

# A comparative study on nutrient cycling in wet heathland ecosystems

## I. Litter production and nutrient losses from the plant

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**Summary.** The term relative nutrient requirement is introduced in order to measure and to compare the nutrient losses from different perennial plant populations and the amount of nutrient that they need to absorb to compensate these losses. The relative nutrient requirement ( $L$ ) is defined as the amount of the growth-limiting nutrient that must be taken up to maintain or replace each unit of biomass during a given time interval (e.g.,  $\text{mg N g}^{-1} \text{ biomass year}^{-1}$ ). It is derived that in a plant community with two competing perennial plant populations, species 1 will become dominant if the relative competition coefficient  $k_{12}$  (sensu De Wit 1960) exceeds the ratio between the relative nutrient requirements of the two species ( $L_1/L_2$ ), whereas species 2 will become dominant, if  $k_{12}$  is below this critical ratio. The above-ground litter production was measured in wet heathland communities dominated by *Erica tetralix* or by *Molinia caerulea* in order to estimate  $N$  and  $P$  losses from the above-ground biomass and to calculate the relative  $N$  and  $P$  requirements of these species. *Molinia* lost during one year 63% and 34%, respectively, of the amount of  $N$  and  $P$  present in the above-ground biomass at the end of the growing season. These losses were in *Erica* 27% and 31%, respectively. The relative  $N$  requirements of the two species show the same difference: 7.5 and 2.6  $\text{mg N g}^{-1} \text{ yr}^{-1}$ , respectively, in *Molinia* and in *Erica*. Also the relative  $P$  requirement of *Molinia* is higher as well as that of *Erica* (0.18 versus 0.08  $\text{mg P g}^{-1} \text{ yr}^{-1}$ ). The relative competition coefficient of *Molinia* with respect to *Erica* ( $k_{me}$ ) is equal to unity under unfertilized conditions but increases with increasing nutrient supply. Under nutrient-poor conditions  $k_{me}$  is below the critical ratio of the relative nutrient requirements of the two species ( $L_m/L_e=2.9$  or 2.3), so that *Erica* will be the dominant species. After an increase in nutrient availability  $k_{me}$  increases and exceeds this critical limit which results in *Molinia* replacing *Erica*. During the last 20 years this replacement of *Erica*-dominant communities by monocultures of *Molinia* has been observed in almost all wet heathlands in The Netherlands along with a strong increase in nitrogen availability.

**Key words:** Nutrient cycling – Litter production – Competition – Relative nutrient requirement

During the last few decades there has been a large increase in the grass *Molinia caerulea* (L.) Moench in wet heathland communities in the Netherlands. These were formerly dominated by *Erica tetralix* L. Nowadays, large areas of heathland are completely dominated by *Molinia*. Fertilization experiments in the field showed that an increase in the availability of nitrogen or phosphorus in *Erica* dominated heathland leads after a few years to dominance of *Molinia* and eventually to the disappearance of *Erica* (Aerts and Berendse, unpublished work). In formerly *Erica* dominated communities an increase in the available nitrogen and phosphorus has occurred during the last decades because of the accumulation of humus and litter. In the first half of this century the accumulation of organic matter in the soil was slowed down or interrupted at regular intervals by agricultural practices such as turf removal, burning or sheep grazing. We have found that in many wet heathlands in the Netherlands the accumulation of humus and litter has led to a high mineralization of nitrogen, i.e. 100–130  $\text{kg N ha}^{-1} \text{ yr}^{-1}$  (Berendse et al. 1987). The second factor that probably has contributed to the increased availability of nitrogen is the increased atmospheric deposition of ammonium, that is brought about by an increased  $\text{NH}_3$ -emission from heavily manured pastures and arable fields that surround these heathlands (Van Breemen et al. 1982).

The questions that we wish to answer are: why is *Erica* able to maintain its dominance under nutrient-poor conditions and why does an increase in nutrient availability result in *Molinia* replacing *Erica* as the dominant species. It is important to understand which plant properties can be regarded as favourable for the plant under nutrient-poor conditions and which properties are favourable in more nutrient-rich environments. In examining these questions it is important to realize that the success of a perennial plant population is not only determined by the amount of nutrients that is absorbed annually by the population, but also by the amount of nutrients that is lost. In environments where nutrient availability limits plant growth, the dynamics of perennial populations are to a large extent determined by the balance between the uptake and the loss of nutrients. An individual or population in a natural environment is continuously losing nutrients. These losses may occur through a variety of pathways: mortality of plant parts (shedding of leaves, flowers etc.; mortality by disturbance; root turn-over); herbivory (e.g. large herbivores, phytophagous insects, root nematodes, parasitic fungi); leaching from leaves etc. (especially of cations); production of seed and pollen and root exudation. The nutrients that are lost

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by the plant cannot easily be taken up again. The plant has to compete with other plants and with microorganisms for the nutrients that remineralize from the litter. Moreover, part of the nutrients that return to the soil may be lost by leaching from the soil profile, denitrification or ammonia volatilization or may be bound in very resistant humus compounds.

The impact of the nutrient availability and the relative competitive ability of the two species on nutrient uptake have been examined by Berendse and Aerts (1984) and by Berendse et al. (1987). In this paper we will discuss the loss of nutrients from the plant by litter production. At a first glance the two species seem to behave very different in this respect. *Erica* is an evergreen dwarf shrub, whereas *Molinia* is a perennial grass that dies off above-ground completely at the end of the growing season. We measured the mortality of the different plant organs and the withdrawal of nutrients from dying plant parts. We restricted our study to the losses of nitrogen and phosphorus, as our fertilization experiments in the field showed that these two nutrients had an important effect on the dynamics of the two species (Aerts and Berendse, unpublished work). In the theoretical section we analyse the consequences of the loss of nutrients from the plant for the dynamics of communities with both *Erica* and *Molinia*.

### The relative nutrient requirement

A plant that loses a large part of its nutrients annually through litter production, grazing, seed production, etc. will have to take up a larger amount of nutrients to maintain its biomass than a plant that retains more of its nutrients. In order to measure and to compare the needed nutrient uptake of different species under natural conditions, we introduced the concept of the relative nutrient requirement (Berendse 1985). The nutrient requirement ( $NL$ ) is the amount of the growth-limiting nutrient lost from a plant individual or a plant population during a given period. This amount must be absorbed by the individual or the population just to maintain its biomass. If it absorbs more, then its biomass will increase; if less, then its biomass will decline. The relative nutrient requirement ( $L$ ) is the nutrient requirement per unit of biomass, i.e. the amount of nutrient that is needed to maintain or replace each unit of biomass during a given time period (e.g.  $\text{mg N g}^{-1} \text{ dry weight yr}^{-1}$ ). Using this definition the cost of biomass maintenance can be calculated in terms of the nutrients that are required. For other purposes it may be useful to calculate the relative nutrient requirement per unit of nutrients present in the plant ( $L_n$ ; e.g.  $\text{mg N mg}^{-1} \text{ N yr}^{-1}$ ). The inverse of this parameter is, under steady-state conditions, the mean residence time of the nutrient in the plant.

We carried out a mathematical analysis of the competition between two perennial plant populations (e.g., *Molinia* and *Erica*) with different relative nutrient requirements. When plant growth is limited by nutrient availability, the dynamics of the two populations are determined by the uptake and the loss of the growth-limiting nutrient. The nutrient requirement or loss of nutrients ( $NL$ ) from the population is:

$$NL = L * B \quad (1)$$

where  $L$  represents the relative nutrient requirement and  $B$  the biomass. The appropriate units of the different vari-

**Table 1.** List of the variables and parameters, that are used in the equations, with their appropriate units

Symbol	Name	Units
$B$	biomass	$\text{g dry weight/m}^2$
$N$	nutrient availability	$\text{mg nutrient m}^{-2} \text{ yr}^{-1}$
$NL$	nutrient loss or nutrient requirement	$\text{mg nutrient m}^{-2} \text{ yr}^{-1}$
$L$	relative nutrient requirement	$\text{mg nutrient g}^{-1} \text{ dry weight yr}^{-1}$
$U$	nutrient uptake	$\text{mg nutrient m}^{-2} \text{ yr}^{-1}$
$n$	nutrient concentration in biomass	$\text{mg nutrient/g}^1 \text{ dry weight}$
$b$	competition coefficient	dim. less
$k_{me}$	relative competition coefficient of species $m$ with respect to species $e$	dim. less
$t$	time	yr

ables and parameters are listed in Table 1. The uptake of nutrients by a plant population is determined by the amount of nutrients ( $N$ ) that is available during the growing period (e.g.,  $\text{mg N m}^{-2} \text{ yr}^{-1}$ ) and by competition with the other population. The most adequate way of describing the partitioning of a limiting factor between two competitors is still given by the competition hyperboles developed by analogy with Raoult's law for the relation between liquid and vapour composition (De Wit 1960). According to this theory the uptake by each population is given by:

$$U_m = \frac{b_m B_m}{b_m B_m + b_e B_e} N \quad (2a)$$

$$U_e = \frac{b_e B_e}{b_m B_m + b_e B_e} N \quad (2b)$$

where  $U_m$  and  $U_e$  represent the uptake by *Molinia* and *Erica* and  $b_m$  and  $b_e$  are the coefficients with which  $B_m$  and  $B_e$  must be weighed to take into account the different competitive ability of the two species.  $N$  represents the rate at which the nutrient that limits growth becomes available for uptake by the vegetation. These equations can be simplified by introducing the relative competition coefficient of *Molinia* with respect to *Erica*  $k_{me} = b_m/b_e$ :

$$U_m = \frac{k_{me} B_m}{k_{me} B_m + B_e} N \quad (3a)$$

$$U_e = \frac{B_e}{k_{me} B_m + B_e} N \quad (3b)$$

The relative competition coefficient  $k_{me}$  measures the relative competitive ability of *Molinia* with respect to *Erica*. The relative competition coefficient is not a constant, but dependent on the length of the time interval after which it is measured. We define here  $k_{me}$  with respect to the length of one year or growing season. Moreover,  $k_{me}$  is here defined just with respect to the uptake of nutrients and not with respect to the dynamics of the biomass. So, the relative competition coefficient is mathematically independent of the relative nutrient requirement.

Combination of expression (1) and (3) yields the two difference equations that describe the dynamics of the biomass of two perennial plant populations:

$$\frac{\Delta B_m}{\Delta t} = \frac{1}{n_m} \left( \frac{k_{me} B_m}{k_{me} B_m + B_e} N - L_m B_m \right) \quad (4a)$$

$$\frac{\Delta B_e}{\Delta t} = \frac{1}{n_e} \left( \frac{B_e}{k_{me} B_m + B_e} N - L_e B_e \right) \quad (4b)$$

The first term between the brackets represents the uptake of nutrients, whereas the second term represents the loss of nutrients. By dividing by the nutrient concentration in the plant ( $n_m$  or  $n_e$ ) the increase or decrease in the amount of nutrients in the plant is converted into the dynamics of the biomass of the two species. Here it is assumed that there is a linear relationship between the amount of the growth-limiting nutrient in the plant and the amount of plant biomass. We have analyzed the equilibrium conditions of (4a) and (4b) by putting both equations to zero and dividing them by each other. We derived that *Molinia* and *Erica* could only co-occur under equilibrium-conditions (nutrient uptake = nutrient loss), if

$$k_{me} = L_m / L_e \quad (5a)$$

*Molinia* will be dominant under equilibrium conditions, if

$$k_{me} > L_m / L_e \quad (5b)$$

and *Erica* will be dominant, if:

$$k_{me} < L_m / L_e \quad (5c)$$

The validity of the results of our analysis was verified by numerous simulations. In these simulations an equilibrium always was established, so that the presented conditions predict the final outcome of the competition between the two species.

We may consider our equations to be an extension of the classical competition theory of De Wit (1960). If the relative nutrient requirements of the two competing species are equal to each other, conditions (5a), (5b) and (5c) are reduced to the analogous conditions in classical theory. However, if the relative nutrient requirements are different, it is possible that *Molinia* wins with respect to the uptake of nutrients (i.e.  $k_{me} > 1$ ), but finally loses in the competition with *Erica*, if *Erica* has a lower relative nutrient requirement. Just when the relative competition coefficient exceeds the critical ratio between the relative nutrient requirements of the two species, *Molinia* will be able to replace *Erica* as the dominant species.

So, we may conclude that in order to predict the dynamics of two competing perennial plant populations we do not only need to know their competitive abilities with respect to each other, but we must also know their relative nutrient requirements. The relative nutrient requirement appears to be a biologically meaningful term in order to measure and to compare the nutrient economy of perennial plant populations.

### Study area

This study was carried out in the Gelderse Vallei in the central part of the Netherlands (52°13' N, 5°32' E). During the Weichselian glacial this area was covered with aeolic sandy deposits. In the beginning of this century extensive wet heathlands dominated by *Erica tetralix* L. were present.

Nowadays, most of these heathlands have been converted into agricultural grasslands and the few remaining heaths are embedded in a matrix of intensively cultivated land. Our study site was located in one of the last large wet heathlands found in the nature reserve, Kruisshaarse heide. Nowadays most of this heathland is dominated by *Molinia caerulea* (L.) Moench, but there still are a few scattered *Erica*-dominated communities. In the *Molinia*-dominated areas a layer of *Erica* litter still can be observed under the layer of *Molinia* litter. The soil is strongly podzolized and is classified on the soil map of the Netherlands as a "veldpodzol". On top of a soil profile of fine sand is a FH-layer of  $4.3 \pm 1.1$  cm. The amount of organic matter in the FH- and the L-layer was measured to be ca. 4 and 1 kg/m<sup>2</sup>, respectively (Berendse et al. 1987). Nitrogen and phosphorus are almost exclusively restricted to the upper 10 cm of the soil. The pH(H<sub>2</sub>O) in this layer varies between 3.8 and 4.5, the pH of the *Molinia*-dominated communities being slightly higher than those of the *Erica*-dominated communities. The water table fluctuates during the year between a few cm above and 1.7 m below the soil surface.

The communities dominated by *Molinia* and by *Erica*, that occurred at our sites had almost identical environmental conditions (cf. Berendse et al. 1987). In both communities almost no other phanerogamic species occurred.

### Methods

We measured during 1983 the litter production and the retranslocation of nutrients from dying plant parts in communities dominated by *Erica* and in communities dominated by *Molinia*. Litter traps underneath the vegetation appeared not to be a feasible method for estimating litter production, so we decided to estimate it using indirect methods. Moreover, we measured at the end of the growing season the standing biomass. Below we describe the methods used for the different plant parts of the two species.

#### *Erica*: standing biomass

On 31 October 1983, 5 sods measuring 20 × 20 cm were cut. The plants were divided up into current year wood, second year wood, current year leaves, second year leaves, older living wood and leaves, flowers, standing dead wood and buried stems. These fractions were dried, weighed and analyzed in order to determine the nitrogen and phosphorus content.

#### *Erica*: leaf and stem litter

During 1983, every two weeks, from 16 May till 3 October 1983, 60 randomly chosen *Erica* branches were cut off as close to the soil surface as possible. In the laboratory these branches were cut into sections at the transitions between the parts of wood grown in successive years (Bannister 1966), down to the point where adventitious roots appeared. The number of whorls, the length and dry weight of the parts of wood and the number and dry weight of the adhering leaves were recorded. In order to determine the nitrogen and phosphorus content, the branches and leaves from the same age classes were pooled, ground and analyzed. The total number of leaves is found from the number of whorls, easily seen from the scars of the leaves on the bark of the branches, multiplied by 4. By subtracting the number of living leaves still attached to the stem from

the estimated total number of leaves one finds the number of fallen leaves. Details of these and other calculations are given in the results.

To measure the loss of weight, and the loss of nitrogen and phosphorus during senescence, it was necessary to collect dead *Erica* leaves. Under normal circumstances a lot of dead leaves can be collected by shaking *Erica* shrubs, but no dead leaves can be collected after a rainshower. This observation led us to conclude that dead *Erica* leaves fall from the shrub soon after they die. Thus, every two weeks from 30 May till 3 October ten samples of ca. 500 dead leaves (which probably recently died off) were obtained by gently shaking the shrubs. These were counted, weighed, ground and analyzed.

On the basis of the dry weight per length of the stems in the different age classes secondary stem growth could be calculated. Moreover, current year stem production was measured at the end of growing season (see above). On the basis of these data a maximum estimate of stem mortality was calculated assuming that no accumulation of living wood occurred.

#### *Erica*: flower and current year shoot litter

In a homogeneous part of the experimental area ten plots of 40 × 40 cm were chosen at random and divided into four 20 × 20 cm subplots, which were randomly allocated to the different series. In the first subplot 20 shoots of *Erica* were marked with waterproof latex paint so that the death of current-year shoots could be detected. In the second subplot all umbels of flowers were harvested as soon as the buds opened. In the third subplot the umbels were harvested when the corolla tubes were coloured brown, about 1.5–2 weeks after the buds had opened. In the fourth subplot both the living and the dead flowers were counted. Living and dead flowers were defined as flowers with a purple or brown corolla tube, respectively. The main aim of counting in the fourth subplots was to compare the number of flowers in these plots with those from the yield plots in order to detect possible harvesting effects on the total number of flowers per unit area. Counting and harvesting was carried out each 2 weeks in all series. During the study period one 40 × 40 plot was destroyed, so the data of only 9 plots could be used.

#### *Molinia*: standing biomass and shoot and basal internode litter

In autumn *Molinia* shoots die off completely above ground except for the basal internodes. These persist through the winter period, give rise to the next year's shoot primordia and die off during the next summer (Jefferies 1916). The potential aboveground litter production is the amount of biomass present at the moment at which the standing crop is at this maximum. This moment, which was taken to be 29 August (1983), 5 sods of 40 × 40 cm were taken from the *Molinia* vegetation. In the laboratory the individual *Molinia* shoots in the sods were separated. A random sample of 20 shoots was taken from each sod. Both the 5 samples of 20 shoots and the remaining shoots in each sod were divided into leaves, culms, panicles, basal internodes and the thick roots that are attached to the basal internodes (cord roots; cf. Jefferies 1915). Leaves were divided into living and dead parts. If the sods still contained internodes from the previous year (which were always dead), then these

were also kept separately. For each sod we dried and weighed the different plant parts and determined the nitrogen and phosphorus content in it. The length and dry weight of each of the different parts of the 20 shoots were determined. The shoots were then pooled for nutrient analysis.

From 29 August onwards, every 2 weeks 5 samples of 20 shoots were taken from 5 sods, until 7 November, by which time all the above ground biomass had died off. On the basis of the dry weight per unit of length and the nitrogen and phosphorus concentration it was possible to calculate the translocation that might have occurred during senescence. On the basis of the data of the sod samples from 29 August these figures could be used to calculate values per unit area.

#### Chemical analysis

Dry weights were determined after the plant parts had been dried for 48 h at 70° C; then the material was ground. Nitrogen and phosphorus concentrations were determined through the digestion of 200 mg ground material by 30 N sulphuric acid and a mixture of sodium sulphate, copper sulphate and selenium. The diluted digests were analysed colorimetrically on an autoanalyzer using ammonium molybdate for phosphate and indophenol blue with salicylate for ammonium.

## Results

#### *Erica*: standing biomass

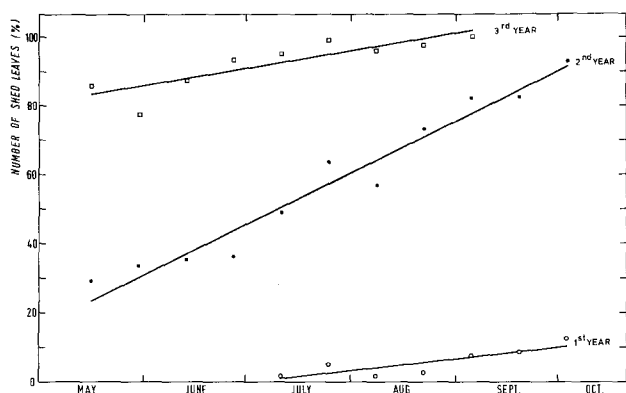
Above-ground standing biomass of the different plant parts of *Erica* at the end of the growing season of 1983 are summarized in Table 2. Most of the previous year leaves had already been shed at this time as had most of the flowers.

#### *Erica*: leaf litter

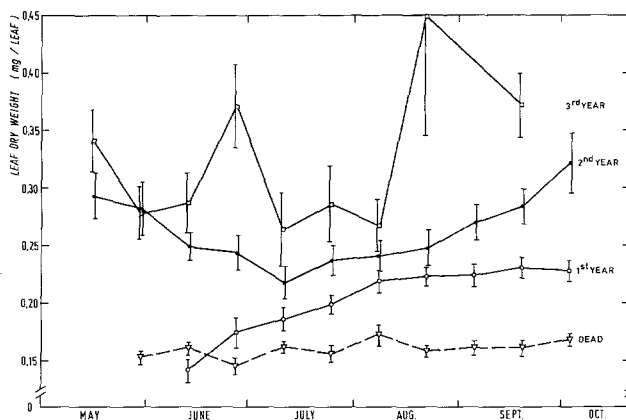
The rate of leaf litter production remains constant over the whole growing season, showing no period of peak fall (Fig. 1). During the third year all leaves that have remained attached to the branches throughout the first two years die off. 23% of second year leaves had already been lost in May, and the remaining leaves nearly all fell off during the second year, so that by October only 9% were left. In July some of the current year's leaves had started falling and by October 10% of them have been lost. From all branches from which the current year leaves started falling,

**Table 2.** The dry weight of the above-ground living biomass (g/m<sup>2</sup>), the nitrogen content and the phosphorus content in the biomass (mg N or P/m<sup>2</sup>) ± standard error of *Erica tetralix* as measured on 31 October 1983 (n=5)

	Biomass	N	P
Current year leaves	152 ± 14	1923 ± 173	53 ± 5
Second year leaves	15 ± 4	168 ± 45	4 ± 1
Current year stems	99 ± 11	869 ± 110	38 ± 5
Previous year stems	492 ± 89	4129 ± 847	112 ± 20
Buried stems	644 ± 89	6625 ± 1073	159 ± 24
Flowers and fruits	13 ± 2	138 ± 15	4 ± 1
Total	1415 ± 83	13852 ± 935	370 ± 18



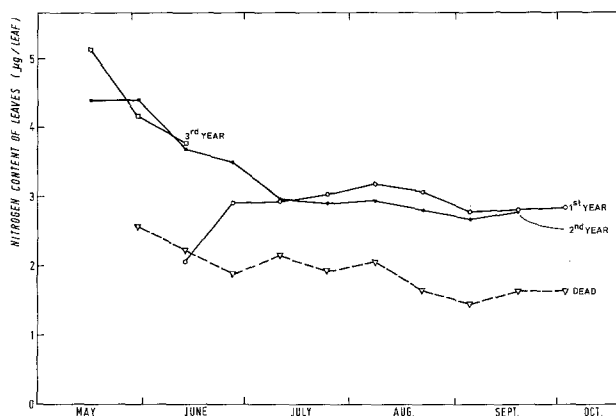
**Fig. 1.** Leaf litter production of first, second and third year *Erica* leaves from 16 May till 3 October, as percentage of the total number of leaf scars that were present in each year class. Regression coefficients and their standard errors for regression of the percentage shed  $S$  against time  $T$  (months) are: 1<sup>st</sup> year leaves:  $S = 0.77 \cdot T$ ,  $b = 0.21$  ( $0.01 < P < 0.05$ ); 2<sup>nd</sup> year leaves:  $S = 3.38 \cdot T$ ,  $b = 0.24$  ( $P < 0.001$ ); 3<sup>rd</sup> year leaves:  $S = 1.14 \cdot T$ ,  $b = 0.26$  ( $0.001 < P < 0.01$ )



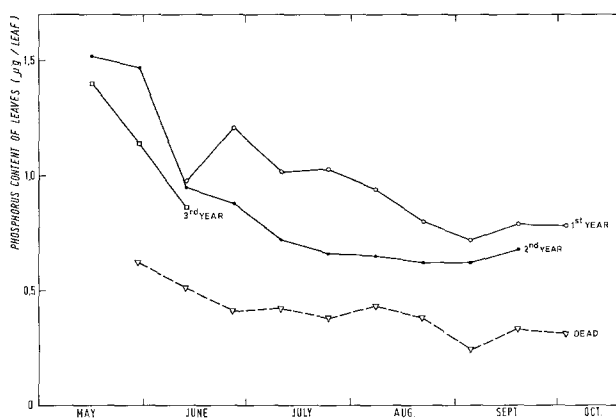
**Fig. 2.** The weight of first, second and third year *Erica* leaves and the weight of dead leaves that are shed, measured from 16 May till 3 October. Vertical bars are standard errors of the mean. Regression coefficients for regression of weight  $W$  (mg/leaf) against time  $T$  (months) are: 1<sup>st</sup> year leaves: 13 June till 8 August  $W = 0.035 \cdot T$  ( $0.001 < P < 0.01$ ), 8 August till 3 October  $W = 0.005 \cdot T$  ( $0.01 < P < 0.05$ ); 2<sup>nd</sup> year leaves: 16 May till 11 July  $W = -0.038 \cdot T$  ( $0.001 < P < 0.01$ ), 11 July till 3 October  $W = 0.031 \cdot T$  ( $P < 0.001$ ); dead leaves: not significant

all second year leaves had already been shed. Because in May there were still third year leaves present and only 23% of the second year leaves had fallen, litter production must slow down or stop during the winter period.

The weight of *Erica* leaves can change rapidly during the growing season (Fig. 2). Current year leaves increase in weight from May till about the beginning of August ( $P < 0.001$ ; deviation regression coefficient from zero using linear regression analysis), after which weight increase per leaf continues but becomes very small ( $P < 0.01$ ). Second year leaves are much heavier in spring than the first year leaves in October. Unfortunately we did not take any measurements during the winter period but it is possible that this weight increase is a result of photosynthetic activity



**Fig. 3.** The amount of nitrogen ( $\mu\text{g}/\text{leaf}$ ) in first, second and third year *Erica* leaves as well as the amount in dead *Erica* leaves, measured from 16 May until 3 October. Regression coefficients for regression of the amount of  $N$  ( $\mu\text{g}/\text{leaf}$ ) against time  $T$  (months) are: 1<sup>st</sup> year leaves: 27 June till 3 October not significant; 2<sup>nd</sup> year leaves: 16 May till 11 July  $N = -0.76 \cdot T$  ( $0.001 < P < 0.01$ ), 11 July till 19 September  $N = -0.09 \cdot T$  ( $0.01 < P < 0.05$ ); dead leaves: 30 May till 3 October  $N = -0.17 \cdot T$  ( $P < 0.001$ )



**Fig. 4.** The amount of phosphorus ( $\mu\text{g}/\text{leaf}$ ) in first, second and third year *Erica* leaves as well as the amount in dead *Erica* leaves, measured from 16 May until 3 October. Regression coefficients for regression of the amount of  $P$  ( $\mu\text{g}/\text{leaf}$ ) against time  $T$  (months) are: 1<sup>st</sup> year leaves: 27 June till 3 October  $P = -0.01 \cdot T$  ( $0.001 < P < 0.01$ ); 2<sup>nd</sup> year leaves: 16 May till 11 July  $P = -0.04 \cdot T$  ( $0.001 < P < 0.01$ ), 11 July till 19 September not significant; dead leaves: 30 May till 3 October  $P = -0.005 \cdot T$  ( $0.001 < P < 0.01$ )

during the winter and early spring. The weight of second year leaves decreases until 11 July ( $P < 0.001$ ), suggesting that carbohydrates are transported from the leaves in the period during which the current year shoots show the largest growth. From 11 July till October there is a steady increase in leaf weight ( $P < 0.001$ ). The few third year leaves that are left are always very large and most of the time heavier than the second year leaves. However, there is no clear pattern during the season, perhaps due to the fact that these third year leaves are rare, and consequently sample sizes are small. The weight of the dead leaves is remarkably constant; regression against time was not significant. So the weight of the leaves that are shed does not seem to be influenced by the weight of the living leaves. Appar-

ently, there is a minimum structure for a leaf and the rest can be translocated. The mean percentage of weight loss during dying off is 35%, measured as the weighted difference between the total weight of first, second and third year leaves that fall in the periods of two weeks, and the total weight of the same number of dead leaves that are shed during these periods.

The nitrogen and phosphorus concentrations in living first and second year leaves and in dead leaves decrease during the growing season (in all cases  $P < 0.001$ ). The amount of nitrogen in the second-year leaves decreases as well ( $P < 0.001$ ; Fig. 3). The three observations on third year leaves show the same decreasing pattern at the beginning. First year leaves reach a constant level of nitrogen already at the end of June. The amount of phosphorus in the second year leaves decreases rapidly in May and June ( $P < 0.001$ ) and thereafter it becomes constant (Fig. 4). Transport of phosphorus takes place from first year leaves as well ( $P < 0.001$ ). The amounts of nitrogen and phosphorus in dead *Erica* leaves are considerably less than in living leaves. The mean percentages of the nitrogen and phosphorus amounts in the leaves that are withdrawn before abscission are 42 and 54%, respectively. These percentages are calculated as the weighted difference between the total amounts of nitrogen and phosphorus in the first, second and third year leaves that fall in the periods of two weeks, and the total amounts of N and P in the same number of dead leaves that are shed during these periods.

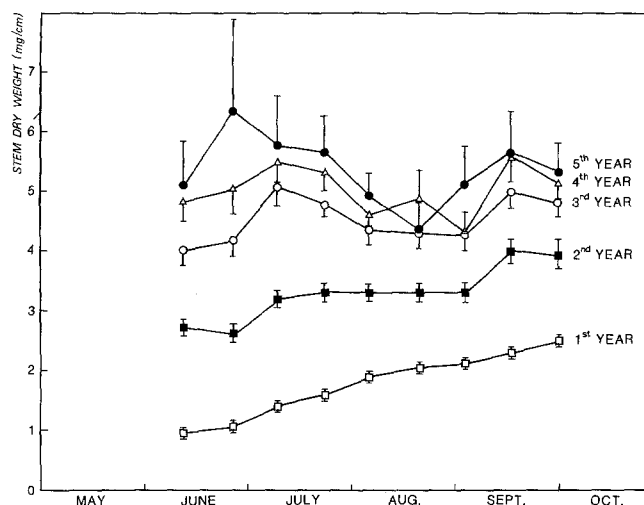
In October 1982 we measured  $7 \text{ g/m}^2$  living previous year leaves at this study site (Berendse et al. 1987). The dry weight of second year leaves (as measured in October 1983) is  $0.32 \text{ mg/leaf}$ . As all 3<sup>rd</sup> year leaves were shed in 1983, the 3<sup>rd</sup> year leaf litter production from October 1982 to October 1983 has been  $7000/0.32 = 21875 \text{ leaves per m}^2$ . Fortunately, the weight of dead leaves is remarkably constant ( $0.16 \text{ mg/leaf}$ ), so that the production of 3<sup>rd</sup> year leaf litter can be calculated to be  $3.5 \text{ g m}^{-2} \text{ yr}^{-1}$ . In October 1982 we measured the biomass of current year leaves to be  $121 \text{ g/m}^2$ . Since in October 90% of the first year leaves are left and after the first year 9% of these leaves have remained, the percentage second year leaf fall is  $(90 - 9)/90 = 90\%$ . The weight of current year leaves in October 1983 was  $0.23 \text{ mg/leaf}$ , so that we can calculate that  $0.9 \cdot 121000/0.23 = 473478$  2<sup>nd</sup> year leaves/ $\text{m}^2$  have been shed. The production of 2<sup>nd</sup> year leaf litter can subsequently be calculated to amount  $76 \text{ g/m}^2$ . In October 1983 the current year leaf biomass was  $152 \text{ g/m}^2$  (Table 2). As 10% of the current year leaves was shed during 1983, we can calculate the current year leaf litter production to be  $(0.1/0.9) \cdot 152 \cdot (0.16/0.23) = 12 \text{ g/m}^2$ . The amounts of nitrogen and phosphorus that are lost by leaf litter production are calculated on the basis of the average nitrogen and phosphorus concentrations in the dead leaves (Table 3).

#### *Erica*: stem litter

Figure 5 shows the course of the mean weight of *Erica* branches of the different age classes. It is clear that almost all secondary stem growth takes place during the period from June to October. Differences between the weights of the parts of branches produced in the successive years were tested, using BMDP-program 4V (URWAS). This was done by means of a two factor (years  $\times$  dates) analysis of covariance with repeated measures (Winer 1971) on log-trans-

**Table 3.** Above-ground litter production ( $\text{g m}^{-2} \text{ yr}^{-1}$ ) and losses of nitrogen and phosphorus by litter production ( $\text{mg N or P m}^{-2} \text{ yr}^{-1}$ ) from *Erica tetralix* during the period October 1982–October 1983

	Litter	N	P
Leaves	92	1098	23
Current year shoots	11	165	7
Previous year stems	86	705	18
Buried stems	112	927	24
Flowers and fruits	52	852	42
Total	353	3747	114



**Fig. 5.** The dry weight of the first, second, third, fourth and fifth year parts of *Erica* branches from 16 June till 3 October. Bars indicate standard-errors of the mean

formed lengths and weights. Length was used as a covariant. The method of repeated measures was used because the parts of wood from the successive years come each time from the same branch, so the years are not totally independent of each other but correlated within the branches. The method of repeated measures accounts for the covariance between the years within the branches. The 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup> and 4<sup>th</sup> year classes were all significantly different from each other ( $P < 0.001$ ). During the 2<sup>nd</sup>, 3<sup>rd</sup>, 4<sup>th</sup> and 5<sup>th</sup> year stems show a weight increase of 59%, 37%, 11% and 5%, respectively. We converted growth per unit branch length into production per unit area on the basis of the total length per year class at the end of the growing season. Total secondary stem growth during 1983 was calculated to be  $99 \text{ g/m}^2$ . The current year stem weight at October 1983 was measured to be  $99 \text{ g/m}^2$  (Table 2), so that the total stem production (minus current year shoot mortality) during 1983 was  $198 \text{ g/m}^2$ .

It is very difficult to measure stem litter production. Mortality of stems seemed at a first glance to be too rare an event to be measured by following marked plant parts. The *Erica*-communities at the study site exist at least for 30 years, and it is probable that the above-ground biomass is near equilibrium, except in those areas in which *Molinia* is increasing. Losses from the above-ground stem compart-

ment occur by mortality of branches and by becoming buried stems. At a certain age the lower parts of the *Erica*-branches bend over, they root adventitiously and litter falls on them. Less than 5% of the above-ground *Erica*-stems have parts that are older than 5 years, which probably means that each year a considerable fraction of the branches becomes buried stems. If the total amount of living wood in these communities does not change over time, the total wood production (net current year stem production + secondary growth previous year stems) equals total mortality of previous year stems. Using the data in Table 2 on previous year stem biomass, it can be calculated that the annual percentage mortality is 17.4%. If the percentage mortality of buried stems and above-ground stems are equal, the litter production of buried and above-ground stems is 112 and 86 g m<sup>-2</sup> yr<sup>-1</sup>, respectively. This estimate of stem litter production does not include current year shoot mortality, which is estimated separately. During 1981, 1982 and 1983 the amount of standing dead wood increased significantly ( $P < 0.005$ ) with 66 g m<sup>-2</sup> yr<sup>-1</sup> (Berendse et al. 1987). The difference between above-ground stem mortality and the accumulation of dead wood may be caused by the fall of dead stem parts into the litter layer. It must be realized that the stem mortality may be over-estimated, as living buried stems may still be accumulating. Nitrogen and phosphorus losses by stem mortality are calculated by multiplying stem litter production by the average nitrogen and phosphorus concentration in the stems (Table 3). We did not find any indication for translocation of these nutrients from dying stem parts, as the concentrations in living and dead wood were equal.

#### *Erica*: flower litter

No differences could be found between the total number of flowers per unit area of the demographic plots and the harvest plots. Thus, the harvesting of living and dead flowers does not seem to influence the total number of flowers per unit area. The total number of produced flowers is estimated to be 19683 ± 1339/m<sup>2</sup> ( $n = 27$ ). The mean weight of living and dead flowers is 2.23 mg and 2.63 mg, respectively. Total losses for flowers and fruits are 52 g/m<sup>2</sup> dry weight, 852 mg/m<sup>2</sup> nitrogen and 42 mg/m<sup>2</sup> phosphorus. These values may be too low since seeds will not be completely ripe at the time they are harvested. A compromise had to be made between too late a harvest, which means that seeds may already be lost, and too early a harvest, when seeds are not yet ripe, and nutrient and weight estimates can be too low. Losses are summarized in Table 3.

#### *Erica*: current year shoot litter

Between 27 June and 11 July there was a large sudden unexplained mortality of first year shoots. About 10% of the marked shoots in the demographic plots died off. In order to estimate how much nitrogen and phosphorus was lost through the mortality of the first year shoots, we used the shoot weight per unit area in June, as found by Berendse et al. (1987) in the beginning of July, namely 104 g/m<sup>2</sup>, and the nutrient content found in living shoots on the date of dying (Table 3). There were no differences in leaf weight or weight per unit of branch length between the dead current-year shoots and the shoots of living plants at that moment, so there was no indication for translocation from these shoots.

**Table 4.** The dry weight of the above-ground living biomass (g/m<sup>2</sup>), the nitrogen content and the phosphorus content of the biomass (mg N or P/m<sup>2</sup>) ± standard error of *Molinia caerulea* as measured on 29 August 1983 ( $n = 5$ )

	Biomass	N	P
Leaves	255 ± 38	4141 ± 607	155 ± 24
Culms	68 ± 12	444 ± 93	23 ± 5
Panicles	22 ± 4	353 ± 68	21 ± 3
Basal internodes	196 ± 32	1500 ± 186	81 ± 14
Total above ground	541 ± 61	6438 ± 640	280 ± 19

#### *Molinia*: standing biomass and shoot and basal internode litter

The dry weight and the nutrient content of the plant parts from the five sods cut on 29 August are given in Table 4. This is the maximum possible litter production. Leaves, culms and panicles die off directly, basal internodes die the following year after having produced that year's shoots.

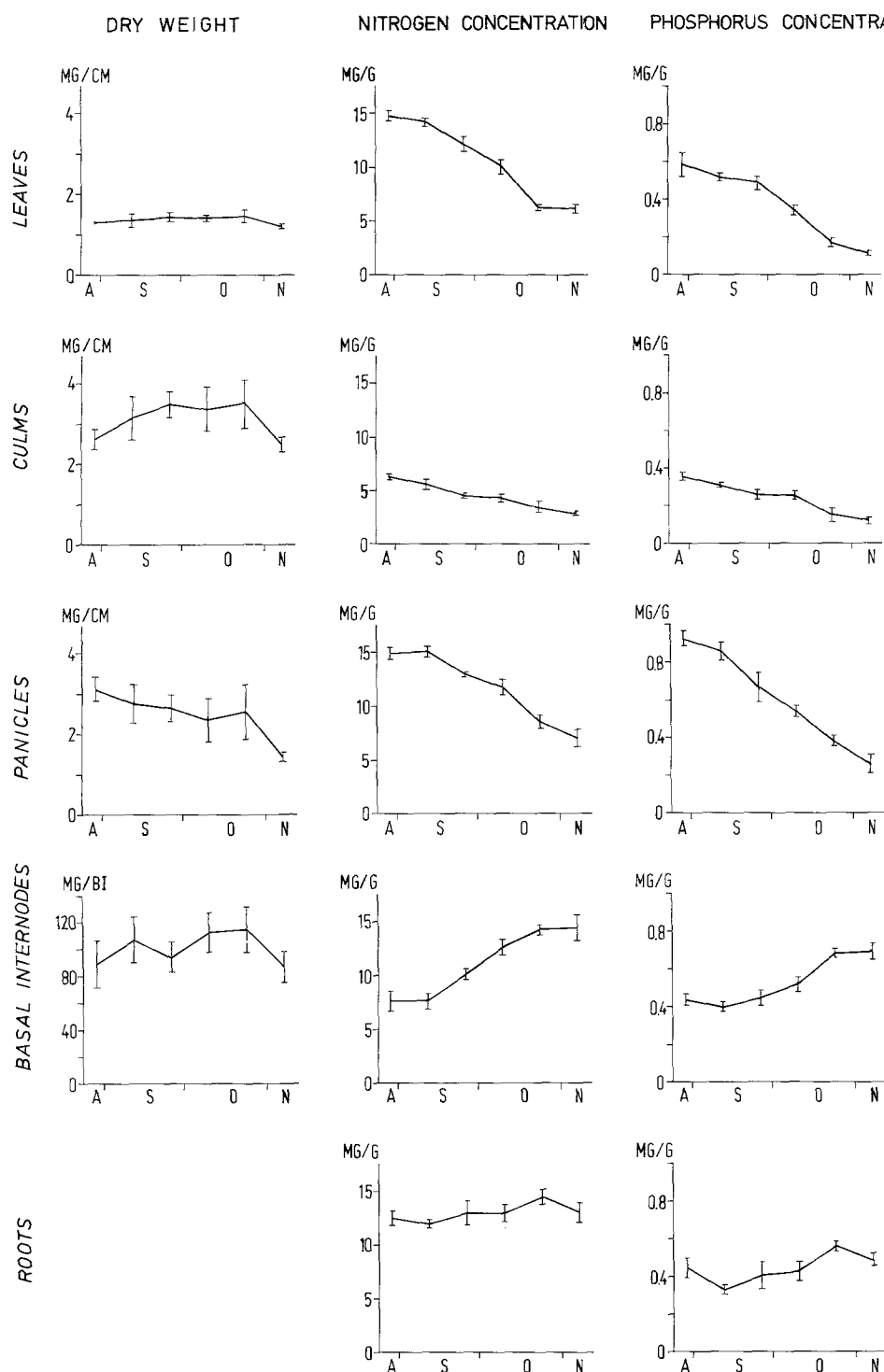
No differences could be found between the weight per unit of length of dead and living leaf material. In the period from 29 August till 7 November, there was no reduction in the weight per unit of length of the total leaf or of the culms (Fig. 6). There was no increase in the weight of the basal internodes. There was not even any difference between the weight of the living basal internodes and the weight of the dead basal internodes from the previous year. The decrease in the weight of the panicles during this period is caused by the release of seeds, which are regarded as lost.

On the other hand there was a significant decrease in the nitrogen and phosphorus concentration in the culms and the leaves, and an increase in the nitrogen and the phosphorus concentration in the basal internodes (Fig. 6). The percentage of phosphorus withdrawn before abscission is higher than that of nitrogen. Table 6 gives percentages and absolute quantities of the translocated nitrogen and phosphorus.

Total losses can be calculated from the reduction in the nutrient concentration and from the nutrient content in the biomass at the time of the maximum standing crop (Table 5). All nutrients in the panicles are regarded as lost. The losses of nutrients per unit area caused by the mortality of the basal internodes are calculated by multiplying the total weight of the basal internodes of the current year by the nutrient concentration in the dead basal internodes of the previous year.

In August – before the withdrawal of nutrients from the shoots – the concentrations of nitrogen and phosphorus in the basal internodes are 8.0 and 0.45 mg/g<sup>1</sup>, respectively. In November – after translocation – the concentrations are 15.1 and 0.71 mg/g<sup>1</sup>. The concentrations in the dead basal internodes of the previous year are 9.5 and 0.21 mg/g<sup>1</sup>. As there were no clear differences between the dry weight of living basal internodes and dead previous year's basal internodes, we may conclude that an important part of the nitrogen and the phosphorus retranslocated to the basal internodes during fall is reused during the next spring.

The cord roots attached to the basal internodes showed a significant increase in nitrogen and phosphorus between 12 September and 24 October, the period in which most nutrients are translocated, but before 12 September and



**Fig. 6.** Dry weight, nitrogen and phosphorus concentration of the different plant parts of *Molinia caerulea*, measured from 29 August till 7 November. Vertical bars indicate the standard error of the mean. The differences between dry weights at the different dates are all not significant. The nitrogen concentrations of the first and the last date are all significantly different except for the roots. The phosphorus concentrations of the first and the last date are all significantly different except for the roots, where only the 2<sup>nd</sup> and the 5<sup>th</sup> date differ significantly (all tested with an analysis of variance followed by a posteriori tests)

after 24 October they showed an unexplained decrease (Fig. 6). There is no difference in the nitrogen content of the living roots attached to this year's basal internodes and that of the dead roots of the previous year's basal internodes. However, the phosphorus concentration in the dead cord roots is 45% lower than that in the living cord roots.

## Discussion

The annual losses of nitrogen and phosphorus from the plant by the mortality of above-ground plant parts are con-

siderable. *Molinia* lost during 1983 63 and 34%, respectively, of the total amount of N and P in the above-ground biomass, whereas these losses from *Erica* were 27 and 31%, respectively (Table 7). It is very hard to believe that nutrient losses of this order of magnitude will not have serious consequences for the population dynamics of perennial plant populations in environments where nutrients limit plant growth. The actual losses are even larger because our study only included part of the possible nutrient losses. We did not measure losses by herbivory, leaching, pollen production and root mortality or root exudation. It may be ques-



**Table 5.** Above-ground litter production ( $\text{g m}^{-2} \text{yr}^{-1}$ ) and losses of nitrogen and phosphorus by litter production ( $\text{mg N}$  or  $\text{P m}^{-2} \text{yr}^{-1}$ ) from *Molinia caerulea* during the period October 1982–October 1983

	Litter	N	P
Leaves	255	1636	25
Culms	68	199	8
Panicles	22	353	21
Basal internodes	196	1865	41
Total	541	4053	95

**Table 6.** Percentages and absolute quantities ( $\text{mg m}^{-2} \text{yr}^{-1}$ ) of nitrogen and phosphorus translocated from the leaves in *Erica tetralix* and from the leaves and culms and to the basal internodes in *Molinia caerulea* during the period October 1982–October 1983

	% N	% P	Amount of N	Amount of P
<i>Erica tetralix</i>				
Leaves	–42	–54	–795	–27
<i>Molinia caerulea</i>				
Leaves	–59	–81	–2427	–125
Culms	–55	–66	–244	–15
Basal internodes	+90	+58	+1342	+47

**Table 7.** Percentage losses of nitrogen and phosphorus by litter production from the above-ground biomass ( $\text{yr}^{-1}$ ) and the relative nitrogen and phosphorus requirements ( $\text{mg N}$  or  $\text{P g}^{-1} \text{yr}^{-1}$ ) of *Erica tetralix* and *Molinia caerulea* as measured during 1983

	Biomass	N	P
Percentual losses:			
<i>Erica tetralix</i>	25	27	31
<i>Molinia caerulea</i>	100	63	34
Relative nutrient requirement (L):			
<i>Erica tetralix</i>	–	2.6	0.08
<i>Molinia caerulea</i>	–	7.5	0.18

tioned whether leaching of nitrogen and phosphate from plant organs is quantitatively important. Morton (1977) found that during and immediately after abscission of *Molinia* shoots an important part of most cations was leached, but he showed that the reduction in nitrogen and phosphorus concentrations was exclusively caused by translocation of these nutrients. Herbivory and turn-over of roots, however, can undoubtedly be significant pathways of nutrient loss. In 1982 we carried out a preliminary study on the dynamics of the root biomass (Berendse et al. 1987). We found that the percentage mortality of the below-ground biomass was much higher than that of the above-ground plant parts, especially in *Molinia*. It is, however, difficult to calculate nutrient losses by root mortality, since we were not able to measure the withdrawal of nutrients from dying root parts. It seems, however, that the total losses of nitrogen and phosphorus expressed as percentage of the amount of these nutrients in the whole plant is significantly larger than the percentage losses from the above-ground biomass

which were given in Table 7. Below we make a few detailed comments on the strategies of the two species. Thereafter we will compare these strategies and consider their consequences for the dynamics of wet heathland communities.

### *Erica*

The long life-span of the leaves of *Erica* (ca. 16 months as opposed to ca. 4 months in *Molinia*) is probably possible because of their relatively high lignin content (44% compared with 24% in *Molinia* leaves; Tietema et al. 1985). Its evergreenness enables *Erica* to continue photosynthesis during the winter period and early spring. There is a remarkable difference between the dry weight of the first-year leaves in October and that of the second-year leaves in May. If this difference is not caused by between-year variability, *Erica* produced about  $39 \text{ g/m}^2$  of leaf weight during the period from October to May.

Withdrawal of nutrients and weight loss preceding the abscission of leaves is a widespread and common phenomenon (Viro 1956; Specht and Groves 1966; Staaf 1982). Unfortunately there are no data for *Ericaceae*, but comparison with data for some species of trees shows that the percentages of the nitrogen and phosphorus amounts (Table 6) that were withdrawn from the *Erica*-leaves are lower than the retranslocated percentages that were measured in the studies on both deciduous and coniferous trees (Viro 1956; Specht and Groves 1966; Staaf 1982).

About 50% of the above-ground litter production in *Erica* was calculated to be stem mortality. The calculation of stem litter production was based on the assumption that the amount of stem biomass in these communities did not increase. It is, however, possible that buried stem biomass is still accumulating. This means that the calculated percentual mortality must be regarded as a maximum-estimation, and real stem mortality may be lower.

### *Molinia*

*Molinia* loses during September and October all its above-ground biomass, so that litter production can easily be calculated. Only the old basal internodes and the very small new shoot primordia survive during the winter period hidden under the litter layer. In a preliminary study it was found that all full-grown shoots remained alive during the whole growing season. An under-estimation error may have occurred, because the leaves of the first series (Jefferies 1916, Loach 1968) may already have been shed at the moment we measured the maximum standing crop. On 28 August, Loach (1968) found the dry weight of the dead leaves of the first series to be  $26 \text{ g/m}^2$ , from which it may be concluded that a possible under-estimation error will be relatively small.

*Molinia* showed an amazingly effective retranslocation of nitrogen and phosphorus preceding the abscission of the shoots. This high retranslocation of N and P in *Molinia* has already been shown by other authors as well (Table 8). The percentages of P withdrawn from the shoots as found in our study are in the same range as those found in the other studies. The percentages of N that are withdrawn are clearly lower than those found in three of these studies. It is possible that because of the high nitrogen availability at our study site (by the high N mineralization and the high input of nitrogen compounds by atmospheric deposition), *Molinia* is less economical with nitrogen than at the

other study sites. It is striking that not only in our study but also in each of the four other studies a more efficient retranslocation of phosphorus than that of nitrogen was found. Kuhn et al. (1982) observed that the increase of nutrients in the basal internodes was larger than the decrease in the upper plant parts. In our investigation the nutrient increase in the basal internodes was not as large as the total decrease in the upper parts (Table 6). These missing nutrients could have been transported to the seeds which were ripening at the time of translocation, or they could have been transported to the cord roots.

#### *Erica* versus *Molinia*

*Erica* and *Molinia* have rather different strategies in order to restrict their nutrient losses. *Erica* is a woody evergreen, that restricts its nutrient losses by a relatively long life-span of its leaves and the inherently low mortality of stems. *Molinia*, on the other hand, is a perennial grass that dies off above-ground completely at the end of the growing season. The main mechanism by which *Molinia* retains its nutrients is a very efficient withdrawal of nutrients from dying shoots. In spite of these different adaptations, there appears to be a clear difference in the success of these strategies between the two species (Table 7). The percent nitrogen loss from *Molinia* is about two times as high as that from *Erica*, whereas the calculated relative nitrogen requirement is almost three times as high. The greater economy of *Molinia* with respect to phosphorus leads to about equal percentage phosphorus losses from both species. The relative phosphorus requirement of *Molinia*, however, is about two times as high as that of *Erica*. One might think that these differences in the loss of nutrients from above-ground plant parts are cancelled by a larger storage of nutrients into the roots in *Molinia*, when it dies off above-ground at the end of the growing season. The increase of the nitrogen and phosphorus concentrations in the cord roots of *Molinia* during September and October point to the transport of nutrients from the dying shoots to the roots. In a preliminary study on root turn-over at the same site during 1982 and 1983 (Berendse et al. 1987), however, we measured that the amount of dead roots in *Molinia* increased rather strongly, whereas the amount of living roots decreased during the period in which the above-ground plant parts died off. On a whole-year basis root mortality was measured to be high as compared to above-ground mortality and the percentage turn-over of roots in *Molinia* appeared to be higher than that in *Erica*. So, if we include the results of this preliminary study on root turn-over the differences between the relative nutrient requirements of *Molinia* and *Erica* would be even larger.

#### Competition between *Erica* and *Molinia*

The results of our measurements can now be compared with the results derived in the theoretical section. The ratios between the relative nitrogen and phosphorus requirements of *Molinia* and *Erica* ( $L_m/L_e$ ) are 2.9 and 2.3, respectively. In the past we carried out a competition experiment with *Molinia* and *Erica* in which we measured the competitive ability of the two species with respect to the uptake of nutrients at different supplies of nitrogen and phosphorus (Berendse and Aerts 1984). The relative competition coefficient of *Molinia* with respect to *Erica* ( $k_{me}$ ) is almost equal to unity under unfertilized conditions, whereas it increases

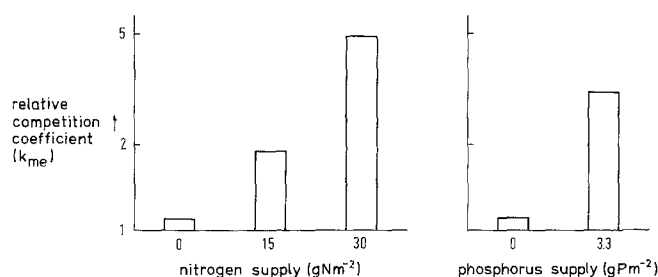


Fig. 7. The relative competition coefficient ( $k_{me}$ ) of *Molinia* with respect to *Erica* at different supplies of nitrogen and phosphorus (after Berendse and Aerts 1984)

Table 8. Percentage decrease of nitrogen and phosphorus in the upper plant parts of *Moninia caerulea* during autumn, as found in different studies

		N	P
Present paper	Leaves/culms	59/55	81/66
Loach (1968)	Leaves	80	80
Morton (1977)	Leaves	75	83
Kuhn et al. (1982)	Upper plant parts	80	90
Lütke Twenhoven (1982) (cited in Egloff 1983)	Upper plant parts	45	87

clearly with increasing nitrogen or phosphorus supply (Fig. 7). From comparison with conditions (5) it is clear that under nutrient-poor conditions  $k_{me}$  will be below the critical ratio between the relative nutrient requirements of the two species, so that *Erica* will be able to maintain itself as the dominant species. Just after an increase in the N or P supply, the relative competition coefficient will exceed the critical ratio and *Molinia* will replace *Erica* and become dominant. This mechanism has probably been underlying the replacement of the former *Erica*-dominated communities by the grass *Molinia*, which has taken place during the last 20 years in wet heathlands in the Netherlands.

Our results suggest that *Erica* is better adapted to nutrient poor environments than *Molinia* is by its better ability to retain nutrients. After an increase in the nutrient availability, however, other plant properties become favourable for the population. Under such conditions it will be especially important for the plant to be able to respond to such a change by a rapidly increased biomass production. At the end of the growing season *Molinia* has invested 48% of its total biomass in photosynthetic tissues, whereas this investment in *Erica* is just 12%. It is not yet possible to calculate a season-weighted investment into green plant parts over the whole year in both *Molinia* and *Erica*, but there seems to be an important difference in this respect between the two species. This difference is essential, since a plant needs a sufficiently large photosynthetic apparatus in order to convert a larger nutrient uptake into a higher biomass production, which enables it to increase its competitive ability. It would be very favourable for a plant species, if it could combine properties that lead to low nutrient losses and properties that lead to a high growth rate after an increase in the nutrient availability. Such a species would be a real generalist. In many cases, however, these two sets of properties cannot be combined without morphological or physiological problems. The carbohydrates and nitrogen

that are allocated to woody structures, structural elements in leaves or defensive compounds (e.g., cyanogenic glycosides, alkaloids) cannot be incorporated into the chloroplast. It seems that there is an evolutionary trade-off between plant characteristics that enable the plant to restrict its nutrient losses and characteristics that lead to a rapidly increased growth rate under relatively nutrient-rich circumstances. The analysis of this trade-off may lead to a better understanding of the adaptation of plant populations to habitats with different nutrient availabilities.

**Acknowledgements.** We would like to thank Dr. C. van der Valk and Mr. R. Aerts for their valuable comments on the manuscript. Moreover, we are much indebted to the "Vereniging tot Behoud van Natuurmonumenten in Nederland", that gave permission to carry out this study in one of its properties.

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Received April 8, 1987