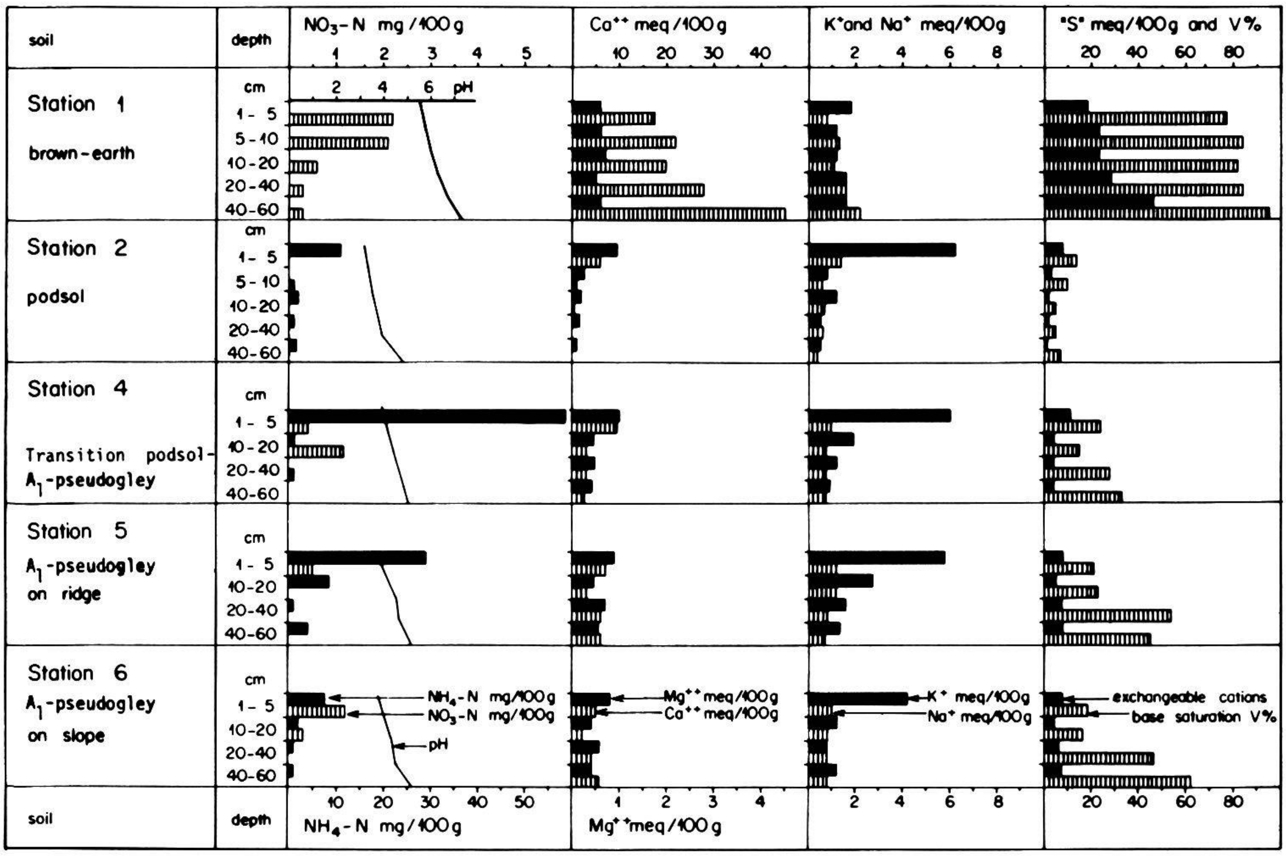


Fig. 14, Chemical characteristics of the different horizons of the soils in the Guberwald. Date of sample collection 3.7.1972.

4.5 Autecological studies

4.5.1 Germination experiments:

Only a few beech seedlings are observed on podsol while plenty of them on brown-earth. The question arises: what factors cause the failure of beech seedlings on podsol? A survey of literature (WATT 1923, SCHMITT 1936, POLACSEK 1954, MAYER-WEGELIN 1949, VIEGHOFFER 1952, BORCHERS 1961 Cf. BURSCHEL et al. 1964, Augustin 1952 Cf. BURSCHEL et al. 1964, MLINSEK 1967)

shows a series of responsible causes, the main cause amoung them being drought which kills seedlings on raw humus. Raw humus-beech forests are common in Europe, hence lack of beech regeneration on thick humus accumulation is of common occurrance. In the present experiments, efforts are made to investigate the causes of beech failure on podsol. Experiments are carried out in the field as well as in the greenhouse.

4.5.1.1 Germination experiments in the field:

Like their seedlings, beech trees are rare on podsol while numerous on brown-earth. Therefore, the amount of beech nut fall on podsol is negligible as compared to that on brown-earth. Beech nuts being heavy and without dissemination mechanism fall below the parent trees or are only slightly carried away by wind and animals. Therefore, it is expected that a small quantity of beech nuts is available on podsol for germination as compared to that on brown-earth. In an experiment in January 1973, an equal number of beech nuts (100) was put on the surface of plots on podsol and brown-earth to assess the effect of soils on germination. Nuts were spread on the surfaces of the plots to provide natural conditions. The observation of the nuts in May 1973 revealed that most of the beech nuts were eaten away by birds and rodents (Table 8). Only 5% of the nuts germinated on brown-earth while only 1% on the undisturbed humus layer of podsol. This shows the effect of birds and rodents, particularly when a small quantity of nuts is available for germination. In poor mast years, the loss of beech nuts caused by birds and rodents even on brown-earth is very significant. In the years of full mast, even after the loss caused by birds and rodents, enough beech nuts are left behind for germination on brown-earth. In all the years, only a small quantity of beech nuts is available for regeneration on podsol. Therefore, the loss caused by these animals in all the years is nearly 100%, thereby affecting the natural beech regeneration on podsol. On the other hand, there are factors which afford protection to beech nuts on brown-earth:

On the brown-earth, earthworms being very abundant, some of the beech nuts get burried in the soil as a result of worm activities. A high rainfall also helps in mixing the beech nuts in the soil and soil frosts may bring the nuts in the soil. Surface runoff coming down the slope brings the beech nuts into the soil depressions and covers them with soil. Autumn leaf fall covers the nuts thereby protecting them from birds. On account of these factors on brown-earth many nuts remain hidden in the soil. These hidden nuts are not only provided with protection but also with good soil contact for imbibition with water. Also the evaporation of water is prevented from the beech nuts since they remain covered with soil. Thus these factors play an important role in protecting the nuts and in providing proper conditions for germination. However these factors do not operate on podsol. The surface layer of podsol is composed of litter from fir and spruce and mosses. Therefore, rainfall and frost have no influence in bringing nuts into the soil or fine humus. Fir trees shed the leaves throughout the year, hence do not afford any protection to the beech nuts against the birds. On account of absence of the above factors, not only beech nuts are not provided with protection but also with proper germination conditions. The factors responsible for fir seed germination on podsol are quite different. A large quantity of fir seeds falls on podsol where losses of seeds caused by birds and rodents does not seem to be great. Therefore, a large quantity of fir seeds is available on podsol for germination.

After assessing the effect of birds and rodents on beech nuts, measures were taken to protect the nuts from these animals. Therefore, wire mesh cages were installed. The results of this experiment showed that on brown-earth, germination was only 8% while on podsol only 5%. Nuts sown under the soil showed a still smaller percentage of germination. This may be on account of the damage caused by fungi. MUELLER (1958, Cf. BURSCHEL et al. 1964) states that under high temperature and humidity, damage caused by fungi to beech nuts is very high.

4.5.1.2 Germination experiments in the greenhouse:

Experiment 1: In the first phase of germination studies, beech nuts were spread on soils in pots as mentioned in table 10 after testing their viability. They were watered daily for two months. There was no germination of beech nuts except on mixed raw humus. Beech nuts were removed and tested for viability by casual observation and by slightly pressing. Infected nuts became blackish white, therefore, infection could be observed directly. Afterwards, nuts were put in water and kept for 24 hours. The nuts settled at the bottom were taken as viable and the ones floating as nonviable. The following table shows the number of nuts rendered nonviable after putting them on the soil.

Soil type	% of nuts rendered nonviable
A_1-pseudogley	35
Undisturbed humus from podsol	33
In competition with Vaccinium myrtillus	31
Sand control	29
Brown-earth	18

This shows that on podsol and A_1-pseudogley there was a average 30% loss of beech nuts within a period of two months. Loss of beech nuts on brown-earth is smaller than on the above soils.

Experiment 2: The viable nuts from experiment 1 were inserted into the soils and watered daily. The germination percentage is expressed in table 10 .

Experiment 3: Again in December 1973 seeds of fir and beech were sown in pots and watered daily. Results were noted in March 1974 and are expressed in table 11.

Fir seeds germinate on the surfaces of the soils while beech nuts do not. Beech nuts germinate on the surface of mixed humus. When inserted into the soils,both beech and fir seeds germinate.

Discussion of germination experiments:

The results of all the germination experiments in the greenhouse show that beech nuts do not germinate on the surface of brown-earth. In the field, however beech nuts do germinate on the surface of brown-earth. The question arises: why do beech nuts not germinate on the surface of the brown-earth in the greenhouse? The answer to this intriguing question could give an information as to why beech nuts do not germinate on podsol. In section 4.5.1.1 it has already been mentioned that natural factors operating on brown-earth in the field, bring the nuts in contact with the soil thereby providing good germination conditions. This is not the case if beech nuts are put on the surface of brown-earth in the greenhouse. The contact with soil is so poor that even on moist soil, nuts do not germinate. Experiments carried out by WATT (1923) clearly illustrate this fact. According to him, direct access of liquid water is essential for beech nuts refuse to germinate in a saturated atmosphere even when freshly collected and before any appreciable amount of water has been lost by evaporation. Further he mentions " Neither the nuts suspended over water nor those exposed on a soil surface are supplied with requisite condition but partial immertion of the former and burrial of latter induce germination." DAUBENMIRE (1959), in this regard, states that seeds of some species which become dehydrated while dormant may not germinate readily unless soil moisture exceeds the field capacity for a time. This is due to the fact that seeds can exhaust growth water only from the points where they make cantact with soil particles and since physical contact between nuts and soil is so poor that they may not thus obtain sufficient moisture from these points to exude their radicles. DAUBENMIRE's view seems to be true in the case of beech nuts on account of the following factors:

1: Structure of beech nuts: Beech nuts are tetrahedral in shape with thick seed coat which seems to be much less permeable to water than that of fir seeds. The micropilar end of beech nuts has a fibrous lining which extends into the nut cavity, along with a ridge of tetrahedral seed. Effective water imbibition for germination of nut, seems to be carried out by this special structure. Therefore, proper contact of beech nuts with soil is a prerequisite for germination.

2: Since beech nuts are tetrahedral, one fourth of their surface comes into contact with soil while three fourth lose water by evaporation.

This shows how critical the contact between nut and soil is for germination.

Compared to the surface of brown-earth in the greenhouse, the surface of podsol is much less moist. It consists of the litter of fir and Vaccinium. Whatever water comes to this litter layer through rainfall, flows through (permeability coefficient for water saturation according to RICHARD 1971 is 2288 cm/day). Contact between beech nuts and litter layer is so poor that nuts can not imbibe enough water for germination. Therefore, beech nuts are found to germinate on podsol very rarely.

Beech nuts put on the surface of the humus mixed by hand do germinate. This is because the showers of water bring the beech nuts in good contact with fine humus which retains water. Therefore, beech nuts imbibe enough water to make germination effective. A similar situation is observed in the field where beech nuts when come to lie on a fine mass of humus, germinate. The course of soil water tension in the humus layers during the growth period shows that water remains in the range of availability (see section 4.3.).

The situation with fir seems to be different than that with beech. Fir seeds germinate on the surfaces of the soils in the greenhouse. The question arises: Why do fir seeds germinate on the surface of the brown-earth which is moist and also on the surface of podsol which is comparatively dry? The answer to this question seems to lie in the ability of fir seeds to imbibe water quickly and effectively. In the greenhouse when watered daily fir seeds germinate on sand and also on the surface of podsol. Compared to beech nuts, fir seeds have the following advantages:

1: Fir seeds have a fine seed coat which can imbibe water quickly and effectively.

2: The seeds are bilaterally symetrical and hence one half of their surface comes in contact with soil.

Beech nuts also do not germinate on moss polsters and in Vaccinium herds also due to lack of proper moisture conditions. BURSCHEL et al. (1964) stated that when a humus layer is stripped off before the nuts fall, the nuts germinate. This is on account of an exposed mass of fine humus with which nuts mix under the influence of rainfall. BURSCHEL et al. thought that it was on account of exposed mineral soil which provides room for establishment. Author thinks that this is primarily important in providing favourable germination conditions. The role of water conditions in the germination substrate is clarified by the following fact:

As water conditions in the germination bed of beech improve, the germination percentage of the beech nuts increases accordingly (Fig. 16). On the sand and undisturbed humus, beech does not germinate. When inserted in the humus layer 13%, in mixed humus 15%, in sand 17% and in brown-earth 20% germinate. Water conditions improve from the undisturbed humus ⟶ mixed humus ⟶ in sand to brown-earth. From the comparison of beech nut and fir seed germination, it becomes clear that favourable water conditions in the germination bed are greatly important for beech nuts than for fir seeds. Therefore, a high percentage of fir seed germination is found even on the undisturbed humus layer of podsol in the field.

Though primarily, water and lack of good contact are the controlling factors for beech nut germination, pH of the soil also seems to play a small role. Fig. 15 shows the relation between nut and seed germination and pH of the germination medium. On a medium having pH 3, germination percentage of beech nuts is only 9% while that of fir is 12%. As pH increases germination percentage also increases. But the effect of low pH is greater on beech nut germination than on fir seeds. The effect of low pH is due to the damage caused by fungi to nuts and seeds. On a medium with low pH, nuts and seeds are found to be more infected by fungi than those on a medium with higher pH. The longer the resting period of the nuts on a low pH medium, the greater is the loss caused by fungi to the nuts. Because of lack of proper moisture conditions on the undisturbed humus layer of podsol, beech nuts rest for a longer period and therefore, loss of beech nuts is nearly complete. Fir seeds on the contrary, do not rest on humus layer of podsol for a long period. As soon as snow starts melting, the seeds start germinating. Therefore, in this regard too, fir seeds have an advantage on beech nuts.

Thus the sequence of events that affects beech nut germination on podsol can be described as follows:

1: There is invariably a small quantity of beech nuts on podsol as there are no beech trees.

2: The loss caused by birds and rodents to beech nuts is nearly 100% since the factors (mentioned on pp 52) protecting the beech nuts on brown-earth do not operate on podsol.

3: The structure of beech nuts demands better contact with soil for effective germination. Undisturbed humus layer of podsol, where beech nuts come to lie neither provide enough water nor good contact.

4: In the absence of proper germination conditions, beech nuts rest for a long time on the surface of humus layer where they are infected by fungi and are rendered nonviable.

Table 7 . Comparison of the seeds of beech and fir.

Beech (Fagus silvatica)	Fir (Abies alba)
- 16.2% average yearly seed production (SCHWAPPACH 1895, Cf. DENGLER 1930)	34.4% average yearly seed production (SCHWAPPACH 1895, Cf. DENGLER 1930)
- Seeds heavy	Seeds light
- Seeds without dispersal mechanism	Seeds with wings for dispersal
- Seeds covered with thick tetrahedral seed coat	Seeds covered with thin seed coat
- Seeds tetrahedral with broad base and pointed micropilar end.	Seeds nearly flat
- A fibrous thread enters into the seed coat chamber from micropilar opening with fibrous lining which absorbs water from the soil.	Such a special structural arrangement is absent in fir seeds.
- Seed coat contain resin glands	Seed coat with resin glands
- Seeds fall below the tree or are carried away by the animals to some distance	Seeds fly large distances
- Seeds are preferred for eating by animals	Seeds with strong arromatic smell are not preferred by animals for eating

Table 8 , Results of beech nut germination experiment in the field. Replications six (only four on brown-earth)

Plot	pH	Number of nuts/plot	Number of nuts germinated %	Number of nuts eaten by animals %
On brown-earth				
on the surface	5.5	100	5	95
On podsol				
on undisturbed humus	3.5	100	1	99
on moss polsters	3.5	100	0	100
in competition with	3.5	100	0	100
Vaccinium myrtillus	3.5	100	0	100
on 4cm thick humus	3.5	100	0	100
on A_1 horizon	4.0	100	0	100

Table 9 , Results of beech nut germination in the field. Wire mesh cages were installed to protect the nuts from birds and rodents. Replications two.

Plot	pH	Number of nuts/plot	Number of nuts germinated %	Number of nuts not germinated %
Brown-earth- on surface	5.5	100	8	92
under soil	5.5	100	1	99
Podsol- on humus surface	3.5	100	5	95
under humus	3.5	100	4	96
on A_1 horizon	4.0	100	2	98

Table 10, Results of beech nut germination experiments in pots with 30 nuts in the greenhouse.

Substrate	pH	Number of nuts germinated %	Number of nuts not germinated %	Replications
Control sand	5.0	41	59	3
Sand + humus extract	3.7	21	79	5
Mixed humus	4.0	26	74	3
Undisturbed humus layer	3.5	9	91	8
In competition with *Vaccinium myrtillus*	3.5	5	95	3
Brown-earth	5.5	20	80	3
A_1-pseudogley	4.5	17	83	3

Table 11, Results of beech and fir seed germination experiments in pots with 30 seeds in the greenhouse. Beginning of experiment in December 1973, end March 1974. Replications three.

Substrate	Number of beech nuts germinated %				Number of fir seeds germinated %			
	1	2	3	mean	1	2	3	mean
Podsol- on undisturbed humus	0	0	0	0	9	12	18	13
under undisturbed humus	10	6	5	7	11	13	15	13
on mixed humus	17	14	14	15	16	19	25	20
Brown-earth- under soil	20	18	22	20	15	16	20	17
Sand- with pH 3.0, under sand	5	13	9	9	10	10	16	12
with pH 4.0, under sand	13	12	11	12	18	19	23	20
with pH 4.5, under sand	20	17	17	18	17	19	24	20
with pH 5.0, under sand	18	20	16	18	19	20	21	20
in sand control	4	7	13	8	13	9	14	12
on sand control	0	0	0	0	14	9	14	12

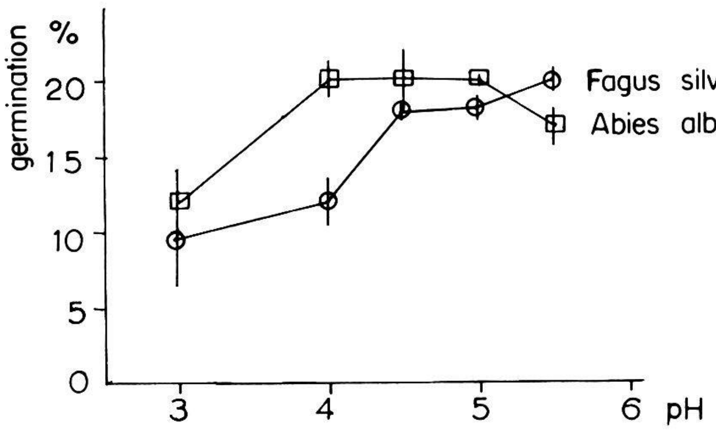


Fig. 15 , Relation between germination percentage of Abies alba and Fagus silvatica and pH of the sand media.

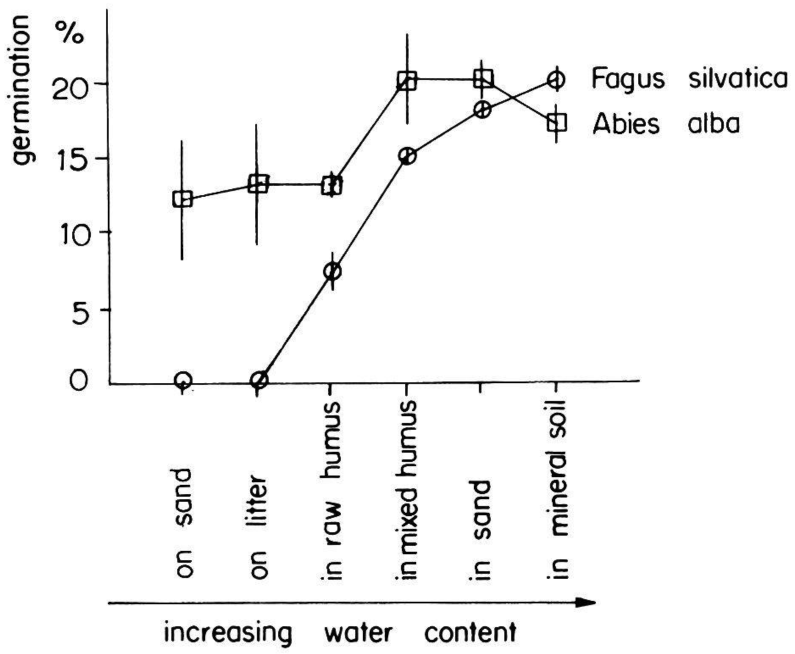


Fig. 16 , Relation between germination percentage of Abies alba and Fagus silvatica and water content of germination media.

4.5.2 Root system and root/shoot ratio

4.5.2.1 Root system:

To remove the intact root systems of beech and fir seedlings and saplings, soil blocks from the field under undisturbed conditions containing the root systems were dug out and washed to clear off the soil. The root systems of these species were studied mainly on brown-earth and podsol. All together 60 seedlings and saplings were investigated.

In brown-earth, the tap root of beech seedling grows profoundly in early age. Secondary roots are fine and short (fig. 17). After an establishment phase of 1-2 years, the tap root sends out longer and stronger lateral secondary roots. At the age of 4-5 years, the root system is well established in the soil. At a latter age, the tap root of beech ceases to function and secondary roots become prominant. The tap root system of fir seedlings in the brown-earth also grows in the same way as that of beech seedlings, but young trees of fir retain the tap root system.

Morphologically, there is a clear relation between humus accumulation and the intensity of root formation. When there is a little humus accumulation, beech forms large secondary root system in the humus layer while the tap root grows deep into the mineral soil. With increasing humus accumulation, the secondary root system enlarges and proportionally the tap root growth is suppressed (fig. 18). In the figure, it is seen distinctly that in the humus a zone of fine roots is formed while the lower portion of the tap root growing in the mineral soil does not have such a profused growth of fine roots. Ultimately, there comes a stage when humus accumulation becomes so thick that just secondary roots constitute the beech root system concentrating only in the humus layer and not reaching the mineral soil. Fir seedlings also form an elaborate secondary root system in the humus layer of podsol but the tap root system extends also into the deeper horizons of podsol. In the humus zone, Vaccinium myrtillus also forms an elaborate root system making the humus layer very compact.

When the root systems of beech and fir are compared, it appears that both have a similar root system on brown-earth. In the humus layer of podsol both form an elaborate secondary root system with long and short roots. Short roots are supposed to be infected by mycorrhiza (HARLEY 1949). From morphological examination of the roots, it seems that in both species, there is a greater amount of mycorrhizal infection on podsol than on brown-earth. A significant difference in the root systems of beech and fir is that the tap root of fir extends into the deeper horizons of podsol while that of beech does not. This different tendency of development of these species on podsol and brown-earth shows that beech root development is adversely affected by some soil factors such as the sequence of organic matter horizons and mineral horizons respectively while that of fir is not. In this regard, KOESTLER et al. (1968) state that fir has a characteristic tap root system which is genetically fixed and is independant of habitat conditions. WIEDMANN (1950,Cf. KOESTLER et al. 1968) also states that fir is very active in building a deep root system particularly under different site conditions. The present investigations are in support of this view. Beech on the contrary, has a heart root system ("Herzwurzelsystem") and changes according to the habitat conditions (KOESTLER et al. 1968).

The intensive development of the root system in the humus layer of podsol is on account of the distribution of nutrients depending on depth. Due to the accumulation of nutrients in the humus layer, plants form intensive root system so as to absorb as much nutrients as possible. Also KOESTLER et al.(1968) state that for ensuring the requirements of water and nutrients on the poor habitats such as podsol, there is a necessity to develop a root system occupying a large area of the soil. BURGER (1930), HARLEY (1949) and MEYER (1961) also reported intensive development of root system on podsol. On brown-earth, plants do not form an intensive root system because nutrients are easily available. An other reason for the development of an intensive root system may be a deficiency of calcium in the soil which has been supposed to induce this mode of growth in the case of fir and beech KRAUSS (1934, Cf. KOESTLER et al 1968). Podsol usually has a small amount of calcium as compared to calcareous brown-earth. WILDE (1962) states that for the development of the root system and particularly for root hairs, calcium plays a great role. Therefore, it seems that the amount of calcium in the soils, to some extent determenes the mode of beech root system. On the other hand, GROSSKOPF (1950) and LAATSCH (1963, Cf. KOESTLER 1968) attribute an intensive development of root system on podsol to nitrogen nutrition. It is supposed that because of the high infection by mycorrhiza, roots receive a greater amount of N-nutrition which results in their enlargement. In this connection it is important to recall that mycorrhizal infection in the humus layer is greater (HARLEY 1949, HARTMANN 1952 Cf. KOESTLER 1968). The author thinks that it is due to combined effect of nutrient deficiency, greater mycorrhizal infection and good aeration.

The tap root of beech in the humus ceases to function in the early years of its development. This seems to be on account of various factors. LAATSCH (1957, Cf. KOESTLER et al. 1968) states that root damage is caused by the poisonous reaction of free alluminium or manganese in acidic soils. Also KOESTLER et al. (1968) mention that alluminium damages the roots. Due to the formation of insoluble alluminium phosphate, there may be a deficiency of manganese or calcium or of both. Furthermore, there may be a lack of phosphate. In the present investigations on podsol, it was observed that in addition to low nutrient content, also ionic complexes are not balanced due to a small Ca/Mg ratio. According to BARSHAD (1960) small Ca/Mg ratio indicates an imbalance in acidic soils. Therefore, multiple factors seem to be responsible for suppressing the activity of tap root of beech seedlings.

Though fir and beech are supposed to have a high nutrient requirements, fir grows well on podsol while beech poorly. This is presumably on account of the specific advantage of fir on these sites in having a long tap root system. Thus fir seedlings receive nutrients from the humus horizons as well as from deeper horizons and therefore, establish well. Furthermore, fir does not meet strong root competition in the humus horizon since it has the advantage of having an alternative source of nutrients. On the other hand, beech receives nutrients only from the humus horizons and therefore, remains weaker, all the more as beech roots meet intense root competition mainly from Vaccinium myrtillus because of its complete dependance on the humus layer.

4.5.2.2 Root/shoot ratio:

Root/shoot ratio in the field as well as in the greenhouse is greater for seedlings growing on podsol than for those on brown-earth which may be attributed to intensive development of root system in the humus layer of podsol. Large amount of carbohydrates and nutrients is used to build up this intensive root system. Therefore, a smaller amount of carbohydrate and nutrients is available for the development of shoots. Experiments carried out by MEYER (1961) show that beech seedlings growing on podsol develop small xerophytic leaves, which probably have a relatively small photosynthesis rate. EIDMANN (1943) states that root respiration of beech is nearly two times higher than that of fir under similar conditions, indicating that beech has to invest more energy for absorption of nutrients than fir. This may be particularly true for the sites such as podsol. Thus energy utilized by beech roots is higher than that used by fir roots. This reveals the adverse effect of this intensive root development on shoot development of beech. BURGER (1930), HARLEY (1949) and MEYER (1961) also reported a greater root/shoot ratio on poor soils. Therefore, a greater root/shoot ratio is indicative of nutrient deficiency and its adverse effect on the growth of shoots.

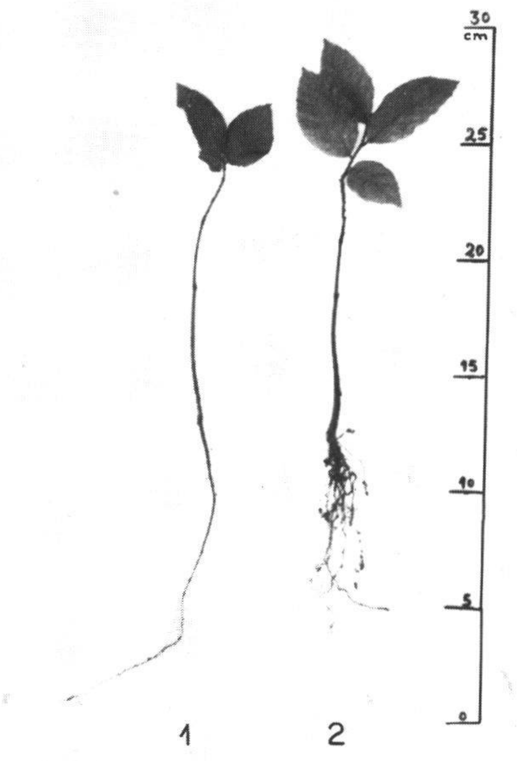


Fig. 17, Root system of young Fagus silvatica seedlings in brown-earth (1) and podsol (2) under field conditions.

Fig. 18, Root system of seedlings of Fagus silvatica in brown-earth (1), in podsol (2=little humus accumulation, 3=5cm humus accumulation, 4, 5 and 6=2ocm humus accumulation)under field conditions.

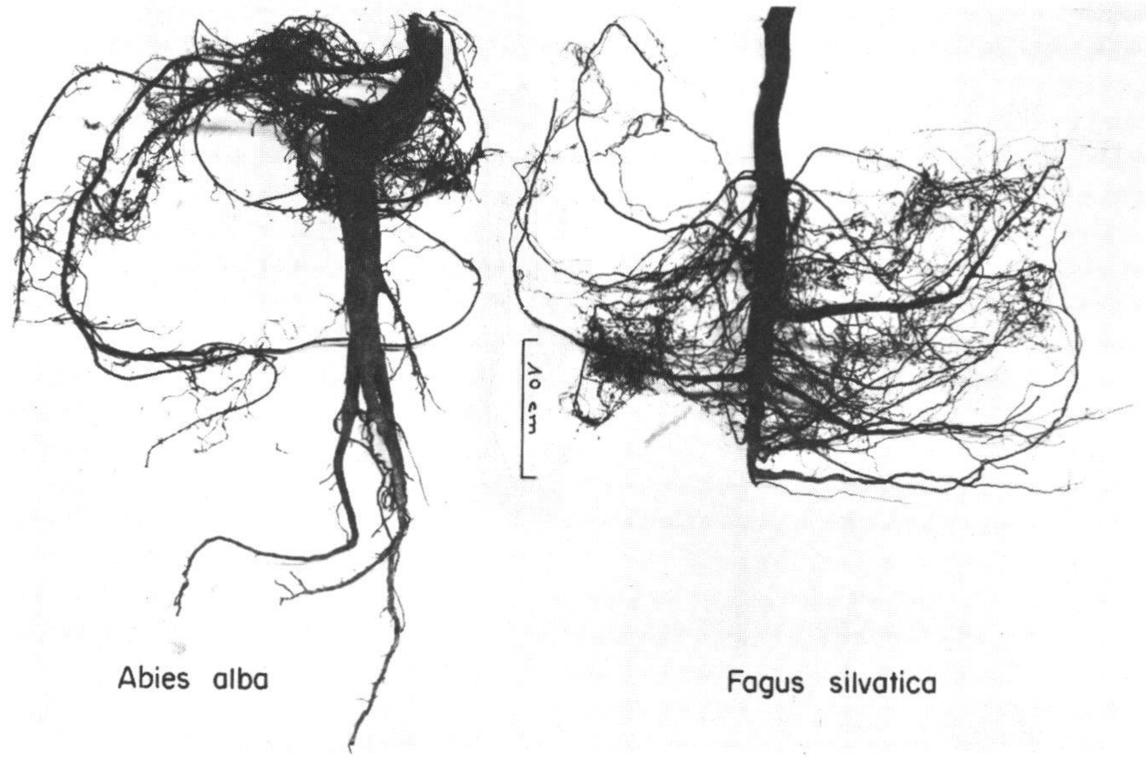


Fig. 18a, Root systems of Abies alba and Fagus silvatica.

4.6 Increment studies of saplings

The early stages of the establishment of beech and fir were investigated by studying the relation between mean annual increment and site conditions. Five saplings of each fir and beech were selected in the field under uniform habitat conditions of every site in respect to humus accumulation, pH of the top soil, and canopy cover. Small parts of the basal stems of saplings were brought to the laboratory. Sections were cut with the sledge microtome for determining the ages of saplings. Care was taken not to take into account the drougth and frost rings. Mean annual height and diameter increment were obtained by dividing height and diameter of sapling by its age.

Saplings:

Fig. 19 shows that as raw humus accumulation increases, the annual height increment decreases. The effect of increasing humus accumulation seems to be very adverse on the growth of beech saplings while not so adverse on fir growth. Beech seedlings probably grow vigourously on weakly acidic brown-earth on gentle slopes under moderate shade conditions. Fir seedlings also seem to grow vigourously on this soil but the rate of growth as noticed in limited sampling of fir saplings (16cm mean annual height increment) is only half of that of beech saplings (32cm mean annual height increment). Vigour of both beech and fir saplings is reduced on the brown-earth on steep slopes. Planted beech saplings grow well on pseudogley- podsol-transition (plateau) where natural beech seedlings and saplings are absent. Here natural fir seedlings grow less vigourously than planted beech saplings. On podsol mean annual height increment of fir (9 cm $\pm$ 0,3) is greater than of beech saplings (7cm $\pm$ 0,2).

Fig. 20 shows that as canopy cover increases, the mean annual height increment decreases. The effect of increasing shade on the growth of beech is more pronounced than that on the growth of fir saplings.

Fig.21 indicates that as the base saturation of soils increase, the mean annual height increment also increases. With fir saplings this relation is less pronounced.

Beech:

The growth of beech saplings seems to be reduced particularly on podsol while on nutrient-rich brown-earth it is enhanced. This shows a negative trend between the growth of beech seedlings and humus accumulation (refer to table 12). In this regard, MEYER's (1961) experiments shows that the slow growth of beech seedlings on podsol humus is on account of nutrient deficiency and therefore, when treated with fertilizer they grow vigourously. There seems to be a high variability in the growth of beech saplings on different soils. A similar observation has been made by KLAUSING (1956) who reports that 115 year old beech trees in Mercurialis forest on dioritic parent material attain 39 m height and produce 13,3 m^3 wood per hectare while on granite 125 year old trees attain only 29 m height and produce 7,5 m^3 wood per hectare. HARLEY (1949) states that the vigour of growth of beech seedlings in neutral to alkaline calcareous soil is greater than on non-calcareous soils. LINDQUIST (1932) and ELLENBERG (1963) express similar views. Therefore, it seems that for the optimal growth of beech, nutrient-rich soil is a prerequisite, particularly in the upper montane zone where competitive ability of beech is reduced by climatic factors.

Fir:

Though the growth of fir also seems to be reduced on poor soils, compared to beech, it relatively grows well. The variability in the growth of fir on different soils is not so high as that of beech. This indicates that fir tolerates a wide range of habitat conditions in this region. The reason for this lies in its capacity to root deeply. Due to this reason fir seems to dominate over beech already in very early age on podsol type sites.

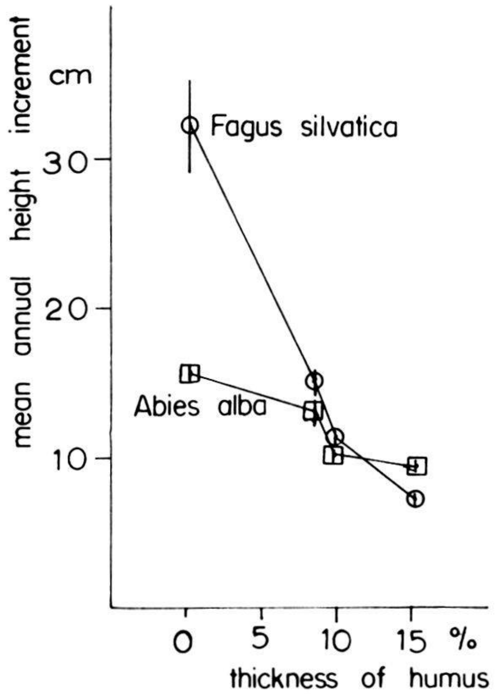
Though fir and beech show some trend, it needs to be clarified with further investigations based on ample data.

Table 12, Annual increment of __Fagus silvatica__ saplings under ecologically comparable conditions in the Guberwald. Measurements were made in September 1973.

Habitat	Indivudals	Sapling Height m	Sapling diameter cm	Sapling age years	mean diameter mm	annual increment aver.	mean height cm	annual increment aver.
__Podsol__	1	2,0	3,5	28	1,2		7	
Humus 15 cm	2	2,5	4,1	30	1,3		8	
pH 3,5	3	1,7	2,3	21	1,2	1,2	8	$7 \pm 0,2$
Canopy cover 20%	4	1,2	1,9	16	1,2		7	
	5	0,8	1,6	13	1,2		6	
__Acidic brown-earth__	1	2,5	2,5	22	1,1		11	
Humus 10 cm	2	3,0	2,8	25	1,1		12	
pH 3,5	3	2,3	2,5	21	1,2	1,2	11	$11 \pm 0,2$
Canopy cover 85%	4	1,9	2,2	20	1,1		9	
	5	1,7	2,1	15	1,4		11	
__Acidic brown-earth__	1	3,4	2,6	22	1,2		15	
Humus 7 cm	2	2,7	3,0	20	1,5		14	
pH 4,0	3	3,0	2,5	17	1,4	1,3	18	$15 \pm 1,4$
Canopy cover 60%	4	2,3	1,9	13	1,4		18	
	5	1,5	1,4	12	1,1		12	
__A_1-pseudogley__	1	3,0	1,7	20	0,8		15	
Humus 0 cm	2	2,5	1,7	18	0,9		14	
pH 5,0	3	3,4	2,0	21	1,0	1,1	16	$14 \pm 0,5$
Canopy cover 60%	4	1,8	1,9	13	1,4		13	
	5	1,2	1,3	10	1,3		12	
__Pseudogley-podsol__	1	6,0	4,0	25	1,6		24	
Planted beech	2	4,6	2,8	18	1,5		25	
saplings	3	3,9	2,3	15	1,5	1,4	26	$22 \pm 2,7$
Humus 10 cm	4	2,5	1,9	12	1,6		21	
pH 4,0	5	2,4	1,5	14	1,o		17	
Canopy cover 30%								
__Brown-earth on__	1	5,0	3,3	18	1,8		27	
__steep slope__	2	3,2	2,9	14	2,0		23	
Humus 0 cm	3	4,4	2,8	17	1,6	1,8	26	$23 \pm 2,5$
pH 5,5	4	2,4	2,6	12	2,1		20	
Canopy cover 60%	5	2,1	1,8	11	1,6		19	
__Brown-earth on__	1	5,2	4,7	16	2,9		32	
__gentle slope__	2	5,0	4,4	12	3,6		41	
Humus 0 cm	3	4,3	3,9	15	2,6	2,8	29	32 ± 6
pH 5,5	4	3,9	3,8	13	2,9		30	
Canopy cover 20%	5	4,1	3,5	15	2,3		27	

Table 13, Annual increment of Abies alba saplings under ecologically comparable conditions in the Guberwald. Measurements were made in September 1973.

Habitat	Individuals	Sapling height m	Saplings diameter cm	Sapling age years	mean diameter mm	annual increment aver.	mean height cm	annual increment aver.
Podsol	1	2,3	2,4	25	1,o		9	
Humus 15 cm	2	3,1	2,8	28	1,0		11	
pH 3,5	3	2,0	2,1	19	1,1	1,0	10	9±0,3
Canopy cover 20%	4	1,5	1,9	16	1,2		9	
	5	1,2	1,6	15	1,0		8	
Acidic brown-earth	1	3,5	3,4	32	1,1		11	
Humus 10 cm	2	3,4	3,5	33	1,0		10	
pH 3,5	3	2,8	2,6	23	1,1	1,1	12	10±0,5
Canopy cover 85%	4	1,6	2,3	19	1,2		9	
	5	1,5	2,2	18	1,2		8	
Acidic brown-earth	1	1,6	2,3	17	1,4		9	
Humus 7 cm	2	3,7	2,0	22	0,9		16	
pH 4,0	3	3,0	1,9	20	0,9	1,1	15	13±1,7
Canopy cover 60%	4	1,8	2,0	16	1,2		11	
	5	2,5	2,5	19	1,3		13	
A_1 pseudogley	1	2,3	2,8	18	1,6		13	
Humus 0 cm	2	2,5	3,0	20	1,5		13	
pH 6,0	3	3,2	3,5	26	1,4	1,4	12	13±0,05
Canopy cover 60%	4	1,7	1,6	13	1,2		13	
	5	3,0	3,1	23	1,4		13	
Pseudogley-podsol	1	3,0	3,5	31	1,1		10	
Humus 10 cm	2	2,3	2,4	21	1,1		11	
pH 4,0	3	1,2	1,7	14	1,2	1,0	9	10±0,3
Canopy cover 30%	4	1,6	1,2	13	0,9		12	
	5	2,7	2,3	26	0,9		10	
Brown-earth on	1	3,5	4,8	39	1,2		9	
steep slope	2	3,3	4,1	29	1,4		11	
Humus 0 cm	3	2,6	2,3	18	1,0	1,1	12	10±0,5
pH 5,5	4	1,3	1,2	12	1,o		10	
Canopy cover 60%	5	1,1	1,6	13	1,2		8	
Brown-earth on	1	4,0	4,6	23	2,0		17	
gentle slope	2	3,7	4,1	25	1,6		15	
Humus 0 cm	3	3,4	4,2	21	2,0		16	
pH 5,5	4	3,0	3,7	19	1,9	1,6	15	16±0,2
Canopy cover 20%	5	2,8	3,3	17	1,9		16	



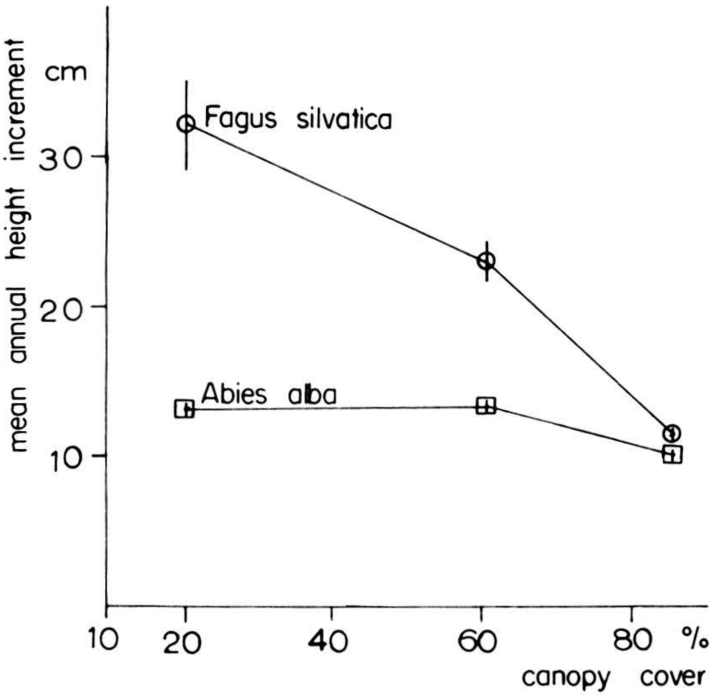


Fig. 19 , Relation between mean annual increment of saplings and humus thickness .

Fig. 20 , Relation between mean annual height increment of saplings and canop cover.

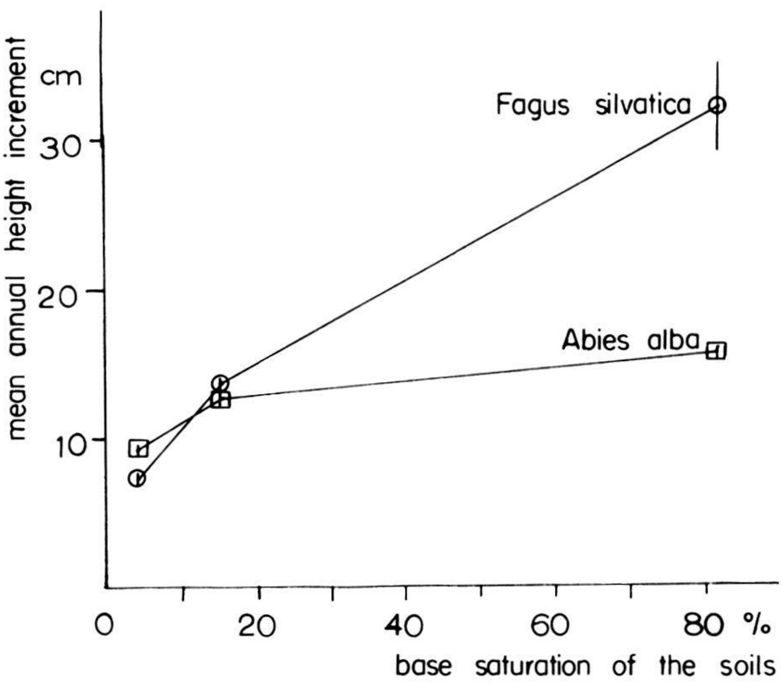


Fig. 21 , Relation between mean annual height increment of saplings and base saturation in the soil.

4.7 Natural regeneration

The problem of natural beech regeneration has been studied by many workers in various parts of the beech area and its failure has been attributed to various causes. Hence a detailed survey of natural regeneration on various soil types was undertaken. Seedlings and saplings of beech, fir and spruce were counted at 60 places on plots of 4 m^2. For each place elevation, aspect, slope, soil type, pH, humus accumulation, canopy cover, ground cover, moss cover, dominant tree percentage and dominant herbs and shrubs were noted.

Elevation:

The investigation area lies between 800 and 1000 m a.s.l. In the Guberwald even at the elevation of 1100 m a large number of seedlings and saplings was observed. Therefore, the elevation gradient in the Guberwald does not play a role in controlling natural regeneration of beech.

Aspect:

Beech and fir regeneration occurs on all aspects of slope and thus it does not play any role.

Slope degree:

A survey of the area shows that beech regeneration occurs mainly on steep slopes. On the plateau and on the gentle slopes, it is observed only occasionally. This seems to be first of all on account of herbaceous vegetation cover, humus accumulation and management practices such as felling timber, weeding of herbs. On the plateau soil, the main cause probably is the formation of a mattress of acidophytic mosses. But on gentle slopes beech regeneration occurs where above management practices are not practiced and soil is base-rich without humus accumulation.

Soil type:

The type of a soil has a great influence on mixed regeneration of the three tree species. Beech regeneration occurs profusely on brown-earth with pH between 5 and 7. On podsol beech regenerates sparsely. Spruce regenerates well on podsol as well as on brown-earth. The highestnumber of fir seedlings in the Guberwald are found on podsol. On pseudogley-podsol and A_1-pseudogley beech occurs rarely but fir profusely. Many specific qualities of these soils are able to influence the regeneration as follows:

Humus accumulation: Fig. 23 shows that as the raw humus increases, beech regeneration decreases. A survey of seedlings under the old beech tree on podsol shwos that in spite of heavy seed fall, there are only a few seedlings. This confirms that humus prevents beech regeneration while allow fir regeneration.

Similar observations have been made by numerous workers (among the WATT 1923, SCHMITT 1956, MAYER 1963 and BURSCHEL et al. 1964). Germination experiments (chapter 4.5.1) show that beech nuts resting on fir needles do not germinate since nuts can not imbibe enough water for germination. Ultimately the nuts are rendered nonviable by the fungus attack. WATT (1923), SCHMITT (1936), HARLEY (1949) and BURSCHEL et al. (1964) state that death of beech seedlings is caused by drought in summer. This is not the case in Guberwald since water remains always in the range of availability even in the humus layer. KUHN (1973) has calculated the frequency of occurence of drought periods of various durations from 55 years of meteorological data. According to him, on Mt. Rigi a 10 days drought period can occur only once in a year and a 28 days drought can occur once in 200 years. Though Guberwald lies at 900 - 1000 m a.s.l., rainfall and temperature are comparable to that of Rigi (1760 m). Therefore, the above observation remains valid for Guberwald. Periodical high precipitation limits the occurence and length of drought in this area. Therefore, drought is not the limiting facotr.

Percentage of beech trees in the stand: Fig. 22 shows the relation between beech regeneration and percentage of beech trees in the stand. Obviously, with a smaller percentage of beech trees in the stand the number of beech seedlings is smaller. With 40% of beech trees in the stand, beech seedlings occur in their largest numbers but above 40%, the number of beech seedlings decreases.

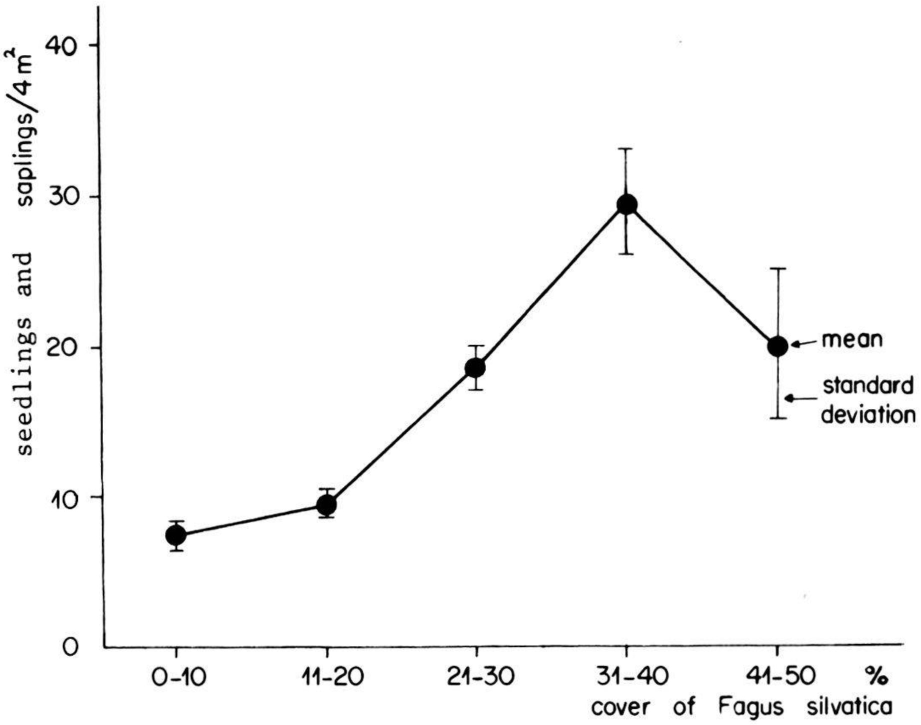


Fig. 22 , Relation between mean number of seedlings and saplings and of Fagus silvatica trees in stand.

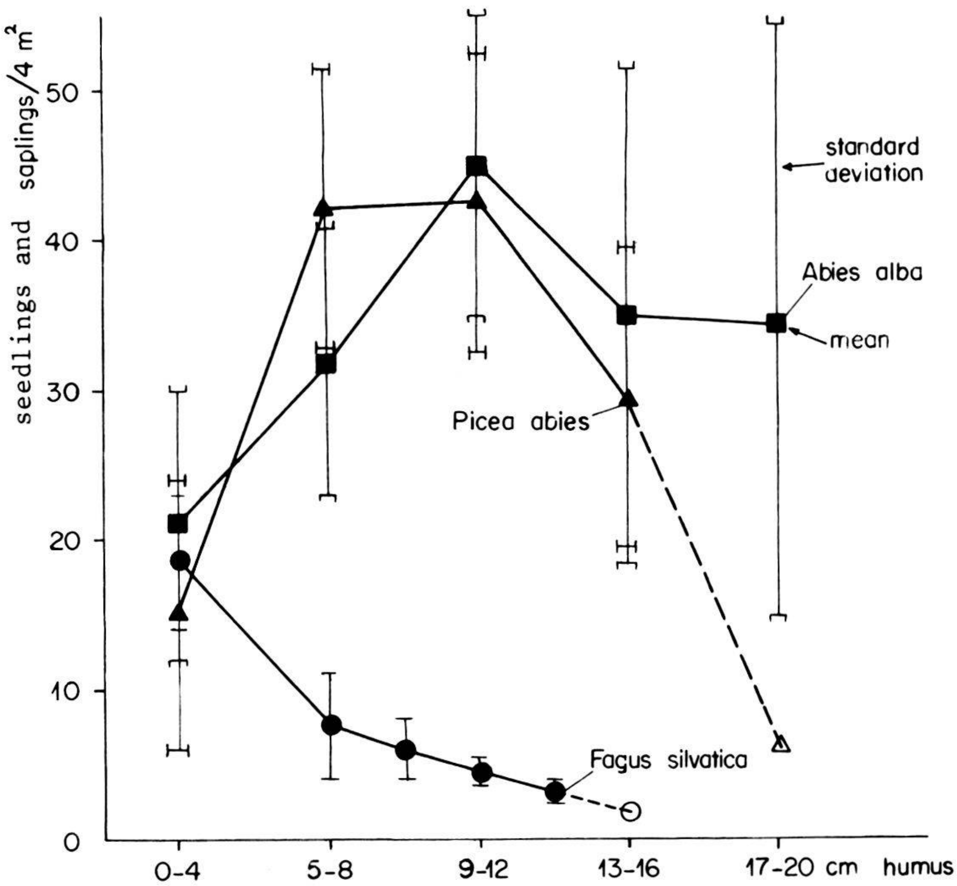


Fig. 23 , Relation between mean number of seedlings and saplings and thickness of humus.

On podsol, beech trees are rare and hence there is no beech regeneration, on account of the unability of beech nuts to be transported to large distances. Fir and spruce, on the contrary disperse their seeds to large areas. Hence they regenerate even in the absence of fir and spruce trees in the stand.

Canopy cover: Under dense stands, beech seedlings are rarely found. They tolerate shade up to 70 % cover. Above that the number of beech seedlings decrease. Fir seedlings are found even under 80 - 90 % cover. ELLENBERG (1963) states that fir is more tolerant of shade than beech.

Ground cover: Beech does not seem to tolerate dense ground cover while fir can stand it best. Maximum regeneration of both species occurs with 30 - 50 % ground cover but with increasing cover beech regeneration decreases drastically and fir regeneration gradually.

Moss cover: Beech does not regenerate on moss carpets whereas fir and spruce regenerate well. Failure of beech regeneration on moss polsters seems to be because of lack of enough water for germination. As compared to beech nuts, fir and spruce seeds do not require large quantities of water for germination since their seed coat is very thin. Therefore, they germinate even on moss carpets and establish well. MAYER (1963) also reported a large number of fir and spruce on moss carpets.

Composition of the stand: SIMAK (1951) investigated tree species generation change ("Baumarten-Wechsel") in planted forests in Switzerland. In the Guberwald under pure spruce plantation of 4 hectares, only fir regeneration was observed. Spruce and beech regeneration is totally lacking. This could be attributed to the "phenomena" observed by SIMAK. Fir is found to regenerate well under pure fir crowns and in mixed stands. Spruce only regenerates under fir crowns and in mixed stands in the Guberwald.

Plant communities: There seems to be a direct correlation between regeneration and plant community (see vegetation table 1) on account of their indicator value for habitat conditions. Beech regeneration has been observed to be associated with the Abieti-Fagetum where the number of species composing the community is high. A maximum number of beech seedlings is observed in association with Mercurialis perennis, Lamium galeobdolon, Veronica latifolia, Ranunculus lanuginosus, Carex alba and Vicia sepium (Abieti-Fagetum typicum Carex alba-variant). Fir regeneration has been found to be associated with Vaccinium myrtillus, Hieracium murorum, Galium rotundifolium, Carex pilulifera and acidophytic mosses as Polytrichum formosum, Dicranum scoparium, etc. (Bazzanio-Abietetum, Abieti-Fagetum luzuletosum). On the other hand there is a negative correlation between Vaccinium myrtillus and beech regeneration. This correlation of regeneration with certain indicator plants is due to specific soil conditions as discussed above. Thus another feature of importance in this respect is that plants of the herbaceous layer are generally good indicators for the habitat conditions of seedling establishment.

Fungi: During census of young seedlings, a small number of beech seedlings were found to be dead because of root disease. Laboratory culture and determination revealed that the parasitic fungus Cylidrocarpon sp. had caused the death of beech seedlings. But this disease does not seem to be very widespread. Many of the saplings were found dead on acidic brown-earth with humus accumulation. The examination showed that the basal portions of the stems near the soil surface were infected by fungi. Diseased stems were brought to the laboratory. Culture and determination showed the presence of parasitic fungi, Armillaria mellea Vahl. and Melogramma spinifera (Waller.) De Not. This diease was found widespread on seedlings under dense shade.

Birds and rodents: As has been proven by germination experiments in the field, heavy losses by these animals occur particularly on podsol carrying only a small quantity of beech seeds (see chapter 4.5.1). WATT (1923) also reported 100 % loss of beech seeds due to these animals. Therefore, they play an important role in controlling beech regeneration particularly on podsol where beech nuts are not covered by litter or soil.

Deer: During the survey of natural regeneration, many saplings were found with browsing marks. Since the civil law to protect deer came into force, the number of deer has grown steadily. The same time, damage caused by deer has also increased. On podsol most of planted beech saplings are browsed by deer. KLOETZLI (1965) states that beech saplings growing in coniferous forests are most succeptible to deer browsing. Therefore, beech regeneration is adversely affected by deer in such communities. Both Abies and Fagus are palatable and physiologically important since they contain essential microelements. Further KLOETZLI states that fir is the most preferred species by deer in the Swiss Midlands. However, in the Guberwald damage caused by deer to fir saplings is not significant. Therefore, it does not pose a threat to fir regeneration mainly because of abundance of seedlings and saplings of fir. But regeneration of beech is seriously affected by deer on account of the small number of beech seedlings, particularly on podsol. KLOETZLI states that rare plants are preferred by deer.

Competition:

ELLENBERG (1963) classifies V. myrtillus in the group occupying the most acidic forest soils. This reflects on the physiology of V. myrtillus which is adapted to acidic soils (BOGNER 1966, KOPP 1969 and INGESTAD 1974) and is able to utilize water and nutrients from the humus layer of podsol effectively. Therefore, V. myrtillus exerts a strong competitional power on a species like beech which is not so well adapted to acidic soils. Thus beech seedlings growing on podsol encounter a severe root competition from the roots of V. myrtillus and fir. Consequently, the tap root growth of beech is suppressed and can not reach the mineral mull horizon. Therefore, beech seedlings depend exclusively on the secondary lateral roots for nutrient absorption from the humus horizon.

Also in other tree species, the competitional influence of Vaccinium myrtillus is obvious as has been proved by the experiments of LEIBUNDGUT (1964). He demonstrated the effect of root competition of V. myrtillus on the seedlings of pine and larch. According to MEYER (1961), however, this root competition can be overcome by the application of fertilizer. Beech seedlings growing on the humus from podsol, then improved the root/shoot ratio and the seedlings grew vigourously. Thus by adding fertilizers in this particular case, the competition balance is altered in favour of beech.

Germination experiments in the course of present investigations proved that beech seedlings growing in V. myrtillus herds develop a very small root system but their shoots grow vigourously in the first two months. In the third month, the seedlings died. Thus the competition for nutrients between beech seedlings and V. myrtillus, particularly on podsol, seems to determine the fate of beech seedlings.

How fir seedlings can stand root competition from V. myrtillus is not very clear. But it seems that fir is physiologically better adapted to acidic soils than beech. Secondly, it evades competition by rooting in deeper horizons which are not reached by the roots of V. myrtillus.

Vaccinium myrtillus further affects beech seedlings by creating shade. When beech nuts start germinating, simultaneously, Vaccinium develops foliage. Therefore, beech seedlings encounter shade and root competition just after germination. Fir has the advantage of being evergreen and can not be strained this way. Moreover, it is more shade tolerant in an early age than beech (ELLENBERG 1963).