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Interactions Between Vegetation and Soil in a Near-natural Temperate Deciduous Forest

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The interrelationships between geology, physiography, soils and trees were examined in a near-natural temperate deciduous forest in Denmark. Surveys on soil, physiography and geology divided the forest in two parts, one dominated by glacial deposits, and another dominated by lacustrine sediments. On glacial till soils the vegetation distribution reflects the past grazing intensity and hence land use. Beech-ash communities dominate on the steepest slopes, which are considered the least grazed, while oak-beech-ash dominate in the level areas, indicating light open conditions due to grazing in the past. On the lacustrine soils the vegetation reflects texture and drainage regime. Beech-ash communities dominate the dry soils, while oak is present along with beech and ash on the imperfectly drained soils. Ash is omnipresent, apparently independently of soil type or drainage regime. It is concluded that tree distribution mainly is caused by past land use (grazing), and only to a limited extent caused by topography and soil characteristics.

Based on soil analysis it is estimated that the $CaCO_3$ has been leached out of the upper 100 cm of the glacial soils, equivalent to approximately 7500 Mg $CaCO_3$ ha^{-1} in the least disturbed part of the forest requiring approximately 1500 mmoles acid equivalents $year^{-1}$ m^{-1} since the termination of the last glaciation approximately 10,000 years BP. It is concluded that the ecosystem is an open system, continuously releasing nutrients by chemical weathering of the soil minerals and subsequent loss of the released nutrient elements by leaching.

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Introduction

Physiography, geology and soil are determining factors in the distribution of natural vegetation types (Alban 1969; Pritchett & Fischer 1987; Kimmins 1987). Soil and vegetation exist and develop in a mutual dependency where the soil act on the vegetation and the vegetation act on the soil (e. g. Moffat 1990; Alban 1982).

In Denmark the natural vegetation of mixed deciduous forests has been disturbed decisively, and accordingly the soil dependent distribution of vegetation has been strongly altered. Consequently it is difficult to study natural soil forming processes and the natural relation between soil type and vegetation. Hence, knowledge on how the soil and geology determine the distribution of vegetation types, and soil development in natural forest ecosystems is very limited.

Suserup Skov is one of the few near-natural forests of Denmark. This forest was subject to studies of soil development and soil dependent tree distribution, aiming at relating the distribution of tree species to the soil, geology, and physiography and examining the dominant soil processes and soil development under semi-natural conditions. It was hypothesized that the slope, hydrology and soil type in part determine the distribution of vegetation types. It was intended to elucidate whether the size of the forest and the soil variation are sufficient to support different vegetation types, or to determine tree species distribution.

Material and methods

Suserup Skov (19 ha) in eastern Denmark (11°30'E, 55°20'N) has only suffered from minor human impacts, and according to pollen studies a continuous forest cover has probably been present since the initiation of the post-glacial period (approximately 10,000 years BP) (Hannon ~~and~~ Bradshaw, unpublished data). The forest is located on the gentle to steep slopes of the Suså river valley and on a terrace in the valley bottom. The parent material comprises glacial tills made up by paleocene clays and marls along with sedimentary and intrusive rocks from the Scandinavian peninsula. Furthermore, glaciofluvial sand, peat deposits along with lacustrine and glaciolacustrine clay, silt and fine sand occur. Mean annual temperature is 8.1° C, precipitation 635 mm year^{1}. The vegetation is dominated by beech (*Fagus sylvatica L.*), ash (*Fraxinus excelsior L.*), oak (*Querqus robur L.*), elm (*Ulmus glabra Huds.*), and alder (*Alnus glutinosa (L.)* Gaertn.).

The forest was divided in three parts according to the vegetation pattern, described by Emborg et al.(1996). Part A is the least disturbed part, in which the three-dimensional structure of the tree-vegetation apparently is approaching a quasi steady state, while the species composition presumably is changing. Part B has been under human impact in the recent past by grazing early in this century, and by sowing of oak in the beginning of the 19th century, and the vegetation structure is probably not in a steady state. Part B has probably been tilled some time during the medieval. Part C is a narrow zone along the lake shore, dominated by alder. Part C has partly been grazed until 1925 and is still under successional change. The three parts are delineated on the tree species distribution map, Fig. 2.

In this work, the forest was initially divided according to geology and slope class. The soil was surveyed according to a 50m*50m grid. In each grid intersection, soil texture class, stones along with soil horizon sequence (including the C horizon) to a depth of at least 1 m were recorded by augering. In the horizon sequence registration, the humus content were estimated by the extent of dark colouring of the horizons. Based on the survey, 4 sites that represent the most common land units, were chosen. Soil pits were dug to depths of 100-170 cm and soil samples were collected for chemical and textural analyses.

After air drying (room temperature) and sieving (2 mm mesh size) the soil samples were analysed according to the following: Exchangeable cations; Al^{3+}, Ca^{2+}, K^+, Na^+, Mg^{2+} were extracted with 1M NH_4NO_3 (Stuanes et al. 1984) and the concentration determined by atomic absorption spectroscopy (AAS).

Phosphorus was determined after dissolution with 0.1 M H_2SO_4 by the molybdenum blue method (Murphy & Riley 1965). Nitrogen and Carbon were determined by dry combustion and mass spectrometry (EA 1108 Elemental analyser Carlo Erba). pH was measured potentiometrically in a 0.01 M $CaCl_2$ solution in 1:2 soil: solution ratio. Texture was determined by sedimentation (Day 1965). $CaCO_3$ was determined by measuring the CO_2 developed after dissolution in HCl.

Results and discussion

The survey on geology and physiography

The results of the survey are displayed on the map of soil and physiography (Fig. 1). Based on geology and landforms, the forest is divided in "upland" dominated by glacial deposits with minor patches of glaciofluvial sediments and "lowland" a level terrace dominated by lacustrine sediments. The upland is subdivided according to slope classes; level (<2%) undulating (2-10%) and steep (>10%), and soil texture (sandy and loamy). The most common slope class is the undulating (land units 1.2 and 1.5), making up some 70% of the upland area. The sandy till soils are concentrated in smaller areas in the eastern part and the loamy in the western and central parts. The upland soils varied greatly in development (depth to C horizon). The lowland is subdivided according to sediment type in clays/silt and fine sand respectively.

Within the chosen land units, the sites of the profiles were chosen with texture and depth to C horizon as the guiding principles. The four profiles chosen represent i. deeply developed loamy till soil, ii. shallow developed till soil, iii. sandy lacustrine soil and iv. silty and clayey lacustrine soil.

The map (Fig. 1) reveals a rather clear subdivision in lowland and upland. The boundary between these two units are interpreted as a former lakeshore. The upland consists of the slopes of the glacial landscape, and the lowland of a former lake bottom.

The lowland is made up by two distinct land units; a slightly elevated plateau of heavy clay soils, and the lower lying sandy soils. Both sediments are homogeneous in texture and contains very few stones. Both sediments are interpreted as lacustrine. The central part of the lowland (land unit 2.1) is interpreted as a glaciolacustrine lake bottom, created in the terminal phase of the last glaciation where the valley was partly filled with ice. These lakebottoms occur regularly in young glacial landscapes in eastern Denmark. They are closely associated to landscapes created by melting of stagnant ice. In these areas, meltwater accumulates as lakes in depressions, and will often be completely or partly dammed by ice. In the meltwater lakes, fine particles will settle. After the complete melting of the ice in the late pleistocene, the former lakebottoms will remain as small flattopped hills, or kames.

The rest of the lowland (land units 2.2 and 2.3) consists of fine sandy sediments, either deposited at a time where the lake covered the low parts of the terrace. Land unit 2.1 was probably dry at this time and appeared as a small island in the lake. The soils in land unit 2.2 consist of both fine sandy and clayey-silty sediments, reflecting varying sedimentation environments in the lake. Profile 3 (Table 1, 2) represent the sediments dominated by fine sand. Both horizontal and vertical variation in sediment type occur. Also Andersen (1931) identified several terraces in the valley.

The occurrence of peat in the lowland indicates a slow retreat of the water. The inner parts of the lowland are the most subdued and wet, partly due to the high ground water table close to the slope at the edge of the upland. The land strip along the lake is periodically submerged, though the lake is slowly retreating, creating new land.

Parent material and soil development

Data on soil chemistry and texture are given in Table 1 and 2.

Glacial till

The glacial sediments represent some of the extremes of tills in eastern Denmark; both clayey, loamy and sandy tills occur. The patches of glaciofluvial sediments are common features in the region. The variation in depth to Ck horizon (the lime rich parent material) and the extent of Bt horizon (soil horizon with accumulation of clay) is considerable, as revealed by the survey, and expressed in the two soil profiles on glacial till.

The till soils are generally well drained, but very different leaching regimes occur. The leaching intensity, i. e. the amount of water passing through the soil, is dependent on the slope steepness, location on the slope, and soil tex-

Table 1. *Content of P, N, organic C, $CaCO_3$ and texture.*

hor	Depth	P	N	C	$CaCO_3$	Clay	Silt	Fs	Cs
	cm	mg/kg			%				
Profile 1 (land unit 1.2)									
A	0-28	94.7	0.17	3.61	–	7	16	52	25
E1	28-64	157.8	0.001	0.70	–	6	16	52	26
E2	64-108	163.7	0.01	0.60	–	5	13	47	35
Bt	108-144	582.5	0.00	0.34	–	22	10	42	26
Ck	144-	285.9	0.00	0.00	25	15	12	40	33
Profile 2 (land unit 1.2)									
A1	0-14	87.3	0.15	3.11	–	10	10	49	31
A2	14-38	101.4	0.09	1.63	–	14	8	50	28
Bt	38-70	478.3	0.01	0.30	–	25	12	45	18
Ck	70-	301.5	0.00	0.00	22	18	12	38	32
Profile 3 (land unit 2.2)									
A1	0-10	36.1	0.18	2.64	–	9	13	74	4
A2	10-50	445.5	0.18	1.9	–	12	16	73	3
C	50-100	109.9	0.07	0.3	–	6	6	86	2
Profile 4 (land unit 2.1)									
A	0-60	45.6	0.08	1.09	–	20	22	56	2
C	60-100	50.4	0.01	0.10	–	28	28	41	3

Table 2. *Soil content of exchangeable cations, soil pH.*

Hor	Ca	Mg	Na	K	A1	pH
			mmol (+) kg soil^{-1}			
Profile 1 (land unit 1.2)						
A	11.18	1.29	0.59	0.13	20.61	4.09
E1	15.36	1.13	0.52	0.11	18.66	4.78
E2	15.16	1.22	0.55	0.11	10.32	4.84
Bt	86.72	2.72	0.23	0.53	1.77	5.23
Ck	–	3.85	0.81	0.13	0.03	8.48
Profile 2 (land unit 1.2)						
A1	28.63	0.92	0.61	0.96	18.34	5.01
A2	41.78	0.99	0.44	1.04	15.11	4.77
Bt	134.10	0.92	0.22	1.02	2.31	5.51
Ck	–	0.8	0.71	1.05	0.01	8.2
Profile 3 (land unit 2.2)						
A	9.55	78.78	0.27	1.8	41.77	5.21
A	112.02	46.84	0.67	1.35	0.77	5.11
C	4.15	0.84	0.44	0.32	22.11	5.54
Profile 4 (land unit 2.1)						
AC	119.03	103.00	0.21	3.27	6.88	5.98
C	80.75	1.69	0.87	1.83	8.19	6.16

ture. The dissolution of $CaCO_3$ and leaching of base cations occur obviously easily in most soils. The dissolved Ca is transported down slope with the seepage water and at the slopes at the boundary to the lowland it is precipitated by contact with the atmosphere as secondary limestone in spring areas. Secondary limestone is visible in soil exposed in the root stumps after windthrows.

One of the most prominent features separating the soils of Suserup Skov from other soils in the same setting is the micro relief. The uprooting by windthrow will occasionally disturb the upper soil layers, partly initiating the soil development (Beatty & Stone 1985). The uprooting turns the soil horizons upside down, exposing parent material (C horizon) to the surface, and burying the A and B horizons. The micro relief created from windthrow is visible in the forest as small heaps of soil, long after the stem has been decomposed. However, this initiation of soil development are probably only restricted to the upper 50-100 cm. Compared to other forest ecosystems, no organic matter is removed by harvest, and there is a significant input of decaying wood, contributing to organic carbon content of the soil.

The loamy tills have a relatively high content of stones and boulders as compared with the sandy tills. The border between the two coincides in part with the extent of the least disturbed part of the forest (Emborg et al. 1996) as delineated on Fig. 1. The sandy soils dominating in the most disturbed part have probably been easier to cultivate in the medieval.

The profiles 1 and 2 represent land unit 1.2 developed on glacial till.

The soil forming processes in the upland till soils, represented by profile 1 and 2, are incorporation of organic matter in the mineral soil, dissolution and leaching of easily weatherable minerals (in particular $CaCO_3$), and eluviation

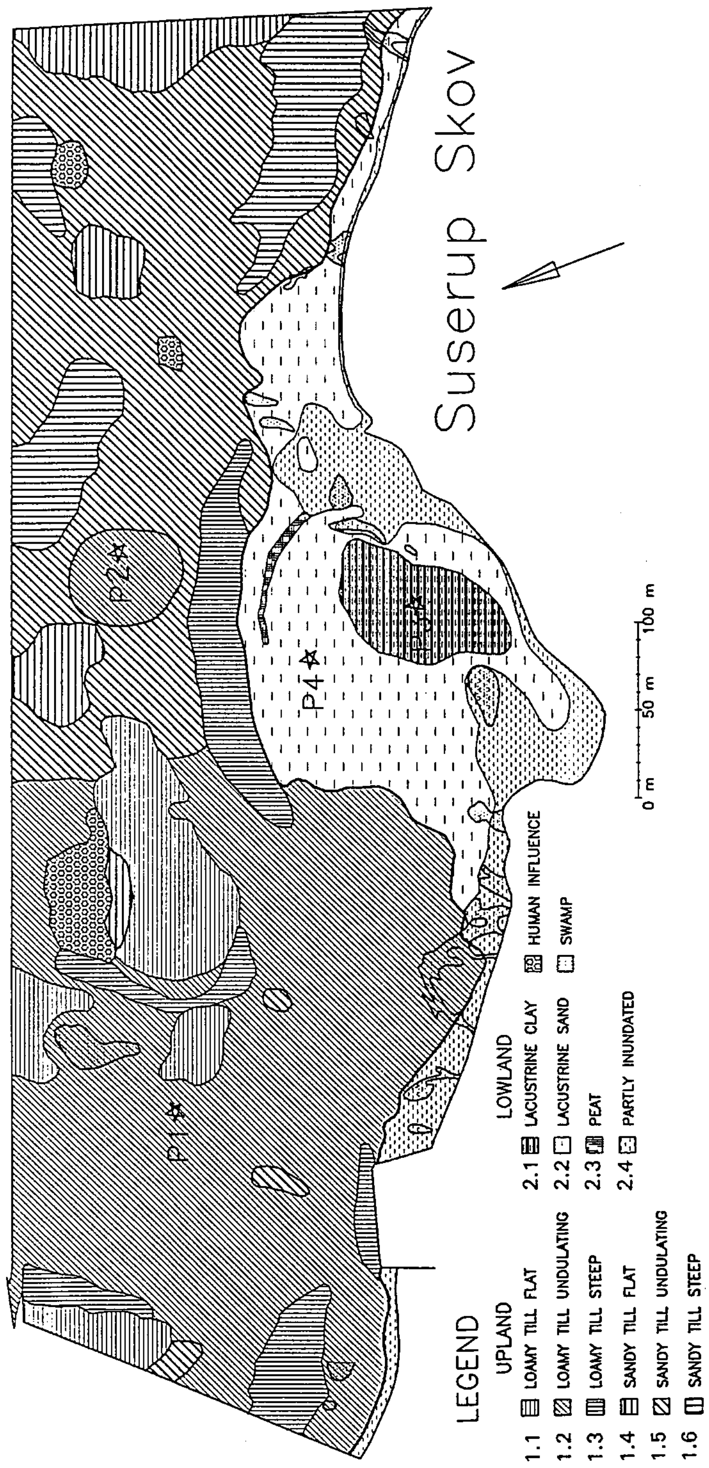

Fig. 1. *Land Unit Map, sediment and soils. P1-P4 indicate location of soil pits.*

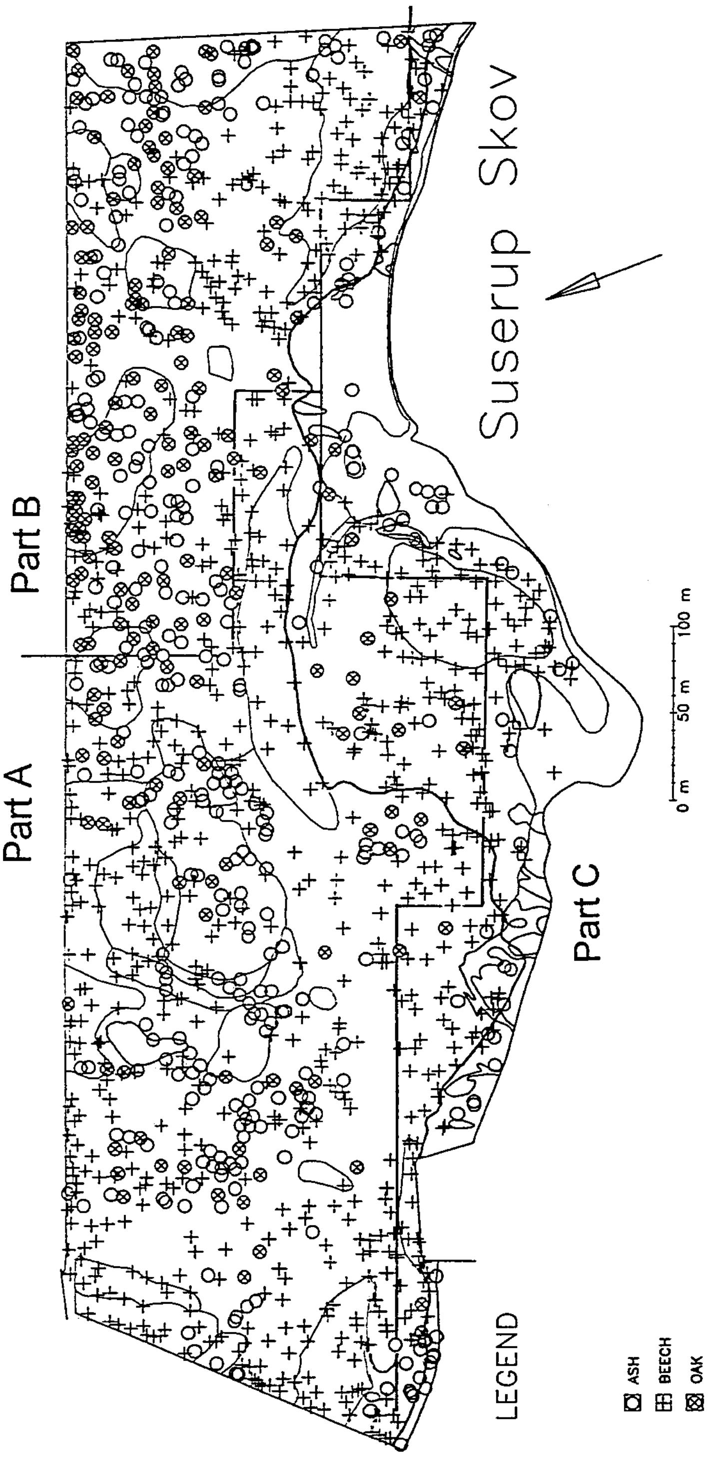

Fig. 2. *Distribution of tree species (≥ 29 cm dbh) according to land units. Deliniation of soil types as figure 1.*

of base cations and clay. These processes have developed the horizon sequence of L-A-E-Bt-Ck, indicating a slight accumulation of tree litter on top of a darkened, humus rich A horizon followed by the bleached, eluvial E-horizon (only in profile 1) which has been deprived of base cations and clay. The Bt horizon is enriched with illuvial clay, while the Ck horizon represents the parent material, the lime rich glacial till. The most notable feature is the position of the acidification front, the boundary between the Bt horizon and the lime containing Ck horizon. The pH increases and the content of exchangeable Al decreases accordingly across this boundary. The textural differences between the two profiles reflect the natural variation in the glacial till. The exchange complex is in the upper horizons (A and E) dominated by Al and Ca, while the Bt horizons are dominated by Ca. Profile 2 lacks a distinguished E horizon, is more shallow, contains more exchangeable cations and is less leached than profile 1. The weaker profile development might be due to another location on the slope. Profile 2 is located on the uppermost part of a slope, whereas profile 2 is located at the lower part. The percolation of water through soil may be more intense on the lower part of the slope, increasing the rate of soil development. Furthermore, in periods of soil erosion, profile 2 may have been in a zone of net soil loss, thereby removing A horizon material. Alternatively the parent material in profile 2 may originally have been richer in $CaCO_3$, increasing the acid buffer capacity of the soil. Both soils are, however, considered nutrient rich, well drained and very suitable growth medias for forest trees.

Lacustrine sediments

Profile 3 represents the clayey/silty sediment of the glacial lakebottom, while profile 4 represents the more recent deposits of lacustrine fine sand. Despite differences in age and textural composition, both profiles have features as homogeneity, absence of stones, very small content of coarse sand, weak soil development and restricted drainage in common.

Profile 3 has a very high content of fine sand (73-86%) and a significant amount of clay and silt. The soil development is very limited, possibly due to poor drainage. The contents of organic carbon and nitrogen are relatively high in the upper 50 cm, and the organic matter is only slightly decomposed, part of which may be organic lake sediments (gyttja). The site is one of the driest of the land unit (2.2), in the wettest areas of this land unit a peatlike deposit dominates the upper 10-15 cm. The content of P is highest in 10-50 cm, presumably because of the higher clay content. The tree growth appears as vigorous as in the glacial part though the drainage is bad in some parts, restricting the root development as compared with the glacial soils.

Profile 4 has a very high clay+silt content (42-56 %.). This high content of fine particles, combined with the almost absence of coarse sand, makes the soil very compact. The contents of organic C and N are very low, both compared to the upland soil and profile 3. The CEC, and especially the contents of exchangeable Ca and Mg, is very high. The exchangeable K content is the highest of all profiles excavated, partly explained by the high clay content of which illite may be dominant. The biological activity is apparently very high, indicated by a rapid litter decomposition. The input of C to the soil through litter fall, and the litter decomposition rate is not known, however. The high rate is estimated based on the observation, that very few leaves remain in the forest floor after 1 year of decomposition.

In summary, the soil development in the lacustrine sediment soils is much weaker than in the glacial soils. The soil forming processes are dominated by incorporation of organic matter and a slight weathering of the uppermost layers, indicated by a weak topsoil acidification in profile 4.

The weaker soil development in the lowland soils is probably caused by the high water table, which restricts the downward water movement to the upper 50-60 cm. Below this zone, the soil is water saturated most of the year, which exclude the soil forming processes of the well drained soils in the glacial upland land units.

Tree distribution and soil types

In Fig. 2 all stems of beech, ash and oak ≥ 29 cm dbh are plotted (data from Emborg et al. 1996). The correlation between tree species distribution and land units was made visually.

In part A, the distribution of oak seems to be dependent on slope steepness. At the steepest slopes, oak is almost absent, while it is well represented in the level and undulating land units of the glacial part. If the presence of oak is an indication of former more light open conditions as suggested by Fritzbøger and Emborg (1996), it may be inferred that the grazing or cutting of hay has taken place in the level and undulating part of the forest rather than on the steep slopes. An ecological reason for the absence of oak may be the activity of seepage water in the steep sloped areas, but there are no records of beech being more competitive than oak on steep slopes. Moreover, oak sown in the beginning of the 19th century thrives on the steep slopes in part B.

On the lake sediments, the hydrology apparently in part determines the distribution of the tree species. The fine sand sediments have shallow ground water tables, and oak probably has a competitive advantage to beech on these waterlogged soils. On the more well drained, slightly elevated plateau of lacustrine clay, beech dominates while oak is almost absent. It may appear conflicting that the fine textured soils are the driest, and the coarse textured the wettest. The clayey glacio-lacustrine sediments appear as a slightly elevated plateau, while the fine sandy soils are low-lying and have the highest ground water table, in particular at the base of the upland slope. On the hydromorphic soils of the terrace *Alnus* dominates completely the vegetation.

It should be stressed, that the species composition is changing towards a pure ash-beech forest with elm in the understorey, slowly excluding oak (Emborg et al. 1996). Regeneration of oak is very limited in any part of the forest. Although some coincidence between physiography, soil and species distribution can be detected, it is probably rather caused by the influence of physiography on the former land use than by the species distribution per se, in particular on the till soils. The lacustrine soils are characterized by two very different hydrological regimes, and the soil conditions may therefore be more causal in determining the species distribution, though a difference in land use is not excluded.

Ash is not confined to any particular land unit. It lacks in land unit 2.2 (the clay rich lacustrine sediments), and is only sparsely represented in the steep sloped areas of the upland. The general picture is that ash thrives all over the forest, upland and lowland and well drained as well as imperfectly drained. The map only shows the stems larger than 29 cm dbh, but small ash individuals is omnipresent in large numbers in all gaps generated by death of an overstorey tree. There is no support for the often held conventional wisdom that ash is only suitable on wet sites.

Future development of vegetation and soil

If no new tree species are introduced, the species composition in Suserup Skov will probably homogenize in the long term. Most of the soils would presumably be able to meet the specific requirements of the beech-ash system, probably with the exception of the most waterlogged lacustrine soils and the hydromorphic soils of the lakeshore. The vegetation hence only show a weak level of preference of soil type in this forest. If the species composition develops towards homogenization, it may be discussed which spatial scale or which degree of soil variation is required to create different vegetation types, and whether the development of a soil dependent vegetation distribution is possible. The soil variation is less that possible, if the extremes among Danish soils were represented in Suserup Skov. The most nutrient poor and dry soils of the region, such as coarse sandy glaciofluvial soils, are not represented. The nutrient contents do probably not vary sufficiently, while the hydrology probably plays a role in determining species distribution, particularly on the hydromorphic soils. The driest soils found on the hill tops, may create sufficient variation, but these areas are too limited in size to present detectable differences in the vegetation.

A possibility for the introduction of soil dependent vegetation development would be the reinitiation of the succession after a catastrophic event. The present regeneration mode is a small gap dynamic, and the patch size of the shifting mosaic structure is probably too small to let the vegetation express the soil variation. As a climax forest is more independent on soil conditions than pioneer forests (Kimmins 1987), the expression of soil dependent vegetation patterns may therefore be dependent on the disturbance regime. In large scale disturbances, the soil type determines the pioneer vegetation type, while in small scale disturbances, other factors as light, climate, year, stochastic events may determine the vegetation type.

In the very long term, given the present conditions of a humid climate, the soil will degrade as a consequence of the continuous weathering and leaching (Miles 1985). The rate of changes depends upon tree species, biomass production rate, and site variables, in particular the hydrology, weathering rate and the soil acid buffering capacity (dependent on the assemblage of soil minerals). As fresh deposits often weather very rapidly (Zabowski 1990), the rate may slow down in more weathered soils (Miles 1985) and therefore the weathering rate cannot be considered constant.

To estimate the weathering rate, and hence the future development of the soils, three question must be addressed: The past, present and future weathering rates.

Concerning the past, soil content of $CaCO_3$ may be used as an indicator of the degree of degradation. Based on the present content in the Ck horizons, it is hypothesized that 30% $CaCO_3$ originally was present in the upper 1 m of the glacial till. It is ignored that the soil then was more compact than the present, compensated today to some extent by the decrease in bulk density by loosening of the soil by soil organisms. With this assumption, 0.3 m^3 of $CaCO_3$ has been leached per m^2 since the last glaciation in the glacial soils. This equals 746 kg of $CaCO_3$ m^{-2}, equal to 14.92 kmoles of charge m^{-2}, requiring 14.92

kmoles of acid equivalents m^{-2}. This equals approximately 1500 mmol charge m^{-2} $year^{-1}$ since the termination of the last glaciation, which in this case is set to 10,000 years BP. This historical weathering approach is an acceptable method to determine extent of past weathering (Olsson & Melkerud 1991).

In attempting to model the past acidification regimes, not only the present vegetation but also the development in vegetation through the past 10,000 years, including man made disturbances, (e.g shifting cultivation), and influences (e.g. biomass harvest and grazing by domestic animals) must be taken into consideration. As the vegetation composition and land use have changed, it is likely that the acidification rate has changed accordingly. The major change of the vegetation is the shift from a *Tilia condorta* dominated to a beech dominated system approximately 2500 years BP. (Hannon & Bradshaw, unpublished data). The active acidification of these two tree species is very different, beech being the most acidifying (in terms of acidity produced by organic acids from the degradation of biomass), and the rate at which the two species degrade the soil varies accordingly. Åby (1983) estimated the acidification rate to be 4-5 times faster under beech-oak-birch than under lime in Draved Skov, a near-natural forest of southwestern Denmark. Even if this estimate does not apply to Suserup, it is likely, that the soil development would have proceeded slower without the change in vegetation facilitated by human activities, in particular the shift from the *Tilia condorta* dominated system to the beech dominated. The tree action on the soil can adversely affect the trees themselves, as soil action on trees is an open loop; plant induced soils changes feed back on plants (Miles 1985).

At present, the system has lost a considerable amount of acid neutralization capacity (ANC), but still plenty of ANC is present in the soil, as primary and secondary silicate minerals, and exchangeable cations. The dissolution of $CaCO_3$ is however a more rapid process than the dissolution of silicate minerals. In the pH range in the A and E horizons, the role of carbonic acid is diminishing, and other weathering agents will be dominant, in particular organic acids. Compared to the past, the present situation implies both a decrease in acidification rate, and an increase. The reduction is due to the cease of biomass export, and the increase is due to the deposition of nitrogen and sulfur compounds from the atmosphere. The quantitative contributions from these are not known, however.

With the present acidification regime, the buffering capacity will be lost eventually however, and the system slowly turns into a more poor, degraded state, presumed that no new glaciation or other soil disturbing geological events happen.

The question is at which rate this consumption of acid buffering capacity will occur in the future. The acidification is dependent on the tree species, as different tree species alters the soil with different rates due to differences in litter composition, leachates and through fall/stem flow (Ovington 1953; Jensen 1974; Pallant & Riha 1990).The direction of the future vegetation succession will depend on this soil alteration. The soil change and successive change of vegetation communities should not be considered an anthropogenic facilitated event solely. Andersen (1969) describes the successional natural vegetation/soil development in Denmark in the past three interglacials as consisting of the following main phases: i. Vegetation of light demanding plants without preferences to soils, ii. Woodland on brown earth requiring fertile soils, and iii. Vegetation on acid humus. Suserup is at present in phase ii., but according to the discussion, most of the forest will in the long term, eventually turn into phase iii. The only exception is probably lowland soils, which both receives dissolved nutrient cations with the ground water from the upland soils, and have a weaker soil development and hence slower rates of soil development. The soils may even improve the fertility with the element transport for the upland soils to the lowland soils.

The overall cycle of vegetation-soil development in the system consists apparently of alternating glaciations associated with renewal of the parent material, and interglacials associated with acidification/degradation of the soils (Andersen 1969). In the interglacials, the vegetation changes towards systems of species adapted to more nutrient poor conditions (Iversen 1958). According to Åby (1983) it is necessary to know the succession of vegetation-soil types in the past and the duration of each state when assessing the role of soil genesis in vegetation distribution. However, it is difficult to give precise estimates on duration of vegetation periods. Also cyclic interactions between species in the climax micro succession (over one tree generation) are reported (Miles 1985). The question is whether soil differences in this case can be detected between the phases of the forest cycle succession which in this case consist of a period dominated by ash followed by a period dominated by beech. This problem is still to be solved.

Conclusion

The distribution of tree species in Suserup Skov reflects the former land use rather than the geology, soil, and topography. The land use, however, was partly dependent on soil and slope features. The only soil feature to determine vegetation distribution is believed to be the ground water table. The past development in vegetation succession suggests that the acidity, has changed due to changes in vegetation composition. The degradation of the soil may proceed faster than indicated by the simple average depletion of $CaCO_3$ from the soil since the termination of the last glaciation. The major part of this depletion may have occurred in the latest millennia.

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