



## Carbon and nitrogen in soil and vegetation at sites differing in successional age

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Received 24 December 1998; accepted in revised form 25 December 1999

**Key words:** Carbon, Inland drift sands, Nitrogen, Primary succession, Soil development

### Abstract

We studied vegetation and soil development during primary succession in an inland drift sand area in the Netherlands. We compared five sites at which primary succession had started at different moments in the past, respectively 0, 10, 43 and 121 years ago, and a site at which succession had not yet started. In the three younger sites the vegetation was herbaceous, whereas in the two older sites a pine forest had formed. Forest formation was accompanied by the development of an FH-layer in the soil, an increase in the amount of soil organic matter, and an increase in nitrogen mineralisation rate from 1.9 to 18 g N m<sup>-2</sup> yr<sup>-1</sup>. Soil moisture content also increased, whereas pH showed a steady decrease with site age. The vegetation changed from a herbaceous vegetation dominated by mosses and lichens and the grass species *Corynephorus canescens* and *Festuca ovina* towards a pine forest with an understorey vegetation dominated by *Deschampsia flexuosa* and, at the oldest site, with dwarf shrubs *Empetrum nigrum* and *Vaccinium myrtillus*. At the same time the total amounts of carbon and nitrogen of the ecosystem increased, with a relatively stronger increase of the carbon pool. The establishment of trees during succession greatly affects the dynamics of the ecosystem, especially its carbon dynamics.

### Introduction

The processes that drive vegetation succession and the changes in soil and vegetation that result from it have, despite decades of effort, still not been completely unravelled. During succession, the plants themselves inevitably change the supply of resources (e.g. Vitousek & Walker 1987; Berendse 1990; Hobbie 1992). Competition for these resources is considered one of the main processes regulating succession (Gleason & Tilman 1990; Attiwill & Adams 1993). It has been shown in various ecosystems that nitrogen is the most limiting resource during early succession (e.g. Pastor et al. 1984; Schulze et al. 1995; Zarin & Johnson 1995).

Most studies on succession have either investigated succession within herbaceous vegetations or grasslands (e.g. Daniels et al. 1987; Berendse & Elberse 1990; Olff et al. 1993) or within forests (e.g. Alaback

1982; Frelich & Reich 1995; Schulze et al. 1995; Zarin & Johnson 1995; Finegan, 1996). However, the transition from open, herbaceous vegetation to forest is part of many successional seres (e.g. Hester 1991a,b; Rode 1993). During this transition large changes may take place in the system. As trees differ from herbaceous species in several aspects, their invasion will have a large impact on the carbon and nitrogen cycling through the ecosystem (e.g. Attiwill & Adams 1993; Keenan et al. 1995), especially on the distribution of carbon and nitrogen over plant and soil compartments.

However, as succession from bare soil to forest will take place over rather long time-spans, it is difficult to study it 'as it happens' and chronosequences have therefore become an important means of studying such a succession (Huggett 1998). When data are collected in a chronosequence and not during actual succession, the history of the sites may become important. As atmospheric nitrogen deposition has increased over time

in the Netherlands, older sites may have accumulated nitrogen at a slower rate than younger sites. Nitrogen deposition more than doubled between 1950 and 1980 from less than  $2 \text{ g m}^{-2} \text{ yr}^{-1}$  to over  $4 \text{ g m}^{-2} \text{ yr}^{-1}$ , but probably started to decrease again after about 1988 (Van Oene et al. 1999). Still, comparison of sites of different successional ages is our best opportunity to get insight in carbon and nitrogen distribution over different ecosystem compartments in the course of primary succession.

Inland drift sand areas in the Netherlands provide an opportunity to study the pattern of succession starting on bare soil. Over-exploitation in former centuries created bare areas from which the wind blew away all fertile soil. In parts of these areas succession could start when a site came under the lee of neighbouring tree stands that had been planted in reforestation programmes. Plants could only establish in the hot, bare soil when the weather conditions were sufficiently benign. Pine trees have established in cohorts in such favourable years, which has resulted in a mosaic of stands of distinctly different ages (Fanta 1982).

This study was conducted to investigate the nitrogen and carbon dynamics during primary succession from bare sand to forest, especially during forest formation. We collected data in a sequence of ecosystems on strongly similar sites, that had developed for different periods in time. The youngest of these sites were still in a herbaceous stage, while in the oldest forest had formed.

### Study area

We studied a series of five sites in a drift sand area near Leuvenum, the Netherlands ( $52^{\circ}20' \text{ N}$ ,  $5^{\circ}44' \text{ E}$ ,  $\pm 10 \text{ m}$  above sea level). The ground water is usually present at a depth of about 2.5 m and the soil is mostly freely draining. Rainfall is around 820 mm per year (KNMI, 1984–1994). Average temperature in January is about  $3.3^{\circ}\text{C}$ , in July  $18^{\circ}\text{C}$ . The substrate at the sites consists of calcium-poor material of fluvio-glacial origin with a thin cover of aeolian deposits (Koster 1978; Castel et al. 1983). Fanta (1986) and Prach (1989) have described vegetation and species replacement during succession in this area. After stabilisation of the sandy soil owing to the establishment of green algae and the grass *Corynephorus canescens*, *Festuca ovina* becomes the most abundant vascular plant species in a vegetation dominated by mosses and lichens. Seedlings of *Pinus sylvestris* manage to es-

tablish only during extremely cold and wet summers. When the pines have grown to form a closed canopy, *Deschampsia flexuosa* has become dominant in the understorey vegetation. When herbivory is not very severe, the pine forest will give way to mixed forest with *Betula pendula* and *Quercus robur*, second generation *Pinus sylvestris*, and *Rhamnus frangula* in the lower layer, and *Empetrum nigrum*, *Vaccinium myrtillus* and *Deschampsia flexuosa* in the understorey. The soil development during succession has been described by Emmer (1995).

The selected sites were located on blow-outs. Succession had started at different moments in the past and we considered these sites to represent stages in a chronosequence. The chosen sites included bare sand, grass, grass with young pines, pine wood and mixed forest. The ages of the first generation of pine trees that had established in each of the sites were determined by counting growth rings in wood cores and comparing these data with a sequence of aerial photographs. In 1993, the oldest spontaneously established pines at the three oldest selected sites were on average 10, 43 and 121 years old. Hereafter these sites will be referred to as S-H2 (herbaceous 2), S-PF (pine forest) and S-MF (mixed forest). The two sites without pine trees were assigned the ages  $-5$  (S-NV = no vegetation) and 0 (S-H1 = herbaceous 1) years, based on experience and aerial photographs. In the site assigned age 0, *Pinus sylvestris* seedlings were frequently observed which usually died in spells of hot, dry weather. In 1996, the site S-NV had assumed an aspect similar to how site S-H1 initially looked. Per site five quadrates were established for measurements. Quadrates in site S-H2 were established outside the range of trees, to prevent large inhomogeneities inside or between the quadrates. Each of the sites covered a surface of 0.25–1 ha. Site S-NV through S-PF were located at very close range of each other, while site S-MF was located about 2 km south-west of the other sites. The substrate at the various sites is very similar (Emmer, 1995).

Nomenclature of vascular plants follows Van der Meijden et al. (1990).

### Methods

#### Soil

At all sites soil was sampled to a depth of 10 cm with a soil auger (diameter 8 cm) at two random points in each of the established quadrates in July 1995. Depths

of the combined organic horizons were measured. The samples were divided into litter layer, FH layer, and mineral substrate. A very sharp boundary between the FH layer and the mineral soil facilitated this. Samples from the same quadrat were bulked.

Organic matter and ash content were determined after heating to 550 °C for 2 hours. Carbon and nitrogen concentrations of the organic matter were determined using an element analyser (EA 1108, Fisons Instruments, The Netherlands). To determine pH of the soil solution, samples were taken at every site with a soil auger in April 1994. The samples were divided in the field into mineral layer and organic layer. Soil pH was determined in 1M KCl solution.

From October 1993 till October 1994 nitrogen mineralisation was measured at each of the sites by a sequential *in situ* method (Olf et al. 1994). At each sampling date measurements were done in duplicates in each of the five quadrates per site. Sampling dates were 8 weeks apart except in winter when there was a period of 12 weeks between the sampling dates.

Soil water content was determined gravimetrically in every tube used in the mineralisation measurements. By combining these data with data on soil bulk density from the soil cores, volumetric water content could be estimated.

### Vegetation

In October 1993 and July 1994 above-ground biomass of the understorey species was estimated by means of destructive sampling. Two samples of 50 cm × 50 cm were taken per quadrat and bulked. All vegetation was clipped just above the soil surface. Above-ground plant material was separated by species, plant organs, necro- and biomass. Furthermore, all plant litter was collected from the ground. Root biomass was sampled inside the same 0.25 m<sup>2</sup> squares in soil cores (diameter 7 cm) at 0–10, 10–20 and 20–30 cm from the soil surface. Roots were removed from the cores by sieving and hand-picking, sorted in woody, non-woody and rhizomes. All material was oven dried (48 h, 70 °C), and weighed.

Tree biomass was estimated using allometric tables by Marklund (1988). Height and diameter at breast eight were measured in S-PF and S-MF on all trees in an area of 900 m<sup>2</sup>. In site S-H2 the trees were too small to be estimated using the tables. At this site all trees were counted in a 1200 m<sup>2</sup> area. Five trees were cut down and taken to the laboratory for weighing. These

values were used to estimate the total tree biomass at this site.

Carbon and nitrogen concentration were determined in subsamples of all distinguished types of plant material collected at the harvests, as well as in samples of tree leaves, collected at 22 May 1995, and in wood cores from tree stems. For these measurements an element analyser was used.

### Statistics

Whenever two samples were taken per quadrat, results were averaged before further analysis. Mineralised amounts of nitrogen were summed over dates per quadrat. Differences between sites in the C:N ratio of the organic layer, the C:N ratio of the litter, and nitrogen mineralisation rates were tested with OneWay ANOVA, followed by Duncan's multiple range posthoc tests when the comparison comprised more than two sites. Pearson correlation was used to analyse the relation between soil organic matter content and soil water content.

## Results

### Soil

The FH layer (*sensu* Klinka et al. 1981) first became visible in the 43-year-old site S-PF. The thickness of this layer was 30 (± 5.8) mm on average in S-PF and 60 (± 6.5) mm in site S-MF (Table 1). The amount of organic matter in the upper 10 cm was lowest in S-NV with 0.6·10<sup>3</sup> g m<sup>-2</sup> and highest in S-MF with 10.4·10<sup>3</sup> g m<sup>-2</sup> (Table 1). The C:N-ratio of the organic layer – without the easily removable litter part – was significantly lower in site S-PF, where it was 25, than in site S-MF, where it was 31 (OneWay ANOVA, *p* < 0.01). C:N ratios of litter, defined as the easily removed material on the top of the soil, averaged over both harvests, did not differ between the two oldest stages where it was 31 (± 2.2) in S-PF and 30 (± 0.9) in S-MF (OneWay ANOVA, *p* > 0.05) (Table 1). The pH-KCl of the soil solution in the mineral substrate declined with increasing site age from 4.9 (S-NV) to 3.1 (S-MF) (Table 1). The organic soil layer had a lower pH than the mineral substrate. The amount of water stored in the upper 10 cm soil increased with increasing site age from an annual average of about 5% (v/v) in site S-NV to 50% (v/v) in site S-MF (Table 1). A high correlation was found between soil organic

Table 1. Selection of soil characteristics in five sites of increasing successional age (mean  $\pm$  1 s.d.,  $n = 5$ ).

Site	Depth FH-layer (mm)	Amount of organic matter (kg m <sup>-2</sup> )	Soil water content (v/v)	pH-KCl mineral layer	pH-KCl organic layer	C:N-ratio FH layer (g g <sup>-1</sup> )	C:N-ratio litter (g g <sup>-1</sup> )
S-NV	0	0.61 $\pm$ 0.17	0.052 $\pm$ 0.004	4.86 $\pm$ 0.66	–	–	–
S-H1	0	0.45 $\pm$ 0.05	0.048 $\pm$ 0.002	4.84 $\pm$ 0.72	–	–	–
S-H2	0	1.62 $\pm$ 0.62	0.066 $\pm$ 0.004	3.81 $\pm$ 0.12	–	–	–
S-PF	30 $\pm$ 5.8	4.53 $\pm$ 0.60	0.220 $\pm$ 0.026	3.40 $\pm$ 0.14	2.86 $\pm$ 0.07	25.2 $\pm$ 3.5	31.4 $\pm$ 2.2
S-MF	60 $\pm$ 6.5	10.4 $\pm$ 1.26	0.509 $\pm$ 0.038	3.14 $\pm$ 0.09	2.59 $\pm$ 0.07	31.5 $\pm$ 4.3	29.7 $\pm$ 0.9

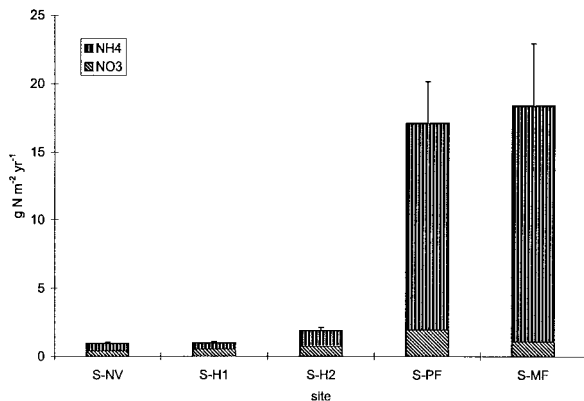


Figure 1. Nitrogen mineralisation rates ( $\text{g N m}^{-2} \text{yr}^{-1}$ ) in five sites of increasing successional age from October 1993 to October 1994  $\pm$  1 s.e., subdivided in nitrate and ammonium.

matter content and water content (Pearson linear regression,  $r^2 = 0.94$ ,  $p < 0.001$ ). The amount of nitrogen mineralised per year in the upper 10 cm of the soil increased from  $1 \text{ g N m}^{-2} \text{yr}^{-1}$  at site S-NV to  $17 \text{ g N m}^{-2} \text{yr}^{-1}$  at site S-PF, but no significant difference was found between the pine forest, site S-PF and the older mixed forest, site S-MF (Figure 1). Of this mineralised nitrogen the proportion of  $\text{NO}_3^-$  was high at the herbaceous sites (S-NV, S-H1, and S-H2), while at the forest sites S-PF and S-MF the proportion of  $\text{NO}_3^-$  was very low (Figure 1).

### Vegetation

Plant species composition and successional changes in the vegetation followed the description given by Fanta (1986). No phytomass was present in the first successional site studied (S-NV). There only was bare sand. In site S-H1 a few scattered individuals of *C. canescens* were found, imbedded in a bare sand environment. The amount of above and below ground phytomass was very low (Tables 2, 3). In the third

successional stage (S-H2) the vegetation was closed and dominated by mosses and lichens, *C. canescens* and *F. ovina*. A few small pine trees had established.

The fourth stage studied (S-PF) was the first forest site dominated by first generation pine trees (*P. sylvestris*), with *D. flexuosa* dominating the understorey vegetation. Mosses and lichens and a few individuals of *F. ovina* were still present, but their amount of phytomass decreased strongly compared to the former S-H2 site. The amount of woody phytomass enormously increased up to  $7.4 \times 10^3 \text{ g m}^{-2}$ . The fifth stage studied (S-MF) was still dominated by pine trees. The phytomass of the pine trees remained about the same. However, *B. pendula* and *Q. robur* invaded the vegetation and contributed substantially to the total amount of phytomass (Table 2). *D. flexuosa* no longer dominated the understorey vegetation. In addition dwarf shrubs, *E. nigrum* and *V. myrtillus*, had established with rather high amounts of phytomass.

The amount of below ground phytomass differed enormously between the five sites studies (Table 3), with increasing amounts of woody, wood, and coarse roots and stumps in the forested sites, S-PF and S-MF.

### Carbon and nitrogen pools

The total amount of carbon in the plant and soil compartments increased with increasing site age. Carbon stored in the vegetation increased from 0 to  $6.9 \times 10^3 \text{ g C m}^{-2}$ , while carbon stored in the soil increased from  $0.4 \times 10^3$  to  $6.5 \times 10^3 \text{ g C m}^{-2}$  (Figure 2a). Initially, most C was stored in the soil: at site S-H1 95% of the total C was stored in the soil compartment. This proportion of C stored in the soil decreased to 67% at site S-H2 and it decreased further to 35% and 48% at the forested sites S-PF and S-MF. Consequently, an increasing amount, up to over 50% of total C, is stored in the forest vegetation.

Table 2. Aboveground live biomass in  $\text{g m}^{-2}$  of the most common species at the five sites of the successional sequence. Data for herbs, grasses, and mosses are the average of two harvests ( $n = 5$ ). Data for trees are estimates based on data collected in 1994 using the allometric tables by Marklund (1988).

Species	S-NV	S-H1	S-H2	S-PF	S-MF
<i>Corynephorus canescens</i>	0	$2.7 \pm 2.2$	$24.5 \pm 11.4$	0	0
<i>Festuca ovina</i>	0	0	$1.9 \pm 2.8$	$2.1 \pm 2.7$	0
mosses & lichens	0	0	$426 \pm 146$	$54 \pm 38$	$91 \pm 60$
<i>Pinus sylvestris</i> (1st generation)	0	0	12	7423	7308
<i>Deschampsia flexuosa</i>	0	0	0	$53.0 \pm 16.3$	$34 \pm 40$
<i>Pinus sylvestris</i> (2nd generation)	0	0	0	0	46
<i>Betula pendula</i>	0	0	0	0	1392
<i>Quercus robur</i>	0	0	0	0	615
<i>Empetrum nigrum</i>	0	0	0	0	$13.3 \pm 15.6$
<i>Vaccinium myrtillus</i>	0	0	0	0	$219 \pm 173$
Total above-ground biomass	0	2.7	464	$75 \times 10^2$	$97 \times 10^2$

Table 3. Below ground biomass of the most common species at five sites of increasing successional age. Data for smaller roots (fine, woody, wood < 1cm, rootstocks) are the average of two harvests measurements in the upper 30 cm soil ( $n = 5$ ). Data for trees (coarse roots and stubs) are estimates based on data collected in 1994, using data tables from Marklund (1988) and Cannell (1982).

Root type	S-NV	S-H1	S-H2	S-PF	S-MF
Fine	0	$8.3 \pm 3.6$	$20 \pm 13$	$54 \pm 44$	$112 \pm 52.9$
Woody	0	0	$1.5 \pm 3.3$	$344 \pm 51.8$	$0205 \pm 66.5$
Wood	0	0	0	$532 \pm 734$	$161 \pm 139$
Rootstock	0	0	0	0	$323 \pm 341$
Coarse roots and stubs <sup>a</sup>	0	0	2	2096	4933
Total root biomass	0	8.3	21.7	3026	5734

<sup>a</sup>Coarse roots and stubs was estimated once for the whole site. No replicates were available, so no standard deviation could be calculated.

The total amount of nitrogen present in the vegetation and soil compartments also increased, as expected, with increasing site age. The amount of nitrogen present in the vegetation increased from  $0 \text{ g N m}^{-2}$  in site S-NV to about  $44 \text{ g N m}^{-2}$  in site S-MF. Organic nitrogen in the soil increased from  $13\text{--}214 \text{ g N m}^{-2}$ . Including standing dead, total organic N increased from  $13\text{--}258 \text{ g}$  in sites differing about 126 years in age (Figure 2b). The relative amount of N in the soil compartment was initially very high, 96% in site S-H1. After forest formation, it decreased to 80% in S-PF and S-MF, when the soil organic layer had developed. Only 20% of total N was stored in the vegetation at both forest sites.

When trees had established (site S-PF and S-MF), carbon accumulation was relatively faster than nitrogen accumulation, resulting in an increase in ecosys-

tem C:N ratios from about 26 in the youngest three sites to about 53 in the oldest two sites. This increase was caused mainly by the increasing C:N ratio of the vegetation, while soil C:N ratios attributed less to this change.

## Discussion

With increasing developmental time we observed gradual changes in vegetation and soil parameters, with, for a number of parameters, a distinct shift between the latter herbaceous site (S-H2) and the younger forest site (S-PF). In the younger sites (S-NV to S-H2) we observed the development of an herbaceous vegetation dominated by grasses, mosses and lichens, combined with a slow but steady increase of

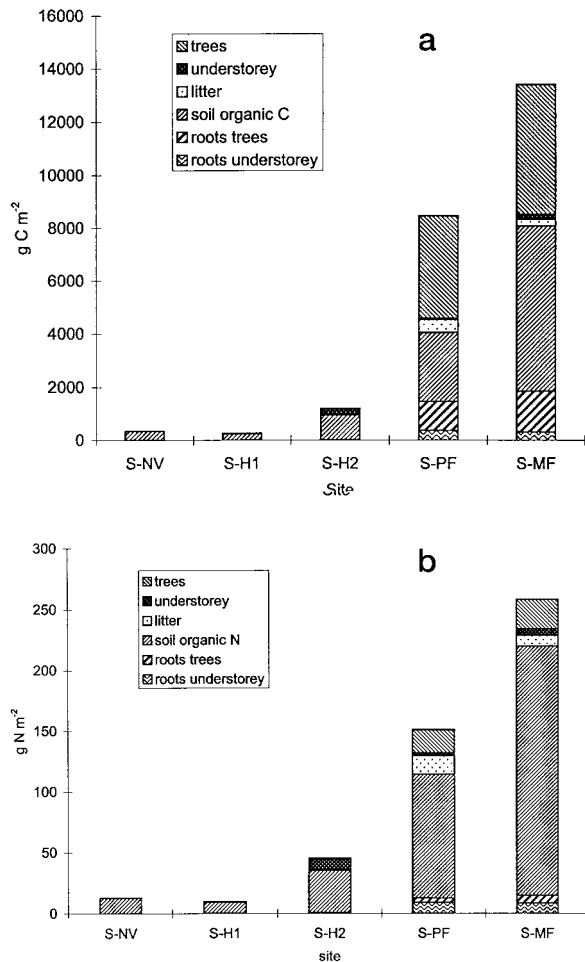


Figure 2. Amount of (a) carbon ( $\text{g m}^{-2}$ ) and (b) nitrogen ( $\text{g m}^{-2}$ ) in different ecosystem compartments at five sites of increasing successional age. Data of soil organic matter were estimated July 1995 ( $n = 5$ ) and trees 1994 ( $n = 1$ ); data for the understorey phytomass are the average of October 1993 and July 1994 data ( $n = 5$ ).

both nitrogen and carbon with site age. Nitrogen mineralisation rate doubled between site S-NV and site S-H2. Between site S-NV, site S-H1, and S-H2 a relatively large drop in soil pH was found. These patterns are comparable with those found in other studies of early primary succession of herbaceous vegetations (Olf et al. 1993). In the younger forest site (S-PF) a closed canopy was formed by *P. sylvestris*, with *D. flexuosa* dominating the understorey. In this site an FH-layer has formed, and associated with it a high soil organic matter content and a high soil water content in the upper 10 cm were measured. The nitrogen mineralisation rate was much higher in this forest site than in the younger sites, resp.  $17 \text{ g N m}^{-2} \text{ yr}^{-1}$  in S-PF and  $1.9 \text{ g N m}^{-2} \text{ yr}^{-1}$  in S-H2. In particular the

release of  $\text{NO}_3^-$  was much lower in the younger sites (see Vitousek et al. 1989). Plant production has been shown in other studies to be proportional to nitrogen mineralisation in nitrogen limited systems (e.g. Pastor et al. 1984; Berendse 1990), so probably plant production was also much higher in S-PF than in the younger sites. An important consequence of forest formation was a stronger increase in the size of the carbon pool, relative to the nitrogen pool. This is expected in a stage of forest formation, because woody tissue with a low nutrient content is being formed, but little is shedded yet because of its long life-span. Owing to this accumulation of carbon in the trees, most carbon at the forest sites was found to be stored in the vegetation, whereas at the herbaceous sites the larger proportion of both C and N was found in the soil compartment.

In the younger and older forested sites, resp. S-PF and S-MF, the nitrogen mineralisation rates were about equal, though the total amounts of carbon and nitrogen stored in the soil and the vegetation were about twice as high in the older site as in the younger. This pattern in nitrogen mineralisation is comparable to that found in other studies on succession in sand dunes (Robertson & Tiedje 1984 as cited in Vitousek et al. 1989). Mineralisation rates depend on the amount and quality of the produced litter both in the current and in previous years. The lower turnover rate of the available nitrogen in the soil may have been caused by the addition of wood, with its low C:N ratio, to the litter flow (Busse 1994). The C:N-ratio of the litter layer in site S-MF was, however, similar to that in site S-PF. The C:N-ratio of the soil organic matter, in contrast, was lower in site S-MF than in site S-PF, which suggest accumulation of nitrogen-poor substances of low decomposability. The thickness of this organic layer was twice that in site S-PF. Elgersma (1998) has suggested that the soil organic matter changed from a moder humus into a mor humus during formation of a pine forest, due to the low decomposability of pine needles. Vegetation composition changed from a pine forest with *D. flexuosa* dominating the understorey at site S-PF towards a mixed forest with young individuals of *B. pendula* and *Q. robur* and an understorey vegetation with besides *D. flexuosa* also *E. nigrum* and *V. myrtillus* at site S-MF.

The study of primary succession by comparison of sites on which vegetation and soil started to develop at different moments in the past will give rise to some problems. Nitrogen deposition increased during the last century, which is likely to have caused higher N

accumulation rates at the younger sites studied. Also, atmospheric carbon dioxide concentrations increased during the last century. With the design we used, five subplots within each successional stage, the problem of pseudoreplication cannot be avoided, since the factor successional stage cannot be truly replicated. The sites studied were all located on blow-outs with similar soil material, ground water levels and macro-climatic conditions, so initial values of these conditions could be considered very similar.

Nitrogen accumulation is likely to have been dictated mainly by the input from atmospheric deposition, as was shown in other studies (Berendse 1990; Berendse et al. 1998), though trees can increase capture of dry deposition from the air relative to herbaceous species (Ivens 1990). In site S-H2, the accumulation rate had been  $3.6 \text{ g N m}^{-2} \text{ yr}^{-1}$ , while N deposition was estimated to be  $5.5 \text{ g N m}^{-2} \text{ yr}^{-1}$  on average over the period 1984–1993 (Van Oene et al. 1999). The estimation of  $5.5 \text{ g N m}^{-2} \text{ yr}^{-1}$  is wet and dry deposition and, as there are only small trees on site S-H2, it overestimates what S-H2 will really have received. However, about 65% or more of the nitrogen that entered the system was retained. The average nitrogen accumulation rate was  $3.3 \text{ g N m}^{-2} \text{ yr}^{-1}$  at site S-PF, and  $2.1 \text{ g N m}^{-2} \text{ yr}^{-1}$  at site S-MF (taking S-H1 as a baseline). Historical nitrogen deposition rates were calculated to be 4.0 for the period 1951–1993, and  $2.6 \text{ g N m}^{-2} \text{ yr}^{-1}$  for the period 1873–1993 (Van Oene et al. 1999). This means that ca. 20% of the nitrogen entering the system over the period of succession was lost, probably through leaching to the lower groundwater. Judging from the lower retention of nitrogen in the younger site, relatively higher losses may have occurred before closure of the vegetation. Carbon accumulation had been  $0.9 \times 10^2 \text{ g m}^{-2} \text{ yr}^{-1}$  in S-H2,  $1.9 \times 10^2 \text{ g m}^{-2} \text{ yr}^{-1}$  in S-PF and  $1.1 \times 10^2 \text{ g m}^{-2} \text{ yr}^{-1}$  in S-MF. Carbon accumulation did not show such a historically based pattern as the nitrogen accumulation, but had been highest at the youngest forest site S-PF, in the middle of the successional sequence.

In conclusion, this sequence of successional sites on inland drift sand blow-outs showed increasing carbon and nitrogen amounts with site age, with a relatively accelerated carbon accumulation during forest formation. Forest formation and accompanying changes in vegetation composition coincided with the formation of a soil organic layer, increasing soil water content and a high, but levelling, nitrogen mineralisation rate.

## Acknowledgements

This work was supported by the Dutch National Research Programme on Global Air Pollution and Climate Change. We thank Natuurmonumenten for their permission to work in the Leuvenumse Bos. We thank Harmke van Oene for valuable comments on an earlier draft of this manuscript.

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