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Effects of dominant plant species on soils during succession in nutrient-poor ecosystems

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Abstract. During the initial phases of succession on nutrient-poor, mineral substrates dead plant material accumulates rapidly in the soil. This accumulation of soil organic matter can result in a more than 10-fold increase in nitrogen mineralization within a few decades. These changes in soil features have important consequences for plant growth and the competition between plant species. During succession in heathlands an increase in nutrient mineralization leads to species with low maximum growth rates and low biomass loss rates being replaced by species with high potential growth rates and high biomass losses. The plant properties responsible for reduced biomass loss rates appear to result in the litter produced being poorly decomposable, whereas the litter from plants with high potential growth rates decomposes more easily. Model simulations suggest that such combinations of plant features greatly influence the increase in mineralization and the change in plant species composition during ecosystem development. Studies in the field and garden plot experiments confirmed this hypothesis.

Introduction

Plants and microorganisms have an extremely important impact upon the chemical and physical properties of the environment. Average air temperature and atmospheric pressure would increase strongly if all living organisms were to disappear from the earth (Lovelock 1989). Lovelock (1979, 1989) even hypothesized that living organisms have a stabilizing effect on the physical and chemical conditions of our planet as a whole. This hypothesis, which he illustrated using his theoretical Daisyworld model, has been greeted with much skepticism to date (e.g., Kirchner 1989). One of the major criticisms of the concept is the virtual impossibility to test such a hypothesis at a global scale.

At a local scale, however, the effects of organisms on substrate and atmosphere are also extremely relevant. Van Breemen (1993) reviewed a large number of studies on the influence of plants, soil animals and microorganisms on their physical substrate and concluded that these organisms affect soil fertility and soil moisture content in such a way that over time the substrate becomes more favourable for their growth and survival. At a scale from 1 m^2 to 1 ha such hypotheses can easily be investigated and even tested.

Competition between plant species and the resulting species composition of the plant community is strongly affected by changes in nutrient supply (Berendse 1983; Tilman 1988). We measured a more than tenfold increase in nutrient mineralization within a few decades during succession in nutrient-poor ecosystems in the Netherlands (Berendse 1990). Such changes have major effects on the establishment and the outcome of competition between plant species. So, it is clearly impossible to ignore the effects of plant species on the soil, when analysing or predicting changes in the plant species composition of nutrient-poor ecosystems. In this paper I will therefore analyse changes in soils brought about by dominant plant species that are adapted to nutrient-poor or nutrient-rich soils.

Description of chronosequences

In many cases an analysis of changes in natural ecosystems at a time scale longer than one decade requires reconstruction on the basis of chronosequences, i.e., sequences of adjacent sites that have developed for different time periods. Long-term observations in natural ecosystems frequently only consider changes in plant species composition, whereas in many cases the relevant soil and plant processes have not been monitored. In chronosequences all parameters considered to be relevant can be measured, using the latest measurement techniques. Nevertheless, reconstruction of succession by a comparative study of neighbouring ecosystems which have developed during different time intervals is a risky enterprise. Mineral substrate, groundwater level and climatological conditions should be similar at all sites. Miles (1985) distinguished between stable substrate characteristics such as textural composition of the subsoil and labile characteristics such as organic matter content and acidity of the upper soil layer, and used several stable properties to measure the similarity between sites. One other point of consideration is the trivial, but often neglected fact that in chronosequences the various sites developed partly in different time periods in which important driving factors such as atmospheric N deposition and CO_2 level were different.

In the last 12 years we studied several chronosequences. Here I present some of the data collected in two sequences on sandy substrates, one sequence is characteristic of dry inland dunes and the other characteristic of heathlands on substrates with intermediate soil moisture levels, in the Netherlands. It was possible to reconstruct the sequences in heathlands because in these areas turf had been regularly removed for many years to encourage the growth of heather. The date of turf removal and the techniques applied had always been precisely recorded. We checked the number of years after turf removal against counts of annual stem rings in the the oldest *Calluna vulgaris* stems in each plot. In all plots there was complete agreement between the two estimates of the time period during which succession had proceeded. In the inland dunes, *Pinus sylvestris* was one of the first vascular plant species that was able to establish, together with the grass *Corynephorus canescens*. *Pinus* seedlings were only able to establish in years with extremely cold and wet summers, which occurred at a frequency of less than 0.1. It appeared that each site was dominated by one even-aged cohort of spontaneous pine trees. We defined the start of ecosystem development as the year in which pine seedlings established succesfully, and measured the time elapsed since then by counting the annual rings in the thickest pine trees at each site. At both the heathland and the inland dune site the mineral subsoil consisted of aeolian sandy deposits that can be considered to be homogeneous over relatively large areas. Groundwater levels were similar at all sites within one sequence and the plots were always sufficiently close to avoid any significant difference in climatological conditions.

In each of the chronosequences a strong accumulation of litter and dead root material was observed (Figure 1a). In the inland dune and the heathland sequence about 2 and 3.5 kg organic matter/m^2, respectively, had accumulated in the litter and the FH-layer within 50 years starting from a bare mineral substrate. Within this period, the accumulation of dead organic material in the soil was accompanied by an increase in annual N mineralization from less than 1 g m^{-2} yr^{-1} to 13 g m^{-2} yr^{-1} in the heathland area to as high as 17 g m^{-2} yr^{-1} in the inland dunes (Figure 1b). It is inconceivable that such changes will not have had important impacts upon plant productivity and upon the competitive balance between the different plant populations. In the heathland sequence, above-ground productivity was strongly linearly correlated with N mineralization and increased from 120 g m^{-2} yr^{-1} to ca. 550 g m^{-2} yr^{-1}. Both the accumulation of soil organic matter and the rate of increase in N mineralization decline during the later phases of ecosystem development.

In both sequences soil moisture increases as a consequence of the accumulating soil organic matter (Figure 1c). The accumulation of soil organic matter apparently has a strongly regulating effect upon soil moisture in these dry ecosystems. The soil moisture content during the initial phases of the heathland sequence is higher than that in the inland dune sequence, but after 50 years this difference was greatly reduced. In the inland dune sequence the pH (KCl) in the mineral subsoil declines from 4.9 to 3.1 after 121 years (data not shown).

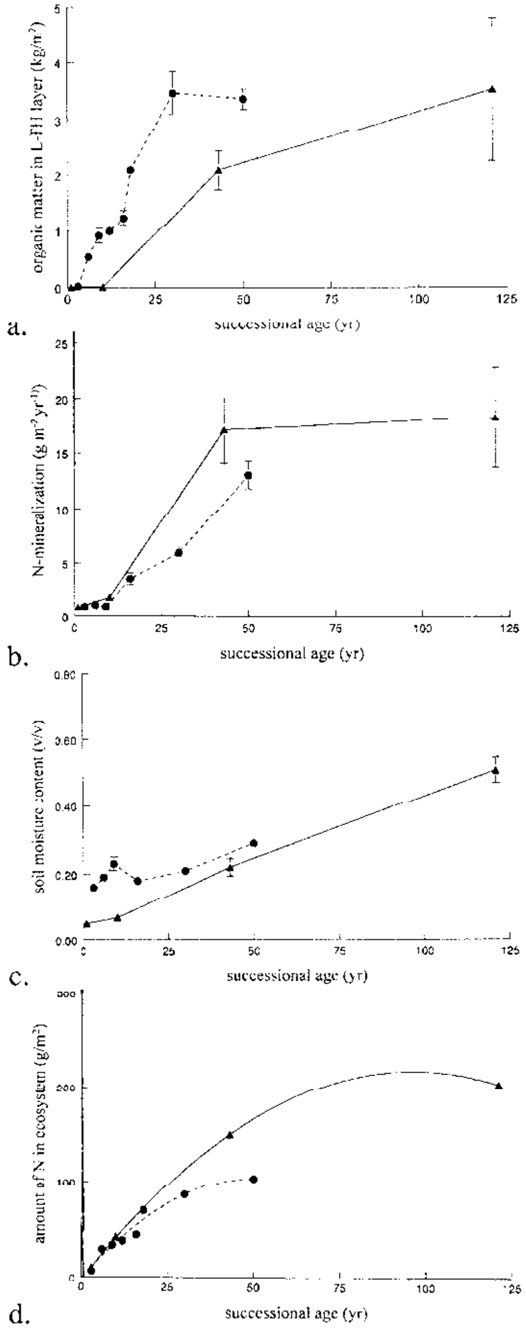

Figure 1. (a) The amount of organic matter in the L and FH layer, (b) the annual nitrogen mineralization, (c) the volumetric soil moisture content in the upper 10 cm and (d) the total amount of nitrogen in the whole ecosystem versus successional age in heathlands and inland dunes. Filled dots: heathland plots; filled triangels: inland dune plots. Bars represent standard errors of the mean.

The accumulation of nitrogen in the whole ecosystem (plant biomass + soil to a depth of 30 cm) is remarkably similar in the two sequences, especially since these ecosystems have attained a completely different structure after about 50 years: a grassy heath versus a pine forest. The initial N accumulation rates are almost equal (4.2 and 4.4 g N m^{-2} yr^{-1} in the heathland and inland dune sequence, respectively) and close to the average N input through atmospheric deposition. This observation implies that during the early phases of ecosystem development essentially all incoming nitrogen is preserved and losses due to nitrate leaching or denitrification are negligible. The presented relation between successional age and the total amount of nitrogen in the ecosystem is clearly curvilinear. This relation is perhaps due to nitrogen saturation during the later phases resulting in increased nitrogen losses by leaching or denitrification. We have to realize, however, that the later phases in the two sequences have experienced on the average lower N inputs as compared to the younger sites. Such differences between plots within one sequence are one of the important pitfalls in the interpretation of chronosequence data.

Adaptation of plant species to nutrient-poor soils

The dramatic increase in nitrogen mineralization during succession as observed in heathlands and inland dunes must have important consequences for plant competition. In recent decades, in many wet heathlands in Europe the ericaceous dwarfshrub *Erica tetralix* has been replaced by the perennial grass *Molinia caerulea*. In competition experiments in containers (Berendse & Aerts 1984) and in field fertilization experiments (Aerts & Berendse 1988; Aerts et al. 1990) *Molinia* is able to outcompete *Erica* at increased nutrient levels, whereas *Erica* remains dominant under nutrient-poor conditions. In dry heathlands an increased nutrient supply may lead to a strong increase in the grass *Deschampsia flexuosa* replacing the dwarf shrub *Calluna vulgaris*. But because older *Calluna* plants are able to overtop the relatively low *Deschampsia* individuals, *Deschampsia* increases only after the *Calluna* canopy has been opened up by heather beetle attacks or frost damage and the grass plants receive sufficiently high light intensities (Aerts et al. 1990; Berendse et al. 1994).

The grass species are able to outcompete the ericaceous species after an increase in nutrient mineralization because they respond much more rapidly to an increased nutrient supply. In a field experiment lasting three years we applied four nutrient levels (0, 5, 10 and 20 g N m^{-2} yr^{-1}) to monocultures of *Erica*, *Calluna* and *Molinia* (Aerts et al. 1990). The potential above-ground productivity of the grass *Molinia* was much higher than that of the dwarf shrub *Erica* (Table 1). Doubling the dose of N (and corresponding quantities

Table 1. Relative biomass loss and relative nitrogen loss rates (expressed as fraction of the quantities of biomass and nitrogen present at the end of the growing season), potential growth rates (after Aerts et al. 1990) and decomposition rates weighted for the contribution of different litter types to total litter production (Van Vuuren et al. 1992, 1993) in neighbouring populations of *Erica tetralix* and *Molinia caerulea*

	Erica	Molinia
relative biomass loss rate (year^{-1})	0.58	1.48
relative nitrogen loss rate (year^{-1})	0.22–0.32	0.64–1.00
potential growth rate (g m^{-2} yr^{-1})	769	$\geq$ 1794
litter decomposition rate (yr^{-1})	0.06–0.09	0.24–0.26

of P and K) from 10 to 20 g N m^{-2} yr^{-1} did not increase the above-ground biomass of *Erica* but doubled that of *Molinia*. This difference in potential productivity between the two species could be attributed to (a) allocation of less nitrogen to the photosynthetic system in *Erica* than in *Molinia* and (b) the greater biosynthesis costs of *Erica* tissues (amongst others due to their higher lignin content).

These differences between the species explain why *Molinia* is more successful after an increase in nutrient supply, but do not explain the success of the dwarf shrubs under nutrient-poor conditions. In habitats where the nutrient supply strongly limits plant growth, the long-term success of plant populations is determined by the balance between nutrient uptake and the loss of nutrients through litter production, root turnover and herbivory. We measured nitrogen losses from populations of *Molinia* and *Erica* plants in adjacent sites for two years. Estimates of total nitrogen loss strongly depend on the assumptions about the retranslocation of nitrogen from dying roots, which we could not measure. Total losses of nitrogen from *Molinia* plants varied between 60 and 100% per year of the total amount of nitrogen present in the plants at the end of the growing season (Table 1). We calculated the lower turnover rate assuming that 50% of the nitrogen in roots was withdrawn preceding abscission, whereas the higher figure was calculated assuming that no retranslocation took place. Losses of up to 100% clearly have important consequences for the success of a population in an environment where nitrogen limits plant growth. Nitrogen losses from *Erica* were much smaller (ca. 30%). These reduced losses seem to be an important adaptation to the nutrient-poor habitats that are dominated by this species. Nitrogen losses from *Erica* plants are much smaller because their leaves, stems and roots live much longer than those of *Molinia* (Table 2). Similarly, Escudero et al. (1992) found that the life span of leaves of tree and shrub species in the Pyrenees varied by a few orders of magnitude and that this variation was strongly correlated with the variation in soil fertility. Plant species dominant on infertile

Table 2. Leaf life span, lignin content and biosynthesis costs of leaves of *Erica tetralix* and *Molinia caerulea*

	Erica	Molinia
leaf life span (yr)	1.3	0.35
lignin concentration (%)	33	24
biosynthesis costs (g glucose/g biomass)	1.8	1.4

soils had leaves that lived longer than species that were abundant on more fertile soils. Recently we carried out an experiment in which 14 plant species of Dutch grassland and heathland communities were grown in monocultures in experimental plots. Here the direct effects of different soil characteristics were excluded. We found a strongly significant inverse relationship between a species' average leaf life span as measured in these plots and its nutrient index. The nutrient index is a parameter that ranks the average soil fertility in the habitat in which the species is most frequently found.

Erica leaves live about four times longer as *Molinia* leaves, thanks to their higher lignin content resulting in an increased thoughness of the leaf. Lignin is more expensive to biosynthesize than compounds such as cellulose. We calculated that the costs of biosynthesizing *Erica* tissue were about 30% higher than those of *Molinia* tissues (1.8 versus 1.4 g glucose/g biomass). From this we conclude that the adaptation to nutrient-poor environments by minimizing the loss of nutrients has an important negative side effect: biosynthesis costs of tissues are increased, which results in a reduced potential growth rate, which is an important disadvantage when soil fertility increases (Berendse 1994). Apparently, plant properties that determine nutrient losses and potential growth rates are strongly interconnected.

Another important feature that is affected by the ability of plant species such as *Erica* to minimize their nutrient and biomass turnover is the decomposability of the dead material from these species. Lignin concentration often shows a strong inverse relation with litter decomposition rate (Melillo et al. 1982; Berg & McClaugherty 1987; McClaugherty & Berg 1987). There are indications that many other secondary plant compounds that increase leaf life span and reduce herbivory also have adverse effects upon litter decomposition (Grime & Cornelissen 1996). In litter bag experiments we compared decomposition rates of the different dead plant parts of *Erica* and *Molinia* for a periods of three years (Van Vuuren et al. 1993). We weighted the annual decomposition rates of the various plant organs according to their relative contribution to the annual litter production. Such weighted decomposition rates for *Erica* litter are about one quarter of those for the dead material produced by *Molinia* plants (Table 1).

From our comparative studies on *Molinia* and *Erica* we concluded that the adaptation to nutrient-poor environments by reduced nutrient losses is achieved by prolonging the longevity of plant organs. Important side effects of such increased life spans are lower potential growth rates and lower litter decomposability. *Molinia* is adapted to the relatively nutrient-rich phases of ecosystem development by its relatively high potential growth rate, but the corollary of higher maximum growth is shorter life spans of leaves and roots and greater decomposibility of dead material. These three groups of plant features seem to be very strongly intercorrelated. For this reason, I will refer to the combination of low biomass turnover, low maximum growth and low litter decomposability as the *Erica* syndrome and to the combination of high biomass loss rates, high potential growth rates and a relatively high decomposability as the *Molinia* syndrome.

Theoretical analysis

The strong positive correlation between the longevity of plant organs, the maximum growth rate of plants and the decomposability of the litter that they produce has probably evolved in response to the large variation in soil fertility in natural ecosystems, but also has important implications for the effects that plant species may have upon nutrient mineralization during succession. To analyze the effects of plant species with different syndromes on soil fertility during succession we combined models for soil carbon and nitrogen dynamics and for competition between plant species for light and inorganic nitrogen (Berendse 1994). Although the resulting model is simple, the changes in soil organic matter, plant biomass and nutrient mineralization it predicted are very similar those in our real-life chronosequences. A more elaborate version of the model was implemented with parameter values measured in independent experiments and initial values of state variables measured at the field sites involved. This model was successfully validated using our chronosequence data (Berendse 1988).

During succession in hypothetical ecosystems dominated by one plant species, soil organic matter accumulates linearly, resulting in an almost linear increase in nutrient mineralization (Figure 2). During the first five years N is immobilized, because the fresh, nitrogen-poor material that the plants add to the soil raises the C:N ratios in the soil organic matter. After 5 to 10 years an equilibrium C:N ratio has been established because of a balance between the decline in the C:N ratio in the soil brought about by decomposition and the increase in the C:N ratio brought about by the addition of nitrogen-poor litter.

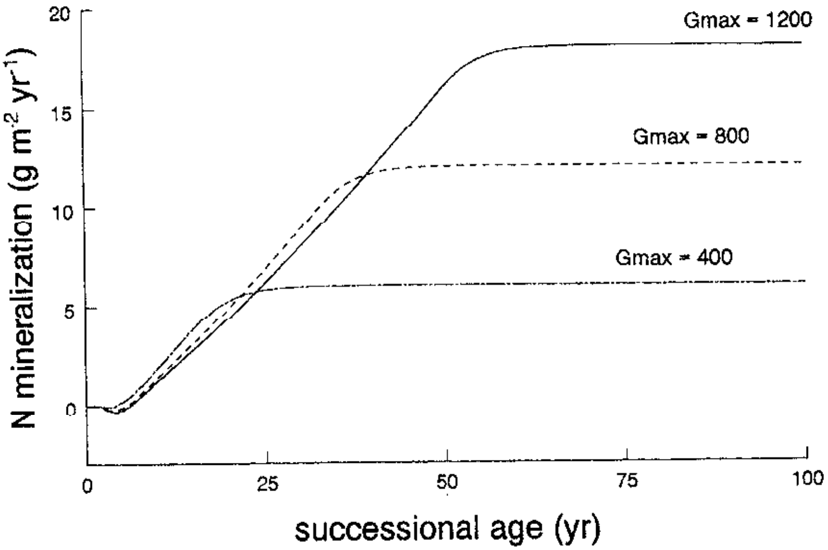

Figure 2. The change in nitrogen mineralization during succession in ecosystems dominated by three plant species with different potential growth rates (Gmax = 400, 800 or 1200 g m^{-2} yr^{-1}). Changes are calculated using a simple model for the carbon and nitrogen dynamics in soils.

As soon as the C:N ratio has reached a constant value the mineralization rate increases linearly. This increase continues up to a maximum that depends on the potential growth rate of the dominant plant species. The accumulation of soil organic matter and the continuous increase in nutrient mineralization during succession on well-drained soils is due to a feedback operating between the positive effect of increased soil organic nitrogen on nitrogen mineralization on one hand, and the positive effect of increased mineralization upon litter production on the other hand. Once plant productivity is at its maximum so that increased nitrogen mineralization would no longer increase productivity, the N mineralization ceases to rise. This analysis leads to the important hypothesis that the final mineralization rate during succession is determined by the potential growth rate of the plant species that is dominant during this final phase. The model predicts that the nitrogen mineralization in this last phase equals the amount of nitrogen taken up by the vegetation when it has achieved its maximum productivity.

The increase in mineralization during succession was calculated for three ecosystems dominated by hypothetical plant species that differed in biomass loss rate and in litter decomposability. The different biomass loss rates (L) and litter decomposition rates (k) had relatively little effect on the mineralization (Figure 3a, b). However, a positive link between biomass turnover and litter

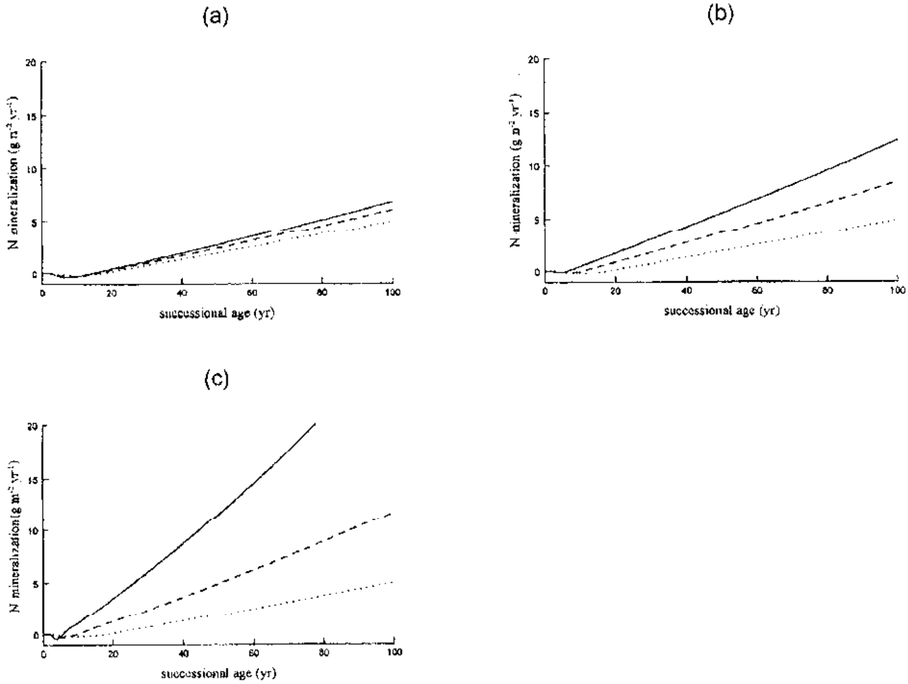

Figure 3. The change in nitrogen mineralization during succession in ecosystems dominated by three plant species with (a) different relative biomass loss rates, L; (b) different litter decomposabilities, k; and (c) different relative biomass loss rates and different litter decomposabilities, L and k. Changes are calculated using a simple model for the carbon and nitrogen dynamics in soils.
(a) solid line: L = 0.4; broken: L = 0.2; dotted: L = 0.1; (b) solid: k = 0.4; broken: k = 0.2; dotted: k = 0.1; (c) solid: k = 0.4 and L = 0.4; broken: k = 0.2 and L = 0.2; dotted: k = 0.1 and L = 0.1.

decomposability greatly enhanced the increase in nutrient mineralization with time (Figure 3c).

As a next step we calculated changes in species composition and nutrient mineralization during succession in an ecosystem with two hypothetical plant species that were identical except in maximum growth rate, relative biomass loss rate and litter decomposability. We compared an *Erica*-like species (low potential growth rate, low biomass losses, low litter decomposability) with a *Molinia*-like species (high potential growth rate, high biomass turnover, producing easily decomposable litter). The *Erica*-like species is dominant during the early phases of succession, when only small quantities of soil organic matter have accumulated and the mineralization rate is below 6 g N m^{-2} yr^{-1} (Figure 4). If accumulation of soil organic matter continues and the mineralization rate increases to sufficiently high levels, *Molinia* replaces

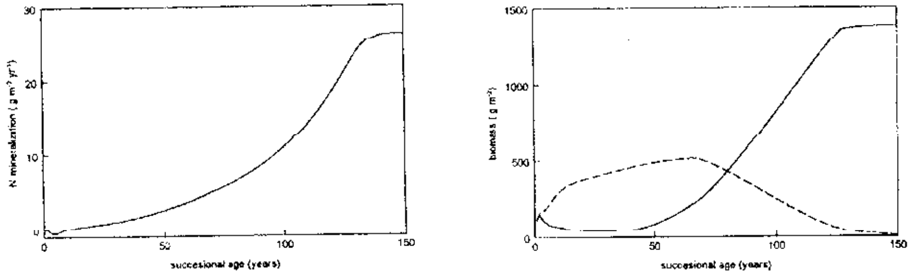

Figure 4. The change in (a) nitrogen mineralization and (b) biomass of *Erica* (dashed line) and *Molinia* (solid line) during succession. Changes are calculated using a simple model for light and nitrogen competition and the carbon and nitrogen dynamics in soils. The two species differ only in potential growth rate, Gmax, biomass loss rate, L, and litter decomposability, k. *Erica*: Gmax = 750 g m^{-2} yr^{-1}, L = 0.6 yr^{-1}, k = 0.05 yr^{-1}; *Molinia*: Gmax = 2500 g m^{-2} yr^{-1}, L = 0.9 yr^{-1}, k = 0.2 yr^{-1}.

Erica rather rapidly because of its higher potential growth rate. After *Molinia* starts to replace *Erica* the increase in mineralization rate is greatly accelerated. During this phase a positive feedback develops between the positive effect of an increased mineralization upon the expansion of *Molinia*, and the positive effect of an increase in *Molinia* upon the mineralization rate. This positive feedback is quantitatively significant only during the early phase of the expansion of *Molinia*. In later phases *Molinia* approaches its maximum growth rate, so that an increase in nitrogen supply does not lead to any further increase in litter production.

Empirical evidence

Our model analysis yielded not only the hypothesis that mineralization will increase over time, up to a certain maximum is reached, but also that the rate of increase is greatly affected by the plant species that is dominant (cf. Wedin & Tilman 1990). The data we collected in the various chronosequences support the first hypothesis. As a first step in testing the second hypothesis we carried out several studies in which we compared the annual nitrogen mineralization in adjacent sites that were dominated by either *Erica* and *Calluna* or by *Molinia* and *Deschampsia*. We compared four groups of neighbouring sites, each of them completely dominated by one species (Berendse et al. 1987; Berendse 1990; Van Vuuren et al. 1992). In the first group we found no significant difference between annual mineralization rates, but within the other groups differences were statistically significant (Figure 5). At these sites the mineralization in plots dominated by *Erica* or *Calluna* varied between 4 and 6 g m^{-2} yr^{-1}, whereas the mineralization in the grass-dominated plots

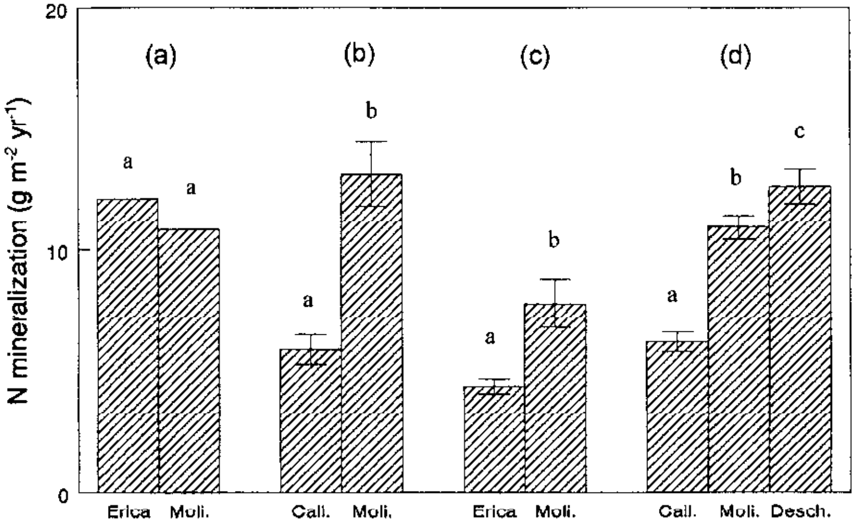

Figure 5. The annual nitrogen mineralization in four groups of neighbouring plots dominated by (a) *Erica* and *Molinia* (Berendse et al. 1987); (b) *Calluna* and *Molinia* (Berendse 1990); (c) *Erica* and *Molinia* (Van Vuuren et al. 1992); (d) *Calluna*, *Molinia* and *Deschampsia* (Van Vuuren et al. 1992). Differences were tested by a one-way ANOVA, followed by Tukey's studentized range test. Different letters indicate significant differences between subsites dominated by the different species.

varied between 8 and 13 g m^{-2} yr^{-1}. The *Calluna* and *Molinia* plots in the second site (Figure 5b) are part of the heathland chronosequence (Figure 1) and had successional ages of 30 and 50 years, respectively. No information was available about the successional age of the plots at the other three sites. These data certainly corroborate our hypothesis, but they do not enable us to distinguish between the effects of successional age and the effect of the dominating plant species. Different mineralization rates could have been caused by the different dominant plant species, but it is also plausible that initial differences in nutrient supply favoured different species and brought them to dominance.

Reliable proof that different plant species have significant impacts upon the increase in N mineralization appears very hard to obtain in realistic field situations. In 1992 we started a garden plot experiment in which we compared monocultures of different plant species planted at the same time. Plots of 1 by 1 m in five replicated blocks were cut out to a depth of 50 cm, where the yellow subsoil was present. The plots were subsequently replenished with sandy soil that was sieved in order to remove old roots and were then planted with monocultures of *Erica*, *Calluna* and *Molinia*. In 1996 we measured nitrogen mineralization during three periods of 8 weeks. Summed mineralization rates were significantly different between the plots planted with the three species (ANOVA; $p < 0.05$). The mineralization in the *Molinia* plots was clearly higher (7.8 g m^{-2}) than that in the plots dominated by the evergreen dwarf shrubs (*Calluna*: 2.8; *Erica*: 4.6 g m^{-2}). These data provide the first convincing evidence that the grass has a positive impact upon the increase in mineralization during succession as compared to the two dwarf shrubs *Erica* and *Calluna*.

Final remarks

During succession on mineral, nutrient-poor substrates the accumulation of dead plant materials results in dramatic changes in the soil. The nitrogen mineralization can increase by a factor of 10 to 15 within a period of 50 years. In the extremely dry inland dunes the soil moisture content increased by more than a factor 10 and converged strongly towards the soil water conditions in the less dry heathland habitats. Such changes are favourable for the establishment and growth of most vascular plant species, if there is no inter-specific competition. But another consequence of soil organic matter accumulation is the strong decline in soil pH and soil Ca content. In the inland dune sequence pH-KCl in the mineral subsoil declined by almost two units within 121 years. Such a change cannot be considered to be favourable for most vascular plant species, especially if the pH reaches sufficiently low levels to increase the Al^{3+}-concentrations in the soil solution.

The ericaceous dwarf shrub and the perennial grass species we focused on showed important differences in the longevity of their leaves and other organs, potential growth rates and litter decomposition rates. For physiological reasons, properties associated with low loss rates and high potential growth rates cannot be combined easily (Chapin 1980). Such a trade-off results in biomass loss rates and potential growth rates being positively correlated. This positive correlation is typified by the *Erica* and the *Molinia* syndromes, but seems to be a more general pattern. In 14 plant species of grassland and heathland communities we measured both the leaf life spans and the relative growth rates at maximum nutrient supply in two independent experiments. Leaf loss rates and maximum growth rates were strongly positively correlated among these 14 species. The *Erica* and *Molinia* syndromes include low and high litter decomposabilities. The long life span of plant parts in the ericaceous species was possible because of the increased concentrations of lignin and secondary, defensive compounds that apparently protected these plant tissues against fungal and microbial attacks even after their death (cf. Grime & Cornelissen 1996).

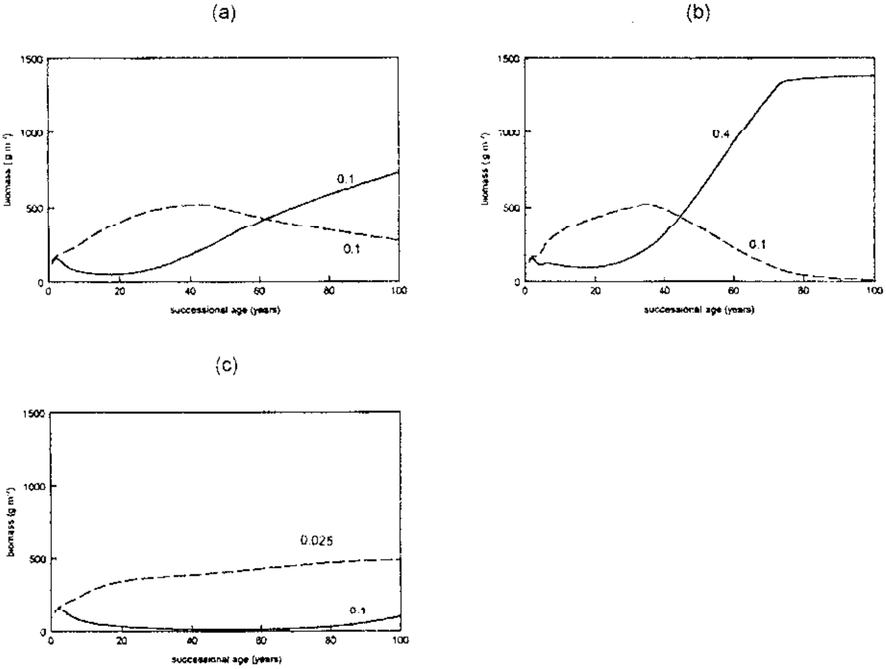

Figure 6. The change in biomass of *Erica* (dashed line) and *Molinia* (solid line) during succession. Changes are calculated using a simple model for light and nitrogen competition and the carbon and nitrogen dynamics in soils.
(a) The two species differ only in potential growth rate (Gmax) and biomass loss rate (L). *Erica* Gmax = 750 g m^{-2} yr^{-1}, L = 0.6 yr^{-1}, k = 0.1 yr^{-1}; *Molinia* Gmax = 2500 g m^{-2} yr^{-1}, L = 0.9 yr^{-1}, k = 0.1 yr^{-1}.
(b) The litter decomposability in *Molinia* is increased (k = 0.4 yr^{-1}).
(c) The litter decomposability in *Erica* is reduced (k = 0.025 yr^{-1}).

Low litter decomposability has probably – at least partly – been evolved as an indirect consequence of natural selection in favour of reduced nutrient losses from the plant. But earlier I suggested that direct selection in favour of low or high litter decomposability can also be expected (Berendse 1994). We modelled the dynamics of an ericaceous species and a perennial grass during heathland succession while varying litter decomposability. When litter of the two species decomposes at equal rates (0.1 yr^{-1}), the ericaceous species is dominant during the early phases, but is replaced by the perennial grass after an increase in N mineralization (Figure 6a). When the perennial grass produces litter that decomposes more easily (0.4 yr^{-1}), the perennial grass appears to become dominant much more rapidly (Figure 6b). On the other hand, when the perennial grass competes with a genotype of the ericaceous species that produces litter which decomposes more slowly (0.025 yr^{-1}), the ericaceous species remains dominant much longer (Figure 6c). These simulation results imply that within one successional sequence in species with low biomass turn-over and low potential growth rates, natural selection might favour genotypes that produce slowly decomposable litter, whereas in species with high growth rates and high biomass losses fitness might be higher in genotypes which produce litter that can decompose more easily. The positive correlation between biomass loss rates, potential growth rates and litter decomposabilities among a wide variety of plant species has important consequences for the effects that plants may have on soil organic matter dynamics and nutrient mineralization. These plant properties not only affect the fertility of the soil, but also determine the outcome of competition if the nutrient supply changes during succession. Species that are able to replace other species after an increase in nutrient mineralization seem to accelerate the increase in nutrient mineralization too. Such effects could greatly speed up the changes in species composition during succession in nutrient-poor ecosystems. The two main groups of vascular plant species that almost symbolise these two sets of interconnected plant properties are the Gymnosperms and the Angiosperms. The burgeoning of many new Angiosperm species during the last part of the Mesozoic might, at least partly, be caused by their growth rates being faster than those of the slow-growing Gymnosperms. During this period most new Angiosperm species had to compete with Gymnosperms which were probably characterized by long-lived leaves or needles that decomposed slowly after abscission. It is possible that the positive feedback between the effects of changes in nutrient supply upon the competitive ability of species and the effects of these species upon soil fertility was partly responsible for the rapid expansion of Angiosperms during the latter part of the Cretaceous era.

References

Aerts R & Berendse F (1988) The effect of increased nutrient availability on vegetation dynamics in wet heathlands. Vegetatio 76: 63–69

Aerts R, Berendse F, De Caluwe H & Schmitz M (1990) Competition in heathland along an experimental gradient of nutrient availability. Oikos 57: 310–318

Berendse F (1983) Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. J. Ecol. 71: 379–390

Berendse F (1988) Een simulatiemodel als hulpmiddel bij het beheer van vochtige heidevelden. CABO, Wageningen

Berendse F (1990) Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. J. Ecol. 78: 413–427

Berendse F (1994) Litter decomposability: a neglected component of plant fitness. Journal of Ecology 82: 187–190

Berendse F & Aerts R (1984) Competition between *Erica tetralix* L. and *Molina caerulea* L. Moench as affected by the availability of nutrients. Acta Ecologica/Ecol. Plant. 5: 3–14

Berendse F, Beltman B, Bobbink R, Kwant R & Schmitz M (1987) Primary productivity and nutrient availability in wet heathland ecosystems. Acta Oecologica/Oecol. Plant. 8: 265–279

Berendse F, Schmitz M & de Visser W (1994) Experimental manipulation of succession in heathland ecosystems. Oecologia 100: 38–44

Berg B & McClaugherty C (1987) Nitrogen release from litter in relation to the disappearance of lignin. Biogeochemistry 4: 219–224

Chapin III FS (1980) The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11: 233–260

Escudero A, Del Acro JM, Sanz IC & Ayala J (1992) Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. Oecologia 90: 80–87

Grime JP & Cornelissen JHC (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. Oikos 77: 489–494

Kirchner JW (1989) The Gaia hypothesis: can it be tested? Rev. Geophysics 27: 223–235

Lovelock JE (1979) Gaia. A new look at life on Earth. Oxford University Press, Oxford

Lovelock JE (1989) The Ages of Gaia. Oxford University Press, Oxford

McClaugherty C & Berg B (1987) Cellulose, lignin and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. Pedobiologia 30: 101–112

Melillo JM, Aber JD & Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621–626

Miles J (1985) The pedogenic effects of different species and vegetation types and the implications of succession. Journal of Soil Science 36: 571–584

Tilman D (1988) Plant strategies and the structure and dynamics of plant communities. Monographs in Population Biology, Princeton University Press, New York

Van Breemen N (1993) Soils as biotic constructs favouring net primary productivity. Geoderma 57: 183–212

Van Vuuren MMI, Aerts R, Berendse F & de Visser W (1992) Nitrogen mineralization in heathland ecosystems dominated by different plant species. Biogeochemistry 16: 151–166

Van Vuuren MMI, Berendse F & de Visser W (1993) Species and site differences in the decomposition of litters and roots from wet heathlands. Can. J. Bot. 71: 167–173

Van Vuuren MMI & Berendse F (1993). Changes in soil organic matter and net nitrogen mineralization in heathland soils, after removal, addition or replacement of litter from Erica tetralix or Molinia caerulea. Biology and Fertility of Soils 15: 268–274

Wedin DA & Tilman D (1990) Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84: 433–441