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Original article

Humus form development and succession of dwarf shrub vegetation in grass dominated primary *Pinus sylvestris* forests

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Summary — Because of its role in nutrient and water supply to plants, the humus form is strongly interrelated with the vegetation and is likely to at least partly control vegetation succession. Causal relations between vegetation succession and soil development are generally difficult to study because of the multifactorial nature of ecology. Primary succession of *Pinus sylvestris* forests on recent inland dunes provides interesting information on succession related humus form development. Humus form characteristics and vegetation composition in these drift sand areas were studied along an age series of Scots pine stands, ranging from 15 to 124 years old, all situated on similar parent materials and lacking antecedent soil formation. From the information thus obtained, successional processes were deduced and the following conclusions were drawn: 1) Chemical variability in the ectorganic profiles under the Scots pine forests concerns a downward decrease of plant available elements as well as allelochemicals, which both may have implications for reproduction and competitive ability of undergrowth species involved in the succession. 2) The concentration of *Deschampsia flexuosa* roots in the F horizon indicates a pronounced niche differentiation, which enables this species to maintain dominance in the herb layer for a long period of time during succession in pine forests. 3) Facilitation in the succession of the undergrowth of the pine forests seems to emanate from horizon differentiation and associated chemical variability. Dwarf shrubs take advantage of the development of an H horizon, leading to a botanically more variable undergrowth vegetation in older pine forests.

humus form / vegetation succession / *Pinus sylvestris*

Résumé — Développement des profils humiques et succession des arbustes nains dans des forêts de *Pinus sylvestris* à graminées. *Une succession primaire de forêts à base de* Pinus sylvestris *sur dunes continentales récentes fournit des informations intéressantes sur les interrelations entre successions végétales et évolution des types d'humus. La caractérisation des types d'humus et la composition de la végétation sur ces sables éoliens ont été étudiées le long d'une séquence de pins sylvestres, allant de 15 à 24 ans, sur roches mères semblables, sans pédogenèse antérieure à l'ins-*

tallation du peuplement. À partir des informations mesurées, les étapes de la succession ont été reconstruites et les conclusions suivantes obtenues : i) sous les forêts de Pinus sylvestris, *les profils ectorganiques montrent la variabilité chimique qui se traduit par une diminution des éléments disponibles pour les plantes et des composés allélochimiques, qui tous 2 peuvent avoir des conséquences pour la régénération et le pouvoir compétitif des espèces herbacées qui participent à la succession végétale ; ii) la concentration dans l'horizon F des racines des* Deschampsia flexuosa *indique une différenciation prononcée en niches, qui permet à cette espèce de prolonger sa dominance pour une période assez longue pendant la succession végétale ; iii) la différenciation en horizons et la variabilité chimique qui en résulte semblent favoriser la succession de la couche herbacée. Les arbustes nains profitent du développement d'un horizon H, ce qui mène à une couche herbacée plus variée dans les forêts de pins âgés.*

type d'humus et succession végétale / pin sylvestre

INTRODUCTION

In the past decades, various models have been developed describing general pathways of primary and secondary succession (*eg* West *et al,* 1981). Environmental factors, such as light intensity, grazing, nutrient availability and allelopathy, have been found to play a role in species competition, and they may act as driving forces behind succession (Muller, 1969; Ahlgren and Ahlgren, 1981; Miles, 1985; Hester *et al,* 1991a, b; Leuschner, 1993). There is, however, still little knowledge about causal relations between soil development and concomitant changes in vegetation composition.

In coniferous forest ecosystems, the ectorganic profile is generally the major rooting environment for the undergrowth vegetation. Furthermore, it determines the conditions under which germination of propagules takes place. Under undisturbed conditions, succession related changes in soils particularly concern the autogenic development of humus forms, as they are controlled by the actual species composition. Humus forms therefore deserve special attention in studies on vegetation succession (Emmer and Sevink, 1993).

Fanta (1986) described a primary succession of *Pinus sylvestris* L forests on poor sandy soils in the Netherlands. In later transient stages, this succession is characterised by the partial replacement of *Deschampsia flexuosa* (L) Trin by *Empetrum nigrum* L, *Vaccinium myrtillus* L and forest mosses, which coincides with the development of an H horizon. Scots pine forests in western Europe commonly have developed as secondary successions on former heathlands or have been strongly influenced by forestry and episodic soil management. The primary succession of Scots pine forests in the Hulshorsterzand area has provided an exceptional opportunity to study the temporal and vertical variability of humus form characteristics evolving from the vegetation development, without interference of antecedent soil formation. The study of temporal and vertical variability of the ectorganic profile in a chronosequence of these forests has been reported by Emmer and Sevink (1994).

The objective of this paper is to describe how the humus form development may control the succession of the undergrowth vegetation in the pine forests.

MATERIALS AND METHODS

The *Pinus sylvestris* forests are situated on recent inland dunes in the Hulshorsterzand area in the Veluwe (5°44'E, 52°20'N, 10–15 m above sea level), the Netherlands. The age series studied spans a period of about 120 years, representing a primary successional sere, thus lacking

antecedent soil formation or pretreatment. The vegetation has been studied by Fanta (1986) and Prach (1989). The initial tree-less stages are dominated by grasses (*Corynephorus canescens* [L] Beauv and *Festuca ovina* L) and moss (*Polytrichum piliferum* Hedw). In young pine stands (less than about 20 years old and with a tree density exceeding 1 500 trees ha^{-1}), ground vegetation is almost absent. Later on, in 40–50-year-old stands, *Deschampsia flexuosa* appears and soon becomes dominant. The species association is described as *Leucobryo-Pinetum* sub association *Deschampsietosum* (Van der Werf, 1991). *D flexuosa* is considered to have increased its surface cover in the past decades due to increased atmospheric N deposition (*cf* Heij and Schneider, 1991). In the following stages of succession (80–100-year-old stands), *D flexuosa* slowly declines and mosses (such as *Pleurozium schreberi* Hedw, *Hypnum cupressiforme* Hedw, *Dicranum scoparium* Hedw and *Dicranum polysetum* Hedw) become more abundant. In 120-year-old stands, described as *Empetro-Pinetum* (Van der Werf, 1991), the herb layer has a much more varied composition, with a co-dominance of dwarf shrubs (in particular, *Empetrum nigrum* and *Vaccinium myrtillus*), *D flexuosa* and forest mosses. The declining vigour of *D flexuosa* has been established from decreasing flowering intensity and increasing dead/living shoot ratios in the 2 oldest stands (Moszynska, 1991). The *Empetro-Pinetum* is considered to be a disclimax vegetation, because the possible development towards the regional climax vegetation (*Betulo-Quercetum robori* or *Fago-Quercetum*; Van der Werf, 1991) is impeded by animal browsing (Fanta, 1986).

The pine stands have been gradually thinned to about 650 trees ha^{-1} during the first 4 decades. The structure of the stands has remained unchanged during subsequent development.

The soils (Haplic or Cambic Arenosols, according to FAO-Unesco, 1988) are well drained and exhibit the development of mor-type humus forms (classified according to Klinka *et al,* 1981), showing a strong horizon differentiation. Climate is temperate humid with a mean annual rainfall of about 800 mm, rather evenly distributed over the year, and with a potential precipitation surplus of 325 mm.

Vegetation descriptions and soil samplings have been carried out along a chronosequence, comprising 15, 30, 59, 95 and 124-year-old stands on sand dunes. Vegetation descriptions concern cover percentages of the herb and moss species and vertical distribution of herb and pine roots in the humus form profile. For the description of the rooting profile in the stands mentioned previously, the soils were sampled to a depth of 40 cm using a soil monolith sampler (surface 42 cm^2; Wardenaar, 1987). These root distributions were obtained using a semiquantitative method for profile descriptions such as outlined by Klinka *et al* (1981). This method distinguishes 6 classes of root abundance, relating to the number of roots counted in a 6.25 cm^2 area for roots smaller than 5 mm in diameter. For the root estimations, soils were sampled in places where the particular herb species had a cover percentage of 80–100%.

In stands 15 and 30, at 12 randomly selected points, the organic layer was sampled by horizon with a 100 cm^2 metal frame. The 12 samples of each horizon were bulked afterwards. In the other stands, 20 profiles were sampled along a nested triangular grid, with minimum distances of 2.3 m between 2 neighbouring points and maximum distances of 63 m. For these samplings, a 25 x 25 cm metal frame was used. The organic horizons were sampled and subdivided into L, F_1, F_2, Hr and Hd horizons (Klinka *et al,* 1981), conforming to L, Fr, Fm, Hr and Hf horizons (Babel, 1971) and approximately to Oi, Oei, Oe, Oea and Oa horizons (Soil Survey Staff, 1981). Samples were analysed separately for organic matter content and elemental composition of the organic matter and of water extracts. Details about sampling and analytical procedures are given by Emmer and Sevink (1994), and Emmer and Verstraten (1993).

In a subsequent sampling, bulked samples (n = 7–10) of organic horizons (L + F_1, F_2, Hr and Hd) were collected in all the dune sites for the analysis of water extractable phenols. For this purpose, in the 3 oldest stands, samples were taken in patches of *D flexuosa* only, to prevent effects of different herb species. An estimation of total water soluble phenols in 1:25 (w/v) extracts was done using the Folin-Ciocalteus reagent (Box, 1983). Phenol concentrations are expressed as tannic acid equivalents in organic matter (mg TAE 100 g^{-1} OM).

RESULTS

The data presented by Emmer and Sevink (1994) concern organic matter accumulation during succession and chemical and

physical properties of organic horizons. During soil development, a subsequent development of L, F_1, F_2, Hr and Hd horizons could be observed. These horizons attain a more or less constant amount of organic matter within the time span of the chronosequence studied (fig 1).

During stand development, the relative contribution of the various horizons to the total amount of ectorganic matter changes markedly in favour of the humus horizons. A survey of ectorganic profiles in the study area revealed that the H horizon becomes visible as pockets after about 30 years of forest development. Distinct vertical gradients in the ectorganic profile can be observed for the elemental composition of the organic matter and the water extracts. It has been shown that during soil development the pH and elemental concentrations in the various horizons remain more or less constant (Emmer and Sevink, 1994). Therefore, it is sufficient only to present data for the stand aged 124 years (figs 2a–d). Figures 2a and b indicate that, except for N and P, the F_2, Hr and Hd horizons have similar concentrations of labile (organic bound, adsorbed plus water-soluble) cations, while the F_1 and L horizons have markedly higher values. Thus, the major vertical change occurs in the upper organic horizons (L and F_1) rather than between the F and H horizons. It furthermore appears that the ratio K/Ca (fig 2a) is below unity and decreases downward. Water-extractable element concentrations (figs 2c, d) also show a strong decline from L to H horizons. Water-extractable K exceeds Ca, in part related to a higher mineralisation rate of the former, but also due to the stronger desorption of K in aqueous extracts. The K^+/Ca^{2+} ratio also decreases downward.

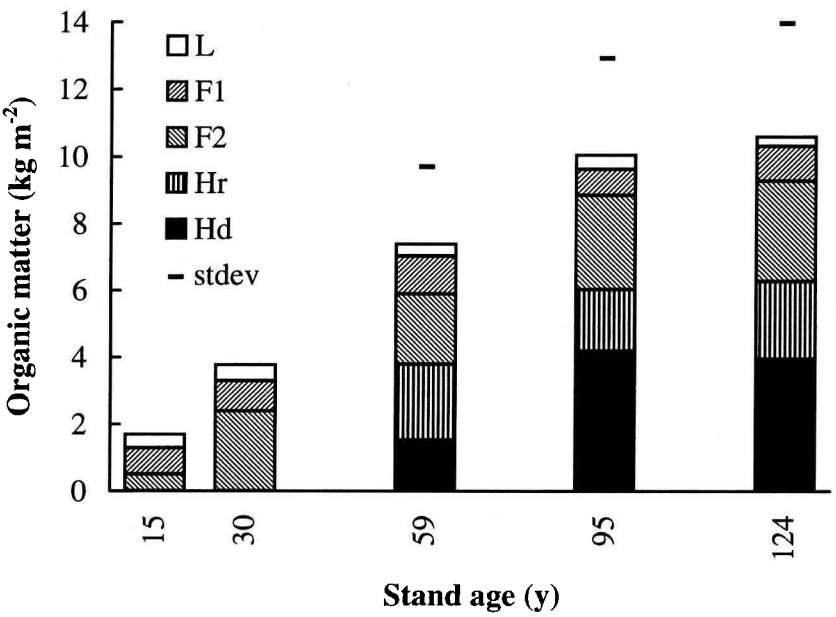

Fig 1. Amount of ash-free organic matter in organic horizons under *Pinus sylvestris* stands on sand dunes, related to stand age. Standard deviations of total organic matter are indicated by horizontal bars ($n = 20$).

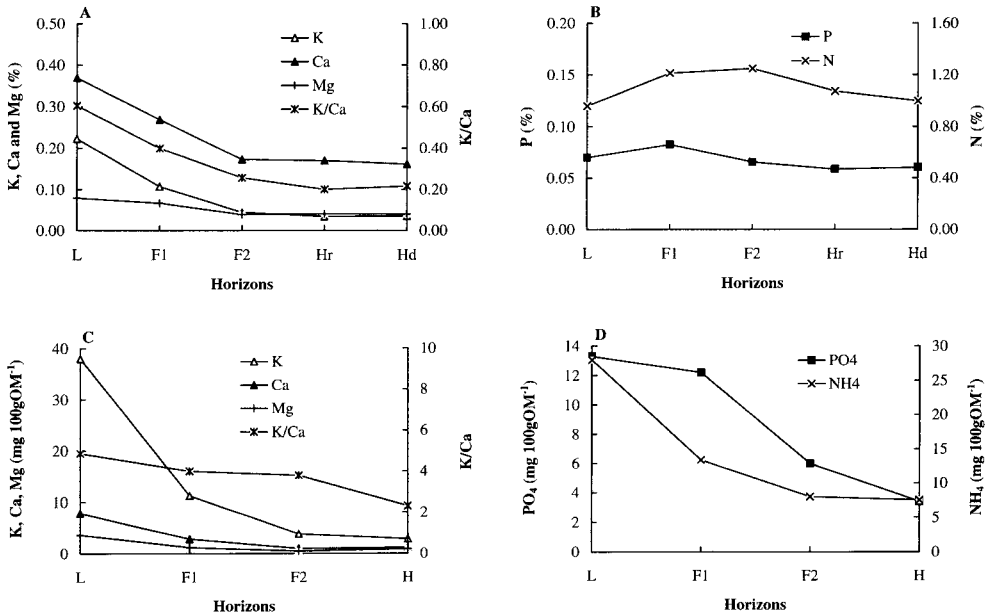

Fig 2. Percental concentrations of labile (organic bound, adsorbed plus water-soluble) elements (**A** and **B**) and concentrations of water-extractable elements, expressed as mg per 100 g organic matter (OM) (**C** and **D**) of the organic horizons in a 124-year-old *Pinus sylvestris* stand on sand dunes (n = 20).

The interpretation of the data on water-extractable phenols (table I) is less straightforward. The tanning action of phenolic compounds is particularly related to the slightly condensed phenols in the cell protoplasm (inherited phenols). The water-soluble phenols in the more humidified layers, formed as the result of biodegradation of lignin and microbial neoformation, are complexed and insolubilised rapidly (Duchaufour, 1982). Moreover, the analytical procedure employed overestimates phenolic acids in all organic horizons, while for the deeper organic horizons, the method is likely to give much higher overestimations due to the interference of higher concentrations of fulvic and humic acids (Box, 1983). For this reason, the results for the Hr and Hd horizons in table I should be considered as too high in relation to those for the L + F_1 and F_2 horizons. As for the extractable elements, the phenol concentrations show a marked decrease from the LF_1 to F_2. The individual compounds are not identified, but Kuiters and Denneman (1987) reported that Scots pine litter contains relatively high concentrations of ferulic acid. Along the chronosequence, the phenol concentrations in the LF_1 and F_2 horizons first show an increase and then a decrease. However, this trend cannot be statistically tested.

The average rooting profiles of the dominant species are presented in figure 3. *P sylvestris* makes use of the F and H horizons throughout the succession, but in later stages rooting of the H horizons prevails. The density of pine root in the upper mineral horizon remains approximately constant throughout the succession. *D flexuosa* is present in the 3 oldest stands and

Table I. Water-extractable polyphenols in the organic horizons in a 124-year-old *Pinus sylvestris* stand on sand dunes (expressed as mg tannic acid equivalents [TAE] per 100 g organic matter [OM], related to stand age [n = 7–10]).

Horizon	*mg TAE 100 g OM^{-1}*				
	15 y	*30 y*	*59 y*	*95 y*	*124 y*
LF_1	1.14	2.86	5.19	2.42	3.00
F_2	0.56	1.45	2.66	1.83	1.43
Hr			1.79	2.11	2.27
Hd			2.40	4.82	4.37

shows strong preference to the F horizon, the scores being much higher than for *P sylvestris*. *E nigrum* has a very dense rooting system in the F and H horizons. This species exhibits a radial spreading, overgrowing *D flexuosa*. *V myrtillus* has a dense rooting system in the F and H horizons as well. *E nigrum* alike, this species propagates itself in a concentric fashion, but making use of rhizomes which are predominantly located in the H horizon. At the edge of *V myrtillus* patches, the rooting profile therefore consists of *D flexuosa* roots mainly in the F horizon and *V myrtillus* roots and rhizomes in the H horizon. Nabuurs (1991) found that, at very low surface covers of the plant (1–10%), *V myrtillus* roots were mainly located in the H horizon. In addition, during vegetation descriptions and soil sampling it was observed that young individuals of the dwarf shrubs had their roots concentrated in the H horizons. The lateral spreading of the dwarf shrubs can be inferred from the macroscopic composition of the organic horizons (*ie* dwarf shrub litter overlies grass litter near the edge of dwarf shrub patches).

DISCUSSION

The development of a well-stratified ectorganic profile in pine forests on poor sandy substrate may have significant implications for the dimension and character of the habitat for forest plants and soil fauna. The latter has been demonstrated for Collembola by Faber (1992) and for soil nematodes by De Goede *et al* (1993a, b). These authors advanced the view that for soil animals the occupation of habitats is, to a large extent, defined by marked vertical gradients in the environmental conditions and substrate availability in mor- and moder-type humus forms. Such gradients may as well give rise to a functional niche differentiation of plant species (Parrish and Bazzazz, 1976; Van den Bergh and Braakhekke, 1978), similar to niche formation in a lateral sense under tree canopies consisting of different species (Lohdi and Johnson, 1989). Differences in resource availability may be partly caused by inhibitive organic compounds in the profile (Rice, 1974). Therefore, the vertical differentiation of the ectorganic profile may be pivotal for succession of undergrowth vegetation in the pine forests studied.

From studies by, for example, Hackett (1964, 1965), Heil (1984), Hester *et al* (1991a, b), Kuiters (1987b) and Kuiters *et al* (1987), growth, germination and competitive vigour of various undergrowth species under specific experimental conditions have been established. Studies concerning the effects of nutrient availability and allelo-

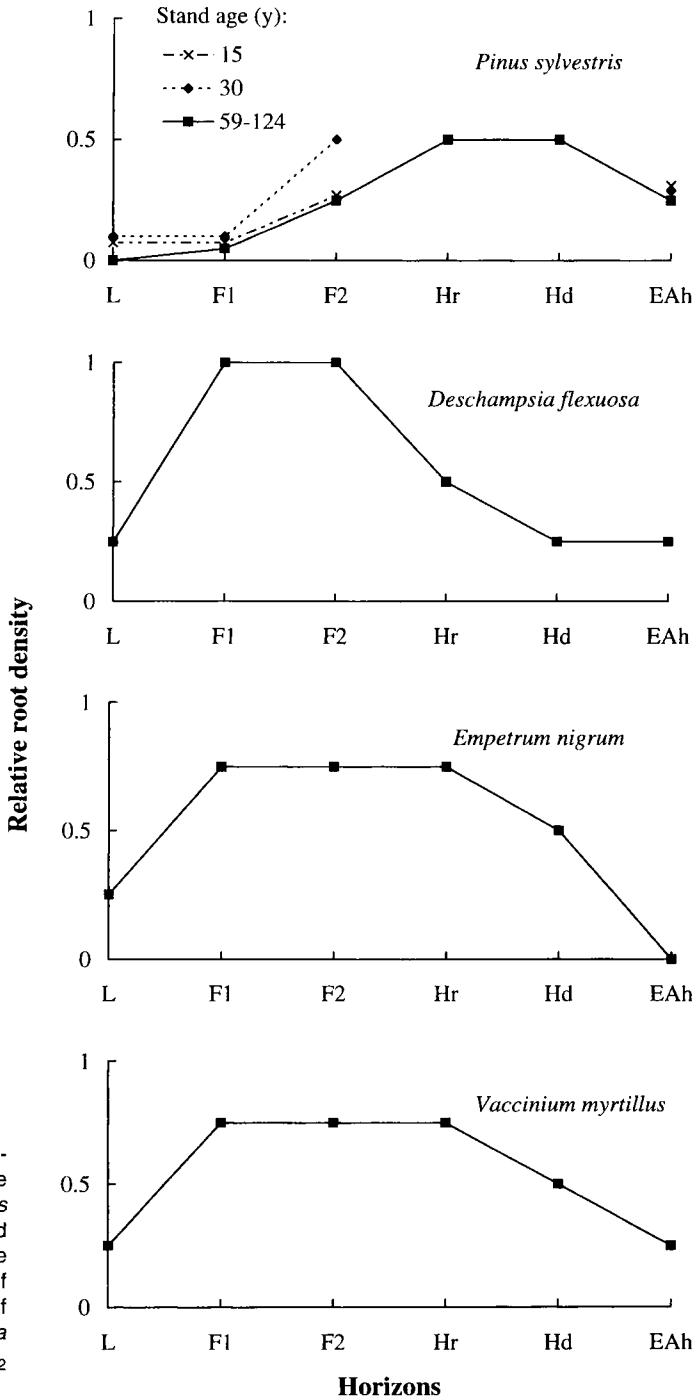

Fig 3. Relative root densities of 4 species in the organic horizons in *Pinus sylvestris* stands on sand dunes. The densities are expressed as fractions of the maximum density of *Deschampsia flexuosa* roots observed in F_1 and F_2 horizons (n = 20–25).

chemicals on species competition involve pot experiments or, in general, consider the soil as 1 compartment. In these experiments, the importance of the vertical distribution of allelochemicals and plant available nutrients in the major rooting environment remain unknown.

Upon decomposition, needle litter releases phenolic acids much slower than most leaf litters, resulting in higher concentrations in the organic layers under coniferous forests (Evans, 1980; Kuiters and Denneman, 1987). During long-term decomposition experiments, extractable phenolic acids were found to steadily decrease after a large initial decline (Hayes, 1965; Berg *et al,* 1982; Kuiters, 1987a). As a result, the H horizon produces much lower amounts of these acids than the overlying horizons, evidently giving rise to vertical gradients, such as found for bioelements. Tam *et al* (1991) and Van Praag *et al* (1991) reported a strong downward decline of water-soluble phenolic acids in the ectorganic profile under pine and spruce, respectively.

D flexuosa is noted for its high competitive vigour. Jarvis (1964) related this vigour to its strong competition for elements and to the inhibitive action of its humus and root exudates on the growth of other plants. Hester *et al* (1991b) showed that under various shading conditions, the competitive vigour of *D flexuosa* exceeds that of *V myrtillus*. This finding agreed with the observation that *D flexuosa* outcompetes *V myrtillus* during succession under birch on previous heather moorland. However, under the *P sylvestris* forests in the central Netherlands in later stages of succession, a consistent process of *D flexuosa* replacement by dwarf shrubs has been observed. With the results of the experiments by Hester probably still valid, the vertical differentiation in nutrient availability and concentrations of allelochemicals observed in this study might explain the observed succession. This will be elucidated later.

Dominance of Deschampsia flexuosa

In the early stages of succession, the ectorganic profile consists of relatively large amounts of fresh and slightly decomposed needle litter, with relatively high concentrations of allelochemicals. Pine-induced allelopathy (Lohdi and Killingbeck, 1982) seems to affect germination of *D flexuosa* less than dicotyledonous species (Kuiters *et al,* 1986; Kuiters, 1987b). The former establishes probably due to large numbers of seeds in seed rain (Hester *et al,* 1991c). For its growth, *D flexuosa* can take advantage of the high mineralisation rates of major cations in the L and upper F horizons. Moreover, in this part of the ectorganic profile, the pH (Hackett, 1964, 1965) and the K/Ca ratio in the soil solution are favourable to growth of *D flexuosa*. Given the fact that *D flexuosa* mainly roots in the F_1 and F_2 horizons, table I suggests that the establishment of this species causes an increase of water-soluble phenol concentrations in these horizons. Jarvis (1964) observed that *D flexuosa* roots produce inhibiting substances in such amounts that they are detrimental to birch growth. These compounds were, however, not identified. The lower concentrations in stands 95 and 124 may relate to the declining vitality, and therefore lower organic matter production of *D flexuosa* in these stands.

Replacement by dwarf shrubs

About 40 to 60 years are required for H horizons to play a role as rooting environment (fig 1). The H horizon is a compartment that meets the germination requirements of dwarf shrubs (*ie* relatively low concentrations of allelochemicals and little competition for nutrients by *D flexuosa*). The theoretical considerations of Berendse (1979), concerning competition between plants with different rooting depths, may very well apply to

the undergrowth vegetation in the pine forests. This theory predicts that the development of an H horizon under the major rooting compartment of *D flexuosa* increases the competitive ability of deeper rooting species, such as the dwarf shrubs.

Once established, *V myrtillus* can propagate itself through rhizomes in the H horizon. Flower-Ellis (1971) measured annual growth rates of 7 cm. *E nigrum* increases its cover by migrating over the grass carpet and overshading it. In this sense, the competition between *E nigrum* and *D flexuosa* seems similar to that between *Calluna vulgaris* (L) Hull and *D flexuosa* in dry heathlands. From an extensive study by Heil and Bobbink (1993), it was concluded that, although perennial grasses are found to be able to replace dwarf shrubs at high levels of available N, closed canopies of *C vulgaris* will prevent this species from being crowded out by *D flexuosa*, even at extreme N deposition rates of 75 kg ha^{-1} y^{-1}.

The development of a well-stratified ectorganic profile, which implies a marked continuous change in the rooting environment, provides *E nigrum* and *V myrtillus* the opportunity to compete against *D flexuosa*, and succession in these pine forests will continue to proceed in their advantage. Elevated N depositions of about 20 kg ha^{-1} y^{-1} at the research site may, however, increase the time period of *D flexuosa* dominance. Whereas Berendse (1990) suggested that a positive effect of N deposition on organic matter accumulation rate would explain the expansion of perennial grasses in heathlands, organic matter accumulation in the pine forest thus seems to have the opposite effect.

The decreasing vitality of *D flexuosa* in the oldest stands is of special interest in view of the changing composition of the undergrowth vegetation and the prospect for forest managers, facing a prolific growth of this grass in younger pine stands in the Netherlands. As *D flexuosa* forms a dense root mat in the F horizon, intraspecific competition may play an important role in the decrease of its vitality, under circumstances where input of bioelements through litterfall decreases as the stand ages (Cole and Rapp, 1981). Furthermore, interspecific competition with forest mosses is likely to increase considerably, as the latter become a co-dominant species in the ground layer, sharing their habitat with *D flexuosa*.

Complex interactions of ecological factors during succession make it difficult to produce conclusive scientific proof, probably even when experimental data are available. Furthermore, implications of soil physical changes due to a gradual development from LF to LFH profiles were not considered in this study. Nonetheless, the successional processes apparent from the inventory of the undergrowth vegetation are likely to evolve from a tight soil–vegetation interaction. Although mainly based on circumstantial evidence, the study of reciprocal soil–vegetation relations in the Hulshorsterzand area has provided a strong indication for facilitative succession. Aspects of inhibition, due to *D flexuosa* dominance during a prolonged phase in the succession, indicate that both facilitation and inhibition may act at the same time, which has also been recognised by Finegan (1984).

Facilitation due to the development of the ectorganic profile in the pine forests also seems to relate to the presumed development towards a *Betulo-Quercetum roboris* or *Fago-Quercetum* in the area (Fanta, 1986). In places along roads in the pine forests, where animal browsing is likely to be much less intensive, oaks, birches and beeches dominate the understorey tree layer. Rode *et al* (1993) suggested that the accumulation of plant available nutrients in the ectorganic profile in pine forests (intermediate successional stage after *Calluna* heather), would explain the development of oak-beech forests. In this primary Scots pine succession, the broad-leaved species induce a mor

to moder transformation of the humus form (Emmer, 1994). A more detailed study of this soil development is needed to determine as to how this may affect the succession of the undergrowth vegetation.

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