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Temporal and vertical changes in the humus form profile during a primary succession of *Pinus sylvestris*

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Abstract

The development of the humus form profile during a primary succession of *Pinus sylvestris* has been studied along chronosequences on dunes and in blow-outs. Attention was given to vertical variation within the humus form and how this changes during profile development. The mor-type ectorganic profile features marked vertical gradients of several soil attributes, while its constituting horizons show no or only small changes of chemical properties during succession. These changes in particular involve increasing calcium and nitrogen concentrations in the organic matter. After an initial high rate of organic matter accumulation in the successive organic horizons, these rates are strongly reduced, suggesting the attainment of a dynamic equilibrium within the time span of the chronosequences on dunes and blow-outs. Blow-outs differ from dunes in the sense that they have a lower amount of organic matter and a higher F/H ratio. This different ratio likely relates to microclimatic conditions less conducive to decomposition.

An attempt is made to explain the vertical trends in terms of processes affecting the characteristics of the organic horizons. Main conclusions are that the development of the ectorganic profile results from a combined effect of decay dynamics, rhizosphere processes and atmospheric deposition, which cannot be unentangled quantitatively with the data available. Furthermore, the distinction between F and H horizons has morphological rather than chemical or ecological relevance, as major vertical changes occur within the F horizon.

Introduction

For many decades vegetation succession received the attention of ecologists and soil scientists, in particular of those who were interested in relationships between vegetation and soil. Emphasis was often given to soil properties that would change over short time spans of less than decades and that would reflect the conditions under which the vegetation developed. Such properties are strongly related to organic matter dynamics and thus to the humus form. Although humus forms adapt quickly to changes in vegetation composition or other external factors, the study of soil-vegetation relationships is often hindered by antecedent soil formation and complex vegetation history. Therefore, primary successions offer the best opportunity to study such interactions. For the development and testing of conceptual models for succession related soil development over periods of several decades, an appropriate tool is the study of chronosequences (Bormann and Sidle, 1990).

Relevant studies are largely confined to freely drained soils in Holocene deglaciated areas (Bormann and Sidle, 1990; Chandler, 1942; Stork, 1963), in recent aeolian deposits (James and Wharfe, 1987; Olson, 1958; Syers et al., 1970; Walker et al., 1981; Wardenaar and Sevink, 1992; Wilson, 1960), or in volcanic deposits (Matson, 1990). Still there is little knowledge about vertical variability of ectorganic profile characteristics and how this may change during succession.

The objective of this study is to describe organic matter accumulation and horizon differentiation during primary succession of *Pinus sylvestris* on inland sand dunes. The soil development on dunes is compared with sites of lower quality and with lower tree density to assess whether the development on the dunes was site and structure specific. Finally, an attempt is made to explain the vertical and temporal trends in terms of processes controlling the soil characteristics described.

Methods

General information on the chronosequences

In The Netherlands large inland drift sand areas have developed, which may date back to the Middle Ages (Koster, 1978). From the first half of the 19th century on, many of these areas were gradually stabilised through the natural colonisation or plantation of *Pinus sylvestris* L.

The forests studied are situated on recent inland dunes and in blow-outs in the Hulshorsterzand area in the Veluwe (5°44'E, 52°20'N, 10–15 m above sea level). The mosaics of primary Scots pine stands of different age and on different sites (e.g. dunes and blow-outs) largely meet the prerequisites for chronosequence studies, viz. similarity of species composition, history, forest management, parent material, relief forms and micro climate. In this area, forest management has been very restricted and well documented. On the dune sites, most of the stands have been planted or sown, while in the blow-outs mainly naturally colonised forests are found.

In the Hulshorsterzand area, vegetation and its succession on various sites, including relatively wet areas, have been described by Fanta (1986) and Prach (1989). The following concise description applies to the succession on dunes and in blow-outs, where soils are freely drained. The initial tree-less stages are dominated by grasses (*Corynephorus canescens* (L.) Beauv. and *Festuca ovina* L.) and moss (*Polytrichum piliferum* Hedw.). In young Scots pine stands (less than about 20 years old) undergrowth vegetation is almost absent (*Cladonio-Pinetum*, Van der Werf, 1988). Later on, in 40-50 years old stands, *Deschampsia flexuosa* (L.) Trin. appears and soon becomes dominant in the herb layer (*Leucobryo-Pinetum* s.a. *Deschampsietosum*, Van der Werf, 1988). In the following stages of succession *D. flexuosa* slowly declines (cover percentage as well as flowering intensity) and mosses, such as *Pleurozium schreberi* Hedw., *Hypnum cupressiforme* Hedw., *Dicranum scoparium* Hedw. and *Dicranum polysetum* Hedw., become more prominent. In stands of an age of about 120 years or older, the undergrowth vegetation has a much more varied composition, with a co-dominance of dwarf shrubs (in particular *Empetrum nigrum* L. and *Vaccinium myrtillus* L.), *D. flexuosa* and forest mosses (this is the *Empetro-Pinetum*, Van der Werf, 1988). In the latter stands, in places *Betula verrucosa* L., *Quercus robur* L. and *Fagus sylvatica* L. have established, indicating a possible development towards a regional climax vegetation. This development is however impeded mainly by roe deer browsing and possibly also by frost damage of *F. sylvatica* (De Blois et al., 1991).

Climate in the Hulshorsterzand area 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. Mean annual atmospheric depositions in the open field (wet and dry), for the period 1978–87, were 20 kg ha^{-1} nitrogen, 4 kg ha^{-1} calcium, 1.9 kg ha^{-1} magnesium, 1.4 kg ha^{-1} potassium, 16.1 kg ha^{-1} sodium, 16 kg ha^{-1} sulphur and 0.1 kg ha^{-1} phosphorus (RIVM/KNMI, 1988).

The highly quartzitic sands are well sorted, with a median of about 175 μm, and are excessively drained, ground water being usually present at a depth of more than 10 m. Accessory minerals are dominantly feldspars (13–16%), with less than 1% heavy minerals (Koster, 1978). The sands are yellowish coloured due to the presence of sesquioxide coatings. Few darker coloured materials also exist, mainly as thin layers, as a result of syn-sedimentation of sand and organic matter or possibly as a result of short periods of stability and the formation of algal mats during dune development.

The dune sands are low in organic matter and soils (Haplic/Cambic Arenosols, according to FAO/Unesco, 1988) exhibit the development of a mor-type humus form (Klinka et al., 1981), featuring a strong acidification and pronounced horizon differentiation. In the upper part of the mineral soil a micro-podzol develops and organic matter accumulation is restricted to the EAh horizon and to a lesser extent to the initial Bhs horizon. In the blow-outs the sands and gravels are also highly quartzitic and exhibit similar pedogenic features, but they practically lack organic matter and are mineralogically much more heterogeneous than the dune sands.

Plot selection

The first inventory studies on initial soil formation on dune sites in the Hulshorsterzand area have been carried out by Van Berghem et al. (1986). They selected five stands to which they assigned ages between 15 and 130 years. The design of the study was to compare stands with known and similar origin, thus giving priority to planted or sown stands. Yet, given the lack of plantations originating from the last decades, the youngest two (15 and 30 years old) were stands which had established naturally.

In the present study these stands have been sampled again. The ages of the stands, as determined using wood cores of selected trees, were 15, 30, 59, 95 and 124 years. The dunes supporting the stands consist of drift sands, overlying podzol profiles which have developed in aeolian cover sands. The thickness of the drift sand layer is on average about 2 m. It has been observed that for their rooting the pines make use of the entire drift sand layer and also of the underlying podzol (Schelling, 1955). The stands have been gradually thinned to about 650 trees ha^{-1} during the first four decades.

For comparison with the dune sites, soils were studied in a blow-out along a transect (blow-out 1), representing a sere from bare sand to a mature pine forest about 80 years old. Another blow-out (blow-out 2) was selected with trees of an age of 105 years on average. This stand represents the extension in time of the sequence observed along the transect in blow-out 1. Furthermore, an isolated blow-out (blow-out 3) was selected supporting a naturally colonised Scots pine stand of about 80 years old trees, neighbouring a planted stand which was 65 years old (about 650 trees ha^{-1}). Naturally colonised stands in the blow-outs have about 200 trees ha^{-1}.

The stands studied cover a surface of at least 1 ha, except for the 15 years old dune stand, which is about half this size.

Soil sampling and analyses

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 all the other stands, except blow-out 1, 20 profiles were sampled along a nested triangular grid, with minimum distances of 2.3 m between two neighbouring points and maximum distances of 63 m. In blow-out 1, 50 profiles were sampled evenly spaced along an almost straight line of 1000 m. For these samplings a 25 × 25 cm metal frame was used. Mineral horizons were sampled to a depth of 40 cm using a soil monolith sampler (surface 47 cm^2; Wardenaar, 1987). Deeper samples were collected using a core auger.

In the dune sites the ectorganic profile was subdivided into L, F_1, F_2, Hr and Hd horizons (definitions according to Klinka et al., 1981). The F and H subhorizons conform approximately to Fr, Fm, Hr and Hf horizons (Babel, 1971) and to Oei, Oe, Oea and Oa horizons (Soil Survey Staff, 1981). In the blow-outs, L, F and H horizons were distinguished without further subdivision.

The time periods required for the F_2, Hr and Hd horizons to become visible in the profile have been obtained by inventarizing occurrences of horizons in various stands and under trees of known age in the study area. The first appearance of the F_1 horizon has been inferred from litterbag experiments with pine needles (Tietema, pers. comm. and unpublished results).

After air-drying and weighing, of subsamples of the L horizons, litter materials of various origin (needles, bark, grass etc.) were separated by sieving and hand picking, and subsequently bulked per type. Element concentrations (see below) in L horizons were calculated as products of element concentrations of constituting materials and their dry weight per sample. Samples of F and H horizons were processed without separation of litters of different origin. "Living" roots and coarse bark and woody materials (> 0.5 cm) were removed from the air-dry samples before analysis and weighed separately. Dry weights were determined after drying for two days at 70°C. Since the samples are contaminated with wind-blown sand and silt particles, it is better to express the organic matter content on an ash-free basis. Ash content of subsamples was determined after heating to 550°C for 16 hours. pH was measured potentiometrically in suspensions of soil material in distilled water and 1 *M* KCl (1:10 and 1:2 weight/volume for organic and mineral samples, respectively). Bulk densities of the organic horizons were estimated using bulk weights and sample volumes. Sample volumes were obtained by multiplying the surface of the sample frame by the mean of the thicknesses measured at the four sides of the sample frame.

Organic subsamples of all plots except blow-out 2 were digested with a mixture of concentrated HNO_3 and H_2O_2 and analysed for base elements and phosphorus in the labile pool (organically bound, adsorbed and water soluble). Evidently, the question whether this digestion is indeed specific to the organic material or causes some release of elements from the mineral admixtures, is important. Experiments, which were carried out to substantiate the validity of the procedure, have revealed that the digestion procedure systematically overestimated the labile element pool, depending on the ash content of the sample. By using a simple correction model, better estimations of the labile pool were obtained (Emmer and Verstraten, 1993).

The organic samples were analysed for total nitrogen by means of a salicylic acid-thiosulphate modification of the regular Kjehldahl procedure (Bremner and Mulvaney, 1982).

Water soluble elements were determined for subsamples taken at blow-out 3 (L bulked subsamples), and for bulked subsamples of dune site 124. They were determined in 1:5 (weight/volume) extracts, prepared by shaking suspensions for 2 hours, centrifugation after 12 hours and filtration of the supernatant liquid over a 0.45 μm filter.

Phosphorus in the HNO_3-H_2O_2 extracts was analysed colorimetrically using the molybdate blue method (Murphy and Riley, 1962). Other elements and phosphate in the water extracts were analysed using a continuous flow auto-analyser and flame atomic absorption/emission spectrophotometry.

Results

Ectorganic profile

The principal humus forms under the pine stands are xeromors under young pines (less than about 30-40 years old) and hemihumimors in older stands (classified according to Klinka et al., 1981). The difference between these humus form groups mainly depends on the moisture regime, which is distinctly xeric in the former. The latter is relatively moist throughout the year.

The field survey and observations of visual changes during litterbag decomposition revealed that the times at which the successive horizons start to develop are approximately 1.5, 10, 30 and 50 years (intervals 1.5, 8.5, 20 and 20 years) for the F_1, F_2, Hr and Hd horizons, respectively. It should be noted that the increasing intervals relate to decreasing decay rates from L to Hd, but that the values evidently dependent on horizon definition. Assuming that the sequence of dune profiles in Figure 1 reflects an accumulation curve of organic matter, accumulation rates can be calculated for the intervals between the stand ages. The average annual net accumulation rate in the ectorganic profile is 0.11, 0.14, 0.14, 0.07 and 0.02 kg m^{-2} y^{-1} in intervals 0–15, 15–30, 30–59, 59–95 and 95–124 years, respectively. These rates correspond with an almost linear increase until about 100 years, after which organic matter accumulation decreases. Only the Hd horizons of stand 59 and the older stands are significantly different, $p < 0.001$ (ANOVA procedure, SAS Institute Inc., 1988). This suggests that on dunes steady state is reached at about 100 years of forest succession. Thicknesses of the organic horizons follow the same trend along the sequence as for the organic matter stocks. In stand 124 the mean thickness of the F_1, F_2, Hr and Hd horizons is 3.8, 5.0, 2.2 and 2.9 cm, respectively, totaling 13.9 cm. Coefficients of variation are between 32 and 43%. The thickness of the L horizon is a few centimetres but is very difficult to measure accurately.

Figure 1 also presents the accumulated ectorganic matter in blow-outs 2 and 3. In the colonised stands there is no increase between 80 and 105 years (average tree ages). The ectorganic matter accumulation along the transect in blow-out 1, as presented in Figure 2, reaches a value of 7.5 kg m^{-2} (2.5 kg m^{-2} for the H horizon) on average in the final 26 m of the transect, where tree ages are around 80 years. This agrees with the values found for the other blow-outs. Figure 2 indicates that in the blow-outs the H horizon becomes visible after about 40 years of pine forest succession. Ectorganic matter accumulation is lower in the blow-outs than on the dunes, while the ratio between the amount of organic matter in the F and the H horizons in the blow-outs is higher.

There is a general resemblance among the dune stands regarding the element concentrations of the organic horizons (Table 1). Nonetheless, calcium shows a significant increase from stand 59 to 124 in the L ($p < 0.01$) and F_1 horizon ($p < 0.001$), and in the F_2 ($p < 0.003$). Nitrogen shows an increase in the L and F horizons along the dune sequence (significant at $p < 0.05$ in the L horizon between stands 59 and 124). It should be noted that values for the L horizon were obtained artificially, as explained in the section on methods. Table 1 shows that potassium concentrations in L horizons in stands 59 and older are distinctly higher than in stand 15 and 30. Moreover, calcium concentrations in L and F_1 horizons seem to decrease between stand 30 and stand 59. These changes after 30 years of succession coincide with the appearance and subsequent dominance of *D. flexuosa*. Its litter contains much more potassium and less calcium than pine

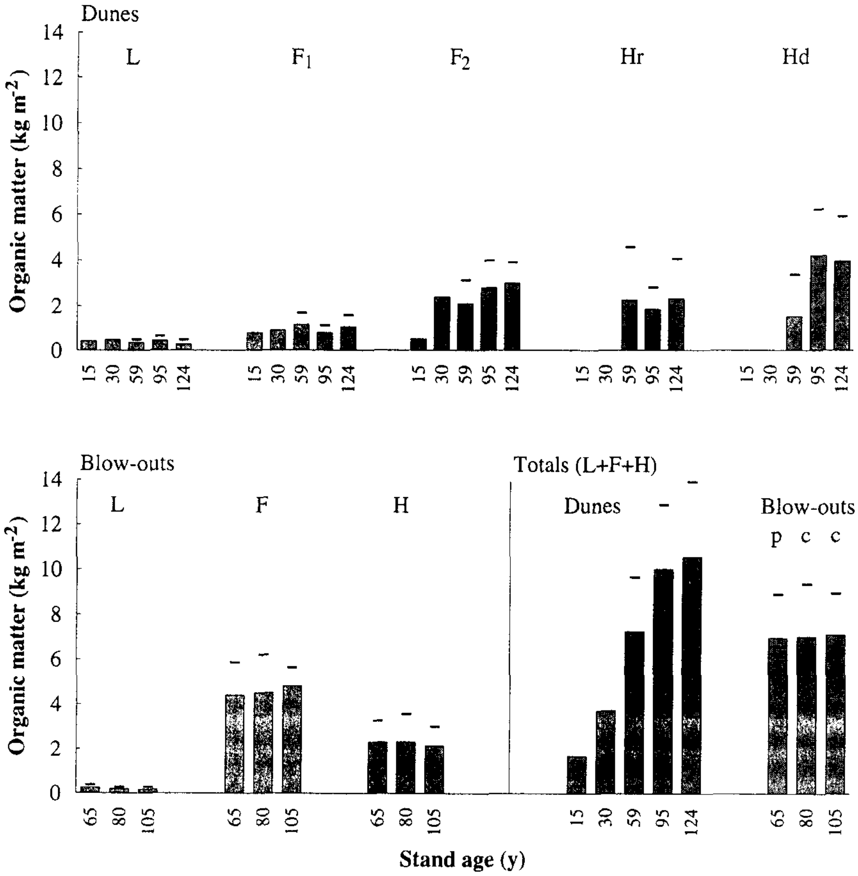

Fig. 1. Amount of ash-free organic matter in organic horizons under *Pinus sylvestris* stands on sand dunes and in blow-outs, related to stand age. If applicable, standard deviations of total organic matter are indicated by horizontal bars (n = 18–20, except Hd of stand 59: n = 10). Planted and naturally colonised stands in the blow-outs are indicated by "p" and "c", respectively.

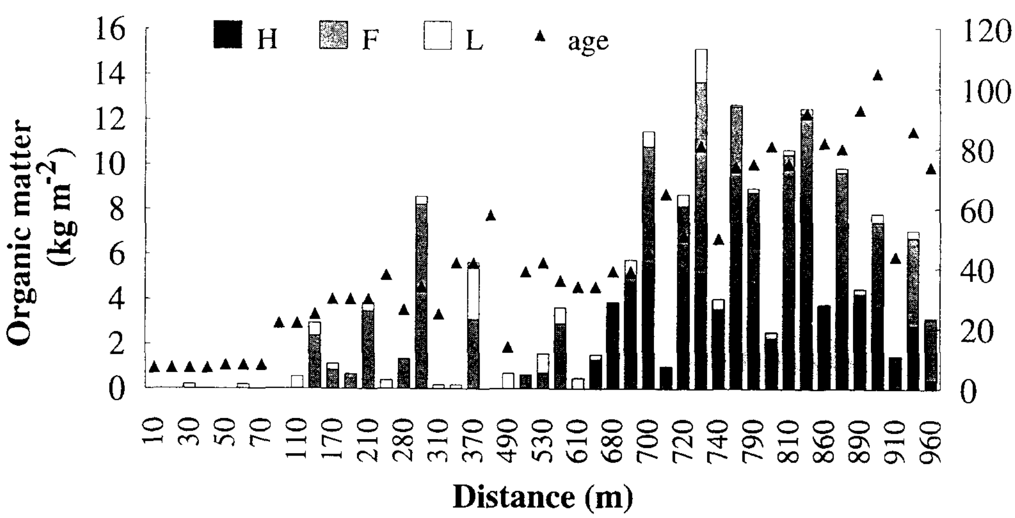

Fig. 2. Age of the pine nearest to the sample point and amount of ash-free organic matter in organic horizons along the transect in blow-out 1, representing a primary successional sere of *Pinus sylvestris*.

Table 1. Elemental composition of organic horizons under *Pinus sylvestris* stands of different age on sand dunes and in blow-outs. Concentrations are on an ash-free basis and corrected for the effect of mineral contaminations; coefficients of variation are between brackets

Horizon	Na	K	Ca	Mg	P	N[c]
	----------	----------	---------- g kg^{-1}	----------	----------	----------
Dunes						
Stand 15[a]						
L	0.35	1.70	2.50	0.69	0.70	7.6
F_1	0.36	0.81	1.97	0.60	0.80	10.0
F_2	0.44	0.50	1.40	0.41	0.58	10.1
Stand 30[a]						
L	0.39	1.65	2.65	0.70	0.67	7.5
F_1	0.32	0.89	2.10	0.53	0.82	11.3
F_2	0.40	0.46	1.63	0.44	0.60	10.8
Stand 59						
L[b]	0.22 (18)	2.39 (46)	2.13 (20)	0.72 (21)	0.59 (25)	7.6 (12)
F_1	0.27 (32)	0.92 (28)	1.97 (18)	0.60 (16)	0.86 (12)	11.5 (10)
F_2	0.40 (48)	0.52 (43)	1.33 (22)	0.46 (33)	0.63 (11)	11.8 (9)
Hr	0.40 (20)	0.35 (16)	1.27 (24)	0.43 (19)	0.36 (42)	9.8 (11)
Hd[d]	0.41 (16)	0.37 (17)	1.14 (30)	0.42 (22)	0.41 (36)	8.9 (23)
Stand 95						
L[b]	0.24 (15)	2.25 (49)	2.26 (20)	0.67 (19)	0.47 (23)	8.1 (13)
F_1	0.22 (31)	0.95 (23)	2.29 (11)	0.64 (14)	0.75 (11)	11.6 (9)
F_2	0.38 (23)	0.51 (25)	1.70 (28)	0.47 (16)	0.65 (18)	11.4 (9)
Hr	0.35 (18)	0.36 (15)	1.61 (18)	0.44 (12)	0.37 (35)	9.9 (8)
Hd	0.40 (17)	0.32 (39)	1.72 (25)	0.45 (17)	0.54 (15)	10.7 (11)
Stand 124						
L[b]	0.22 (20)	2.37 (35)	2.48 (23)	0.86 (18)	0.69 (25)	9.6 (10)
F_1	0.31 (23)	1.07 (41)	2.69 (19)	0.67 (18)	0.83 (14)	12.1 (5)
F_2	0.32 (24)	0.44 (16)	1.73 (19)	0.39 (13)	0.66 (15)	12.5 (4)
Hr	0.36 (19)	0.34 (15)	1.70 (24)	0.41 (14)	0.59 (10)	10.7 (8)
Hd	0.36 (22)	0.35 (15)	1.61 (24)	0.40 (16)	0.60 (19)	10.0 (18)
Blow-out 3						
Colonised						
L[b]	0.30 (21)	2.07 (40)	2.30 (25)	0.70 (17)	0.55 (25)	8.6 (13)
F	0.29 (22)	0.65 (28)	1.64 (11)	0.48 (9)	0.57 (18)	12.1 (6)
H	0.18 (37)	0.52 (41)	1.24 (22)	0.47 (30)	0.54 (37)	10.2 (15)
Planted						
L[b]	0.35 (16)	2.03 (39)	2.40 (22)	0.65 (19)	0.54 (28)	8.9 (14)
F	0.31 (21)	0.70 (14)	1.73 (21)	0.48 (13)	0.59 (14)	11.5 (4)
H	0.31 (40)	0.56 (35)	1.44 (31)	0.50 (21)	0.56 (42)	9.7 (19)

[a] bulked samples.
[b] artificial values (see Methods), means and coefficients of variation are controlled by the relative contribution of litter of different origin.
[c] n = 10–15.
[d] n = 10.

Table 2. Elemental composition of pine and grass litter in dune sites (materials pooled per type and per plot), related to stand age

Stand age	Na	K	Ca	Mg	P	N
			$g\ kg^{-1}$			
Pine litter						
Needles						
59	0.34	1.66	2.61	0.71	0.72	7.8
95	0.44	1.61	3.02	0.71	0.60	8.4
124	0.39	2.23	3.69	0.79	0.83	9.0
Twigs						
59	0.13	0.84	2.10	0.53	0.36	3.1
95	0.13	0.56	2.08	0.48	0.28	3.1
124	0.13	1.06	4.09	0.76	0.48	3.4
Grass litter						
59	0.25	8.18	1.34	1.21	0.97	8.7
95	0.16	6.17	1.38	1.08	0.71	9.1
124	0.18	6.79	1.54	1.21	1.02	9.3

Table 3. pH-KCl of organic horizons under *Pinus sylvestris* stands on sand dunes (related to stand age) and in blow-outs. Coefficients of variation are between brackets

Horizon *Dunes*	15y	30y	59y	95y	124y
L[a]	3.74	3.68	nd	nd	nd
F_1	3.43	3.49	3.22 (7)	3.51 (6)	3.56 (8)
F_2	2.94	2.79	2.64 (4)	2.69 (4)	2.73 (4)
Hr			2.49 (3)	2.50 (4)	2.49 (2)
Hd			2.53 (3)	2.50 (5)	2.51 (4)
Blow-outs			65y p	80y c	105y c
L[a]			nd	nd	3.60
F			2.95 (3)	2.95 (5)	2.91 (5)
H			2.70 (5)	2.71 (4)	2.77 (4)

[a] bulked samples.
[b] planted.
[c] naturally colonised.

litter (Table 2), rendering potassium concentrations in the L horizon higher and calcium concentrations lower. Table 2 also indicates that calcium and nitrogen concentrations in pine litter increase with increasing stand age. For the other elements such trends seem to be absent. pH-KCl values (Table 3) in the F_1 and F_2 horizons increase significantly from stand 59 to stand 124 ($p < 0.05$), while in the Hr and Hd horizons differences among the oldest three stands are not significant (at $p < 0.05$). The relatively high value of 2.94 for the F_1 in stand 15 is probably caused by a lower organic matter content of the samples due to a high content of mineral particles.

When weighted averages of the F_1 and F_2, and the Hr and Hd horizons of the dune sites are compared with the F and H horizons of the blow-outs, it appears that calcium and phosphorus concentrations in both layers are lower and pH-KCl in the H is higher in the latter, while for the other elements no differences were found.

Within the ectorganic profiles there is a pronounced vertical trend, particularly in the case of calcium and potassium. Potassium, calcium and magnesium concentrations of the F_2, Hr and Hd are not significantly different in dune stands 59, 95 and 124, while differences between L, F_1 and F_2 are significant (Tukey's studentised range test in GLM procedure of SAS; $p = 0.05$). Data on water soluble elements (Table 4) also show a strong decrease from L to H horizons. Alternatively, nitrogen and phosphorus concentrations increase from L to F horizons, and decrease from F to H horizons. Differences between L and F, and between F_2 and Hr are significant (Tukey's test; $p = 0.05$). pH-KCl decreases significantly from F_1 (probably from L) to Hr, while the Hr and Hd horizons are not significantly different (Tukey's test, $p = 0.05$).

In the blow-outs the vertical trends within the F horizon are obliterated due to the combined sampling of the F_1 and the F_2 horizons. General trends resemble those found for the dune sites.

Correlations among neighbouring horizons are presented in Table 5. The pH-KCl values are significantly correlated throughout the profile. Correlations of sodium, potassium, magnesium and phosphorus concentrations between F_1 and F_2 are negative, but not significant. Below the F_1, correlations of sodium, calcium, magnesium and phosphorus between neighbouring horizons increase with depth, eventually attaining statistical significance. This trend is most consistent for calcium, including the F_1 horizon, and less prominent for potassium. Nitrogen concentrations of the F_1 and F_2 horizons appear to correlate significantly, while deeper in the profile correlations between horizons markedly decrease.

Bulk densities of the organic horizons have been estimated on an ash-free basis, as high ash contents can unduly influence the calculations. Figure 3 indicates that differences between the stands are small (except for the relatively high value for the F_2 horizon in stand 95), but that bulk densities markedly increase from the F_1 to the Hd horizon.

Table 4. pH, EC and water soluble element concentrations in organic matter of organic horizons under *Pinus sylvestris* on dunes (bulked samples) and in blow-outs (L: bulked samples; other samples: n = 20, all arithmetic means)

Horizon	pH	EC_{25} $\mu S\ cm^{-1}$	K^+	Na^+	Ca^{2+}	Mg^{2+}	PO_4^{3-}-P	NH_4^+-N
			mg kg^{-1}					
Dunes								
Stand 124[a]								
L	4.71	413	380	93	78	36	133	280
F_1	4.68	332	112	57	28	12	122	134
F_2	3.83	209	38	68	10	5	60	80
Hr	3.62	204	31	105	12	9	38	75
Hd	3.67	194	26	110	11	7	33	75
Blow-out 3								
Colonised								
L[a]	4.74	360	782	115	74	67	114	92
F	3.92(3)	173(15)	77(45)	70(21)	13(26)	8(22)	42(22)	48(35)
H	3.75(4)	146(30)	50(41)	86(22)	10(26)	6(40)	25(28)	28(42)
Planted								
L[a]	4.70	344	799	118	79	60	127	108
F	3.88(5)	164(25)	65(26)	74(21)	12(25)	8(28)	65(21)	57(19)
H	3.74(4)	146(24)	43(41)	87(35)	8(34)	5(37)	40(37)	35(46)

[a]bulked samples.

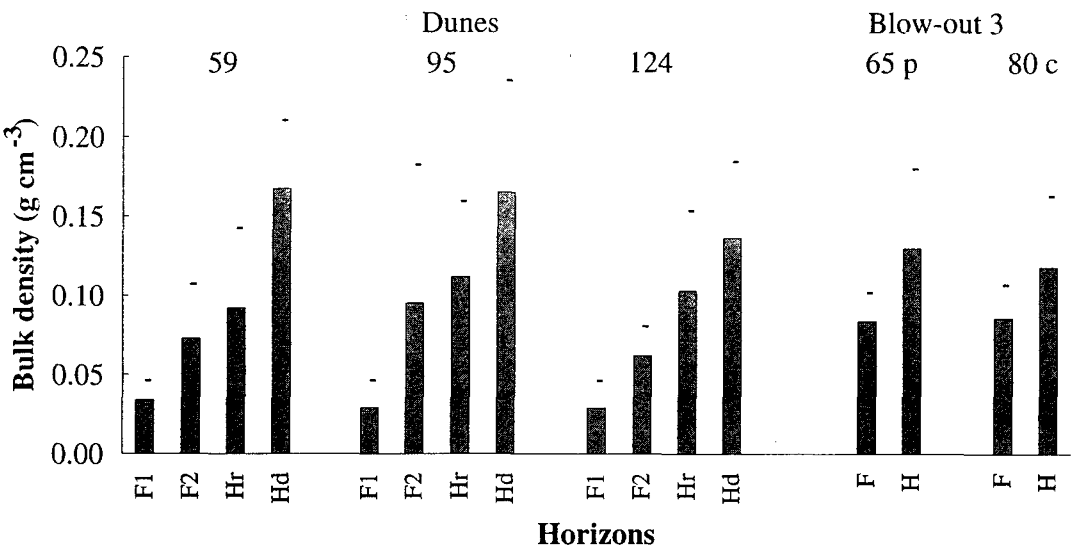

Fig. 3. Bulk densities of organic horizons under *Pinus sylvestris* stands on sandy dunes and in blow-outs. Standard deviations are indicated by horizontal bars (n = 18–20, except Hd of stand 59: n = 10). Planted and naturally colonised stands in the blow-outs are indicated by "p" and "c", respectively.

EAh horizons

The humus forms are of the mor-type, with generally razor-sharp boundaries between the organic layer and the mineral soil. Bioturbation therefore plays a minimal role in the genesis of these humus forms. In the chronosequences studied, soil development in the mineral soil is dominated by bleaching of the upper

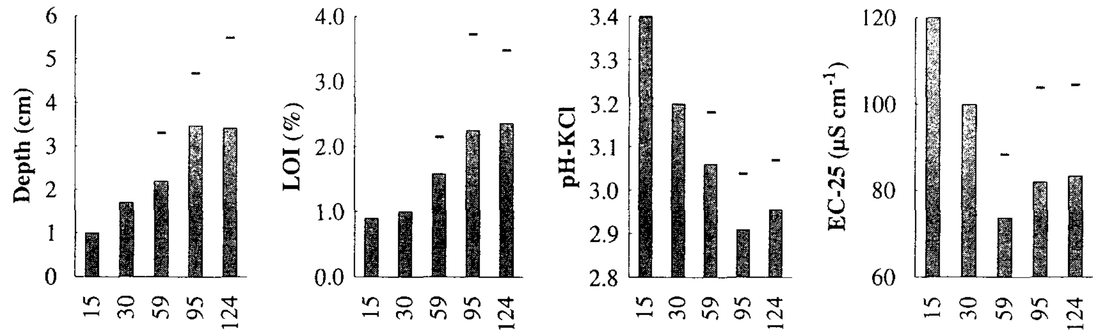

Fig. 4. Properties of the EAh horizons under *Pinus sylvestris* stands on sand dunes, related to stand age. Standard deviations are indicated by horizonal bars (n = 20).

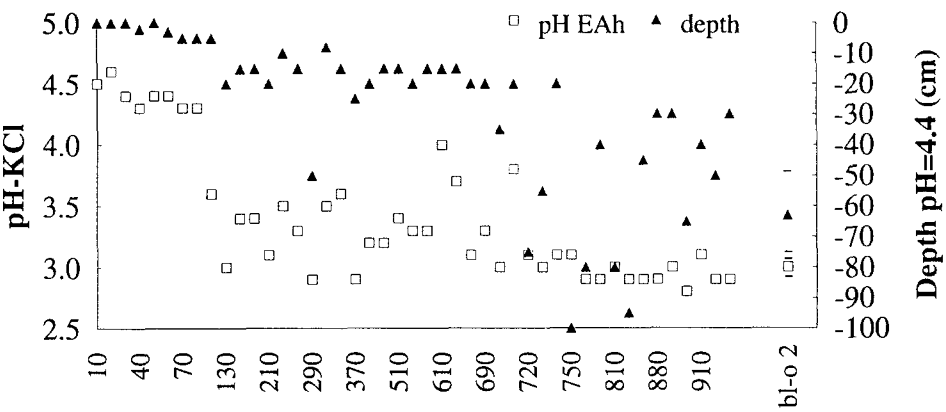

Fig. 5. pH-KCl of the EAh horizons and the depth at which a pH of 4.4 is attained along the transect in blow-outs 1 and 2. The values for blow-out 2 are averages (n = 20), standard deviations are indicated by horizontal bars.

centimetres and formation of an initial Bhs horizon. Some parameters characterising the development of the EAh horizon are presented in Figure 4. Parameters of soil formation, such as horizon depth, organic matter and pH show a marked change along the sequence, but these changes seem to slow down in the later stages, conformable to the development of the organic layer. The electrical conductivity in the water extracts increases after a first strong decline. This trend is probably caused by an initial high rooting activity in the upper part of the mineral soil, while the increase from stand 59 to 124 is due to the increase of soil organic matter.

Along the transect in blow-out 1, the pH-KCl of the EAh horizon shows a gradual decline (Fig. 5). The first 8 datapoints correspond with bare, nonvegetated surfaces and indicate initial pH values of about 4.4. Upon vegetation development the pH decreases about one unit and declines to about 2.9 under old trees, which is a similar trend as observed on the dunes. Another important feature is the depth at which the initial pH value is attained. This indicates the depth to which the parent material has been influenced by soil forming processes. In Figure 5 a gradual increase of this depth to about 50 cm can be observed, with a few extremes near 1 m. This trend is confirmed by the data of the dunes (not shown).

Discussion

Temporal variability

The initial accumulation rate is about the same as estimated for secondary successions of heathlands in The Netherlands (Berendse, 1990). For secondary succes-

Table 5. Pearson correlation coefficients between neighbouring horizons for various elements (labile, see Methods) and pH. Data of stands 59, 95 and 124 are combined, excluding Hd of stand 59

		F_2	Hr	Hd
F_1	pH	0.65***		
	Na	-0.24		
	K	-0.04		
	Ca	0.21		
	Mg	-0.23		
	P	-0.01		
	N	0.69**		
F_2	pH		0.37**	
	Na		0.37**	
	K		0.01	
	Ca		0.56***	
	Mg		0.20	
	P		0.21	
	N		0.29	
Hr	pH			0.60***
	Na			0.44**
	K			0.23
	Ca			0.75***
	Mg			0.42**
	P			0.39**
	N			-0.01

*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.

sions of Scots pine forests in The Netherlands, Van den Burg et al. (1988) found lower accumulation rates of 0.05 kg m^{-2} y^{-1} in the first 100 years. This can probably be attributed to removal of litter from the forests by man, which has been common practice in certain areas, and factors controlling net primary production, such as substrate differences with respect to nutrient availability and depth of the rooting zone. Accumulation rates in secondary successions declined between 70 and 100 years (Van den Burg et al., 1988), as found in this study.

The level at which the amount of organic matter in the dune sites stabilises cannot be established from the data presented, but Figure 1 indicates that after about a century organic matter accumulation decreases markedly, while the stocks in the various horizons are not significantly different between stands 95 and 124. The attainment of a dynamic equilibrium depends on organic matter input as well as its turnover. The literature provides extensive data on organic matter production in coniferous forests. Age related trends have been described for many coniferous species, including *P. sylvestris*, involving, however, secondary successions. Comparisons of primary and secondary successions are lacking. The general pattern apparent from the literature is: net primary production, which is strongly correlated with litterfall and nutrient uptake, shows an initial high rate, but decreases after about half a century (Rodin and Bazilevich, 1967). This chiefly explains the pattern of ectorganic matter build-up observed. The literature further indicates that with increasing stand age the ratio of calcium over potassium in the tree biomass increases (Cole and Rapp, 1981), resulting in an increased ratio in litterfall and in the organic layer. Increasing calcium concentrations are exemplified in Table 1.

Organic matter turnover depends on a quite complicated set of processes, which are to a large extent controlled by physical and chemical properties of the organic matter and physical properties of the ectorganic profile as a whole. Increasing ectorganic matter may produce conditions more conducive to decomposition, because of a higher average moisture level. Xeromors in the *Cladonio-Pinetum* are distinctly dry during large parts of the summer season. The hemihumimors occurring in later stages of succession have higher moisture levels throughout the year. Berg and Staaf (1980) found only small effects of stand age on mass loss in the initial phase of decay, i.e. approximately corresponding to L and F_1 horizons. But improved moisture conditions are likely to be found in the deeper organic horizons and should be evaluated making use of dynamic simulations.

In this study, there is a general similarity of the morphologically defined organic horizons in the various stands and sites regarding their chemical and physical properties, but there are some conspicuous differences. The increase in time of nitrogen concentrations in the organic horizons is about 25% (Table 1). The effect on turnover dynamics is difficult to quantify, but some inferences can be made from other studies. Berg et al. (1987) reported that pine needle litters with 100% higher initial nitrogen concentrations than other needles showed significant higher decay rates during the first year (approximately 10%), but had a similar accumulated mass loss after four years, while differences in nitrogen concentrations were maintained. Other authors (e.g. Fog, 1988) showed that on the long term decomposition may decrease due to higher nitrogen concentrations. Given the observed increase along the chronosequence, the above suggests that decomposition in the F horizons may increase in the order of a few percent, while effects on long term decomposition remain unknown. Increasing element and moisture levels are associated with higher decomposition rates (Swift et al., 1979), but this will probably have a much smaller effect on the levelling of the organic matter accumulation than has the temporal trend in litterfall.

Based on the data presented, blow-outs differ from dunes in the earlier attainment of steady state in organic matter amounts (presumably earlier than 80 years vs. later than 124 years), the lower amount of organic matter at steady state (7 vs. more than 10 kg m^{-2}), the higher ratio between organic matter in F and H (2.0 vs. 0.6), the later development of H horizon (after about 40 years vs. after about 30 years) and the lower concentrations in calcium and phosphorus in the F horizons. The lower amounts of organic matter in the blow-outs probably are due to much lower tree densities (about 200 trees ha^{-1}) in these sites, resulting in a lower net primary production and litterfall per unit area. De Blois et al. (1991) have studied the microclimatologic differences between open drift sand areas and pine forests on dunes and blow-outs in the Hulshorsterzand area. Their study shows that forest development induces less extreme surface and soil temperatures and higher soil moisture contents. It is observed that blow-out areas hold an intermediate position between open sands and dune sites. Therefore, the prevalence of F horizons and the relatively late development of an H horizon in blow-outs is probably caused by lower decomposition rates due to dryer conditions of the organic layer. In conclusion, the combined effect of forest density, site and way of establishment causes only slightly different characteristics of the humus forms and mainly affects the rate of soil development.

Vertical variability

The downward increasing degree of fragmentation in the mor profiles, indicated by a sequence of morphologically distinguishable organic horizons, suggests to reflect a decay continuum. This may particularly be the case in the primary mono-species pine stands studied, which lack antecedent soil formation and where bioturbation is minimal. There are several ways to reveal whether the vertical trends observed truly mimic a consistent ongoing process of decomposition, which will be discussed below.

i) A comparison can be made with decay experiments (e.g. litterbags), although it is hazardous to extrapolate such experiments over the time scale of decades to which humus form development relates. There are various litterbag studies involving Scots pine litter. Tietema (1993) showed that during incubation of Scots pine needles in the same area, the nitrogen immobilisation phase continued until 9 months, which probably explains the increase from L to F_1 in this study. The similar nitrogen concentrations in the F_1 and F_2 indicate a balanced release rate of nitrogen and carbon in the mineralisation phase. Berg and McClaugherty (1989) and Tietema (1993), based on 4 and 2 year litterbag studies, respectively, found a positive correlation between accumulated mass loss and nitrogen and phosphorus concentrations during decay of Scots pine needles. If the vertical trend in the ectorganic profile represents a time scale, the decrease of nitrogen and phosphorus concentrations from F to H seems to be in contradiction with their observations. Possible explanations for this unanticipated trend are: the difficulty to extrapolate the results of litterbag experiments over decades or to compare them with the elemental contents of L, F and H horizons, which was shown earlier by Lousier and Parkinson (1978), and/or the existence of other important sources of organic matter in deeper organic horizons. Concerning the latter, root dominated organic matter input in the H horizon has been suggested by Berg et al. (1982), and indeed pine roots are mainly found in the H horizons. It should be stressed that the vertical trends described apply to grass dominated parts of the forests as well as patches without any undergrowth, so that effects of herbs rooting in the F horizon can be considered modifying rather than decisive for the character of these trends. Pine roots and needles are found to have similar compositions and decay dynamics (Berg, 1984). Therefore, large inputs of pine root litter may induce lower nitrogen and phosphorus concentrations in the H horizons. This is supported by the fact that nitrogen concentrations decrease downwards to attain similar values as for the L horizon. A residual enrichment of bark and wood may partly explain low element concentrations in the H horizons as finer fragments of these materials could not be entirely excluded from the chemical analyses. However, we found no relationship between the contribution of coarse fragments to the bulk samples and element concentrations nor was there any visual observation of high concentrations of fine fragments of wood and bark simultaneously in Hr and Hd horizons.

Declining concentrations of other elements from L to H horizons can be explained by various processes, which will operate simultaneously in the mor profiles. Litterbag studies (e.g. Staaf and Berg, 1982) have shown that part of the potassium, calcium and magnesium is lost by leaching during the first few months of decay. In later stages the release of potassium is approximately proportional to overall mass loss, while calcium concentrations decrease. If these dynamics were to be the only ones determining the vertical trend in the mor layer, the element concentrations would decrease from L to F_1, potassium would remain constant in the deeper horizons, while calcium would decrease. For potassium this is not the case in reality, as concentrations decrease further from F_1 to F_2, which in terms of horizon genesis relates to a time scale of about a decade. Plichta and Kuczynska (1992) presented a valuable approach to the identification of so called disintegration fractions in various organic horizons. Their study suggested that upon fragmentation element concentration changed in accord with trends observed in litterbag studies. However, with increasing botanical diversity, fractions of the same size appeared to show increasingly different compositions between horizons. This supports the assumption of a strong influence of the provenance of litter on vertical trends in chemical properties of the organic matter, but this has to be confirmed in the present case.

Other factors which will induce lower element concentrations in deeper organic horizons include nutrient uptake by roots, and possibly the input of atmospheric protons, the influence of which increases according to the age of a horizon, thus increasing with depth. Exchange processes are likely to play an important role in the elemental status of the organic horizons, as the base elements are principally in the exchangeable form (Emmer and Verstraten, 1993), calcium exchangeability even exceeding 90% in the F and H horizons. Moreover, the contribution of atmospheric element deposition to the element balance of the mor profiles cannot be disregarded. Preliminary data of pine litterfall combined with litterfall figures for the undergrowth supplied by Moszynska (1991) show that litterfall/atmospheric deposition ratios are 82/20 (kg/kg per ha) for N, 20/4 for Ca, 4.4/1.9 for Mg, 16/1.4 for K, 1.2/16.1 for Na and 1.6/0.1 for P. Evidently, the contribution of atmospheric deposition to the element input is appreciable, but it is difficult to evaluate its effect on the vertical trends observed.

ii) A consistent vertical change of the solubility of elements (i.e. the extent to which elements can be extracted with water), expressed as the ratio soluble/total or percent contribution of soluble to total, is an indication for a continuous transformation of the structure of the organic matter. Tam et al. (1991) observed decreasing solubility of elements with depth in a mor layer under ponderosa pine and showed that this was related to an increasing degree of humification. When combining data in Tables 1 and 4, the solubility also decreases markedly with depth. For example, the solubility decreases from 3.1 and 15.9 (L) to 0.6 and 8.6 (F_2) percent for Ca and K, respectively. However, it remains approximately constant further downward. The latter absence of a trend in the F_2 to the Hd is therefore not in line with a distinct change in the visual appearance and presumed degree of humification.

iii) Significant correlations between adjacent horizons are a strong indication for processes acting vertically and thus controlling the vertical trends. Absence of such correlations does not necessarily imply that a vertical direction of processes must be excluded, but makes an interpretation much more difficult. The low correlations between the F_1 and F_2 horizons are not surprising since these horizons consist of relatively young materials of various origin (pines, herbs, mosses), causing a considerable chemical variation, depending on the relative contribution of the species to litter input. These contributions change over time due to seasonal and successional factors. Significant correlations among the Hr and Hd horizons are anticipated as these horizons have a relatively long joint history, under the influence of processes the intensity of which may vary from place to place. Such processes include vertical water and element transport under canopy drip points, preferential water flow paths, decomposition and deposition of woody materials and bark. High correlations between the H subhorizons cannot be explained by the origin of above ground litter, as this would also affect the F subhorizons. In contrast with the other elements, nitrogen shows a significant high correlation between the F_1 and F_2 horizons and low correlation between lower horizons. Nitrogen differs from other elements in its distribution over various pools as it is mainly in the organic bound form, while only a very small part is adsorbed or soluble as ammonium and nitrate. Although conjectural, the high correlation between F_1 and F_2 may be caused by a large contribution of atmospheric nitrogen to total nitrogen deposition (Tietema, 1993 and above) combined with a marked immobilisation phase. Considering the pH, horizons are significantly correlated throughout the ectorganic profile. Skyllberg (1990) also found significant correlations between 1 cm slices for pH in mor profiles under Norway spruce and he suggested that this could be explained by either a downward increasing concentration of organic acids, vertical differentiation in root uptake and mineral acid input affecting deeper organic horizons.

In conclusion, decay dynamics of litter introduced in the ectorganic profile only in part determine the element status of the organic horizons. In the profiles studied, although developed under conditions of restricted botanical heterogeneity and in a primary succession, the sequence of horizons broadly reflects a time scale but results from a combination of decay dynamics of above and below ground litters and exchange processes.

The possible effects of an increased atmospheric deposition of nitrogen and increased acidification in the past decades must not be disregarded in this study. Due to the uncertainties related to acidification of the soil and climatological fluctuations in the past century, there is no incontestable homology between the vegetation and soil development in a specific stand and the development observed along the chronosequence. A number of studies (Berg, 1986a; Berg et al., 1982, 1987) has provided data on effects of various compositions of atmospheric deposition on Scots pine litter decomposition and nutrient release. It was found that high levels of nitrogen caused a significant decrease in long term decomposition (in the order of 10% decrease). However, additions used for these experiments were several times higher than levels of atmospheric deposition in the Hulshorsterzand area in the past decades. Moreover, such heavy additions, for various reasons, are likely to have caused unrealistically low decomposition rates (c.f. Berg, 1986b). Therefore, it can be tentatively concluded that under the intrinsically acid circumstances in these ecosystems decomposition and related differentiation in the organic layer are unlikely to be strongly influenced. It cannot be established whether soil acidification significantly changes the vertical gradient of labile elements in the ectorganic profile due to differential desorption of cations. This should be evaluated making use of dynamic simulation which also consider element uptake and return to the soil by the vegetation.

Conclusions

- The succession of the vegetation is reflected in the development of the organic layer and the systematic build-up of organic matter in its constituting horizons. There is a strong indication that the various organic horizons attain a dynamic equilibrium in the amounts of organic matter within the time span of the chronosequence.
- There are no significant main effects of stand age on bulk density, potassium and magnesium concentration and pH of the organic horizons. Calcium concentrations in organic horizons slightly increase during succession, which corresponds with increasing calcium in the biomass reported in the literature. Nitrogen concentrations also increase, suggesting that ectorganic matter accumulation increases the pool of available nitrogen.
- In blow-outs, the amount of ectorganic matter is significantly lower than on dunes. The amount of organic matter in the F in proportion to the H horizon is higher in blow-outs than on dunes. These results suggest that in blow-outs organic matter input is lower and humification is slower than on dunes. The latter is related to differences in pedoclimate rather than chemical conditions.
- During the succession, the top soil shows marked increases in depth and organic matter content, and decreases in pH. The rates of change slow down concurrently with ectorganic matter accumulation.
- Vertical gradients are distinct for all chemical and physical parameters. Changes occur within the F horizon, more than between F and H. This pattern likely results from autogenic soil developing processes in the ecosystem, including decay dynamics and rhizosphere processes, and exogenic processes such as atmospheric deposition of protons and other elements.
- Vertical gradients are particularly evident if the organic layer is sampled by all its morphologically distinguishable horizons. Such gradients are obscured or even obliterated when only F and H horizons are sampled separately. This implies that important ecological gradients in the organic layer may be overlooked when discriminating only between F and H horizons. The ecologically preferable stratification into L, F_1 and F_2/H horizons implies that the standardised distinction between F and H horizons as employed in the framework of humus form classification is less appropriate in this case study.
- The limited complexity of the soil-vegetation system and the systematic nature of the soil changes during succession provide the opportunity to develop a model describing organic matter accumulation

in various organic horizons. Parameters determining decomposition rate are notably those related to pedoclimate (temperature and moisture), while, in this case, chemical conditions seem less important.

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