Biogeochemistry **15**: 175—190, 1992
© 1992 *Kluwer Academic Publishers. Printed in the Netherlands.*

Root turnover as determinant of the cycling of C, N, and P in a dry heathland ecosystem

R. AERTS, C. BAKKER & H. DE CALUWE
Dept of Plant Ecology and Evolutionary Biology, University of Utrecht, P.O. Box 800.84, NL-3508 TB Utrecht, The Netherlands

Accepted 24 January 1992

Key words: carbon cycling, heathland, minirhizotron, N and P cycling, N and P resorption, root turnover

Abstract. Root production and turnover were studied using sequential core sampling and observations in permanent minirhizotrons in the field in three dry heathland stands dominated by the evergreen dwarfshrub *Calluna vulgaris* and the grasses *Deschampsia flexuosa* and *Molinia caerulea*, respectively. Root biomass production, estimated by core sampling, amounted to 160 (*Calluna*), 180 (*Deschampsia*) and 1380 (*Molinia*) g m^{-2} yr^{-1}, respectively. Root biomass turnover rate in *Calluna* (0.64 yr^{-1}) was lower compared with the grasses (*Deschampsia*: 0.96 yr^{-1}; *Molinia* 1.68 yr^{-1}). Root length turnover rate was 0.75—0.77 yr^{-1} (*Deschampsia*) and 1.17—1.49 yr^{-1} (*Molinia*), respectively. No resorption of N and P from senescing roots was observed in either species. Input of organic N into the soil due to root turnover, estimated using the core sampling data, amounted to 1.8 g N m^{-2} yr^{-1} (*Calluna*), 1.7 g N m^{-2} yr^{-1} (*Deschampsia*) and 19.7 g N m^{-2} yr^{-1} (*Molinia*), respectively. The organic P input was 0.05, 0.07 and 0.55 g P m^{-2} yr^{-1}, respectively. Using the minirhizotron turnover estimates these values were 20—22% (*Deschampsia*) and 11—30% (*Molinia*) lower.

When the biomass turnover data were used, it appeared that in the *Molinia* stand root turnover contributed 67% to total litter production, 87% to total litter nitrogen loss and 84% to total litter phosphorus loss. For *Calluna* and *Deschampsia* these percentages were about three and two times lower, respectively.

This study shows that (1) Root turnover is a key factor in ecosystem C, N, and P cycling; and that (2) The relative importance of root turnover differs between species.

Introduction

Root turnover and root decomposition determine to a large extent the cycling of carbon and nutrients in ecosystems (Caldwell 1979; Vogt et al. 1983, 1986; Aber et al. 1985; Aerts et al. 1989; Raich & Nadelhoffer 1989). Although there is a general consensus about the importance of the measurement of annual fluxes of organic matter and nutrients into the soil due to root turnover, there are relatively few reliable studies of these

processes. A common approach to measuring root turnover is sequential sampling of root mass (Böhm 1979) and estimating root production by adding increments of standing stocks of living and dead roots (McClaugherty et al. 1982). Assuming steady state conditions for the living root system, the input of dead roots into the soil equals root production. However, core sampling can produce rather biassed results due to spatial heterogeneity of root distribution in the soil (Singh et al. 1984; Aerts et al. 1989). More robust estimates can be obtained by combining biomass data and turnover estimates based on observations in minirhizotrons (Vos & Groenwold 1983; Taylor 1987; Aerts et al. 1989; Cheng et al. 1990). The minirhizotron technique allows sequential observations of the same roots under conditions which approach natural growing conditions as much as possible. Nutrient input into the soil can be determined then by multiplying the organic matter input due to root turnover by the nutrient content of the roots (Vogt et al. 1983).

The aim of this study was twofold: (1) Assessing the impact of root turnover on the cycling of C, N, and P in a dry heathland ecosystem; (2) determining the relative contribution of the dominant plant species of an ecosystem to these processes. The study was carried out in three dry heathland stands dominated by the evergreen dwarfshrub *Calluna vulgaris* and the grasses *Deschampsia flexuosa* and *Molinia caerulea*, respectively. Turnover estimates were based on sequential core sampling and observations in permanent minirhizotrons in the field. The aboveground biomass and nutrient dynamics of *Calluna* and *Molinia* are dealt with in Aerts (1989).

Study site and methods

Study site

The study was carried out in the dry heathland area 'Edese Heide', located in the central part of the Netherlands (52° 02′N, 5°50′E). The vegetation was classified as a Genisto-Callunetum (De Smidt 1977). The soils are 'humus podsols' (Kubiena 1953). Some general characteristics are presented in Table 1. These soils are rather acid and most of the organic matter is confined to the upper 10 cm of the soil-profile. The root turnover studies were performed in three adjacent stands, dominated by *Calluna* (mean age: seven years), *Deschampsia* and *Molinia*, respectively. In each stand the biomass of the dominant species comprised more than 95% of total stand biomass.

Table 1. Organic matter content (%) and soil-pH (determined on air-dried material) at different soil-depths in dry heathland communities dominated by *Calluna vulgaris, Deschampsia flexuosa* and *Molinia caerulea.**

	Calluna	*Deschampsia*	*Molinia*
Organic matter			
depth (cm)			
0—5	14.5	21.0	15.4
5—10	4.2	6.5	6.3
10—15	3.2	4.9	5.4
15—25	3.7	3.8	4.0
Soil-pH(H_2O)			
0—5	3.84	3.69	3.89
5—10	3.91	3.72	4.02
10—15	3.96	3.95	4.20
15—25	4.34	4.35	4.45

* Data were kindly provided by S. Troelstra, Institute for Ecological Research, Heteren, The Netherlands.

Root mass, root length, root turnover and nutrient resorption

The methods used for sampling root mass and determining root turnover are described and discussed in detail in Aerts et al. (1989). The vertical root distribution pattern of each species was determined by excavating a monolith of 0.50 × 0.06 m over a depth of 1.00 m and placing this monolith on a pin-board. Roots were washed out in layers of 5 cm and the dry weight of the roots in each layer was determined. Using this pattern, we chose sampling depth in each stand in such a way that at least 95% of total root mass was sampled. Roots were than sampled at monthly intervals from April 1985 until October 1985 and in January 1986 and in April 1986. Root sampling involved the collection of 10 randomly spaced replicate soil cores 2.7 cm in diameter to a depth of 20 cm (*Calluna, Deschampsia*). Due to the uneven horizontal root distribution pattern in the *Molinia* stand, 5 core samples 8 cm in diameter were taken in tussocks and 5 core samples 2.7 cm in diameter between tussocks both to a depth of 50 cm. The dry weights of *Molinia* roots in tussocks and between tussocks were multiplied by their fraction of total cover (in tussocks: 0.45 ± 0.06; between tussocks: 0.55 ± 0.06). After washing the roots from the soil matrix they were separated in living and dead categories using visual criteria (cf. Aerts et al. 1989).

Root production was calculated using the changes in standing stocks of living and dead roots (see 'Root production estimates and statistical analysis'). Root biomass turnover rate (yr^{-1}) was calculated as the ratio between annual root production and average root biomass (Frissel 1981). Root length turnover was determined using permanent minirhizotrons in the field. To this end, five square tubes (made of 4 mm Lexan; outside measurements: 8 × 8 cm) were dug into the soil at 45° to the soil surface (Fig. 1) in each stand. Maximum tube depth equalled maximum rooting depth of each species (*Calluna*: 0.4 m; *Deschampsia*: 0.7 m; *Molinia*: 0.9 m). Preliminary observations indicated that maximum root density occurred 0.1 m below soil surface. Using fibre-glass optics, slides were taken at this depth with six-weekly (summer) or ten-weekly (winter) intervals from April 1986 until April 1989. Living and dead root length on each slide were estimated using the line-intersect method modified by Tennant (1975). Root length production was calculated using changes in the amount of living and dead root length (see 'Root production estimates and statistical analysis'). Root length turnover rate (yr^{-1}) was calculated as the ratio between annual root length production and average living root length.

Nutrient resorption from senescing roots was determined using a split-root technique (Aerts 1990). In April 1989 plants of the three species were collected in the field and grown in pots (2.21) in an experimental

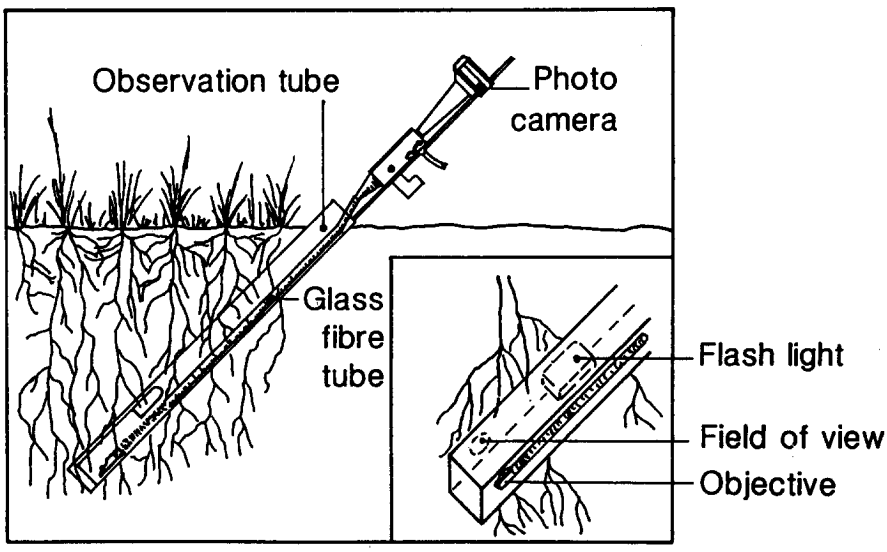

Fig. 1. Schematic representation of the minirhizotron observation equipment in the field.

garden. The plants were grown in soil material from the sites were they had been collected. In October 1989 the plants were transferred to the greenhouse where they were put in pots with a split-root construction. About 20% of the root system of 10 replicate plants was dried out gradually ('dry' compartment), while the roots in the 'wet' compartment received tap-water every day. The experiment was finished after three weeks. Visual inspection showed that about 90% of the roots in the dry compartment had died then. Nutrient resorption was estimated by comparing nutrient concentrations of living roots in the wet compartment and of dead roots in the dry compartment.

Nutrient analysis

After drying living root material for 48 h at 70 °C, N and P concentrations in bulk samples were determined by digesting 200 mg ground material in 5 ml 30 N sulphuric acid and a mixture of sodium sulphate, copper sulphate and selenium. The diluted digestions were analysed colorimetrically on a continuous-flow analyser (Skalar SA-40) using the indophenol-blue method with salicylate for N and the ammonium molybdate method for P.

Root production estimates and statistical analysis

Data were statistically analysed using the General Linear Models procedure of the Statistical Analysis System (SAS Institute Inc. 1985). When variances were proportional to the means, the calculations were done on the log-transformed data. Multiple comparisons among pairs of means were made using Tukey's Studentized Range Test.

Root production (P) was calculated after testing the effect of sampling date on root biomass (L) or necromass (D) with analysis of variance. In case of a significant effect, production was calculated using increments (δ) of mean values according to the criteria of McClaugherty et al. (1982): (a) if $\delta L > 0$ and $\delta D > 0$, then $P = \delta L + \delta D$; (b) if $\delta L > 0$ and $\delta D < 0$ then $P = \delta L$; (c) if $\delta L < 0$ and $\delta D > 0$ then $P = \delta L + \delta D$ or $P = 0$ (in case of a negative P); (d) if $\delta L < 0$ and $\delta D < 0$ then $P = 0$. Annual estimates were calculated by summing the estimates within all sampling intervals within the year. These estimates were further used to calculate turnover rates. Root length production was also calculated using the criteria of McClaugherty et al. (1982), but in this case we took all changes in living and dead root length into account. This was a valid method, because minirhizotron observations are sequentially performed on the same roots.

Results

Root mass and root production

Analysis of variance showed significant effects of species and sampling date on total root mass ($P < 0.0001$ for both variables). The ANOVA revealed a significant effect of sampling date on living root mass of *Calluna* ($P < 0.05$), which showed peak values in spring and early summer (Fig. 2a). Dead root mass was not significantly affected by sampling date ($0.10 > P > 0.05$). Root production of *Calluna* was 160 g m^{-2} yr^{-1} (Table 2).

The living root mass of *Deschampsia* was significantly affected by sampling date ($P < 0.05$) and showed peak values in summer (Fig. 2b). The ANOVA revealed a significant effect of sampling date on dead root mass of *Deschampsia* ($P < 0.0001$), with peak values in winter and low values in summer. Root production of *Deschampsia* amounted to 180 g m^{-2} yr^{-1} (Table 2).

Table 2. Root biomass production (P: g dry weight m^{-2} yr^{-1}), root biomass turnover rate (BTR: yr^{-1}), root length production (RLP: m yr^{-1}) and root length turnover rate (RLTR: yr^{-1}) of *Calluna vulgaris, Deschampsia flexuosa* and *Molinia caerulea* in a dry heathland.*

	P	BTR	RLP	RLTR
Calluna	160	0.64	—	—
Deschampsia	180	0.96	0.27(0.16)[a]	0.75(0.17)[a]
			0.47(0.31)[b]	0.77(0.22)[b]
Molinia	1380	1.68	0.39(0.23)[a]	1.49(0.62)[a]
			0.49(0.12)[b]	1.17(0.36)[b]

* Standard deviations are given between parentheses ($n = 5$).
[a] measured in 1987—1988
[b] measured in 1988—1989

Living root mass of *Molinia* was significantly affected by sampling date ($P < 0.0001$) and showed a very pronounced seasonal pattern with peak values occurring in summer and very low values in winter (Fig. 2c). The ANOVA showed a significant effect of sampling date on dead root mass of *Molinia* ($P < 0.05$). The pattern was more or less complementary to that of the living root mass: low values in summer and high values in early spring and winter. Root production of *Molinia* equalled 1380 g m^{-2} yr^{-1} (Table 2).

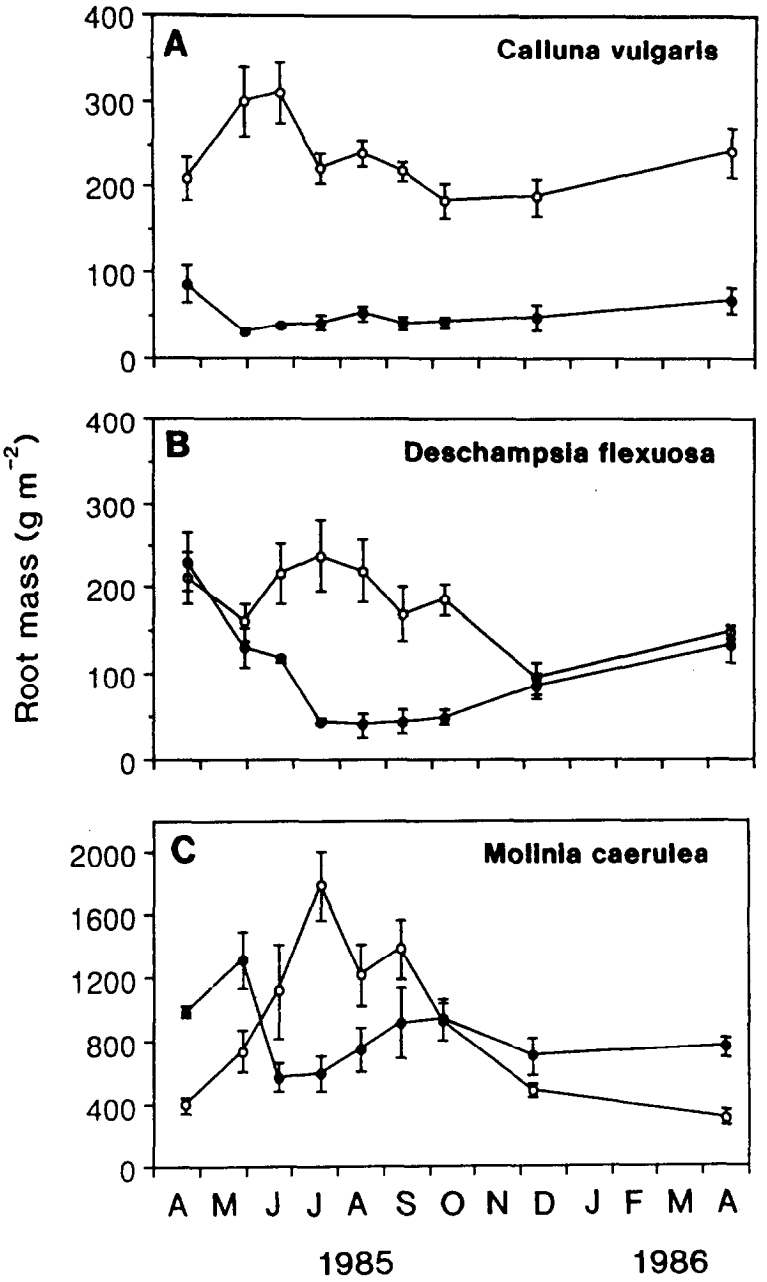

Fig. 2. Root mass (g m^{-2}) of *Calluna vulgaris* (A), *Deschampsia flexuosa* (B) and *Molinia caerulea* (C) in a dry heathland from April 1985 until April 1986. Open symbols: living roots; filled symbols: dead roots. Means ± 1 S.E. are given ($n = 10$).

Root length

Due to very severe frost spells the *Calluna* vegetation in which the minirhizotron observation tubes were installed died completely shortly after the tubes were dug into the soil. So minirhizotron data are only available for *Deschampsia* and *Molinia*. Analysis of variance showed significant effects of sampling date ($P < 0.0001$) and of species ($P < 0.03$) on living root length. In both species there was a clear seasonal pattern in living root length: peak values during the summer and low values in winter (Fig. 3). During the three years of observation, the amount of living root length kept increasing, especially after the mild winters of 1987—1988 and 1988—1989. Due to these mild winters there was very little root mortality, so the amount of dead root length was always very low (Fig. 4). As a consequence, the root systems were not in a steady state. Since the root systems were obviously disturbed after installation of the tubes, root length production (RLP) and root length turnover (RLTR) data are only presented for the second and third year of the study (Table 2). For both species, RLP in the third year of the study exceeded that in the second year, but these increases were not significant. Neither were there within each year significant differences in RLP between species.

Turnover estimates

The root biomass turnover rates of *Calluna*, *Deschampsia* and *Molinia*

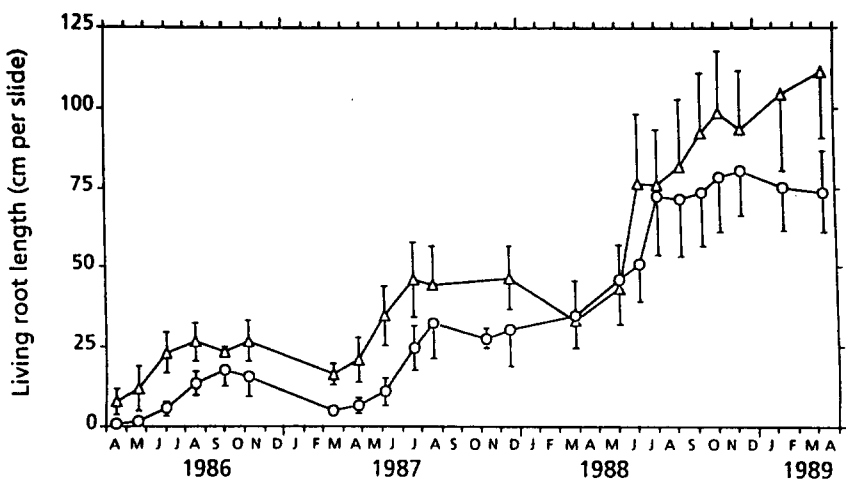

Fig. 3. Living root length (cm per slide) of *Deschampsia flexuosa* (triangles) and *Molinia caerulea* (circles) in a dry heathland from April 1986 until April 1989 as determined by minirhizotron observations. Vertical bars indicate 1 S.E. ($n = 5$).

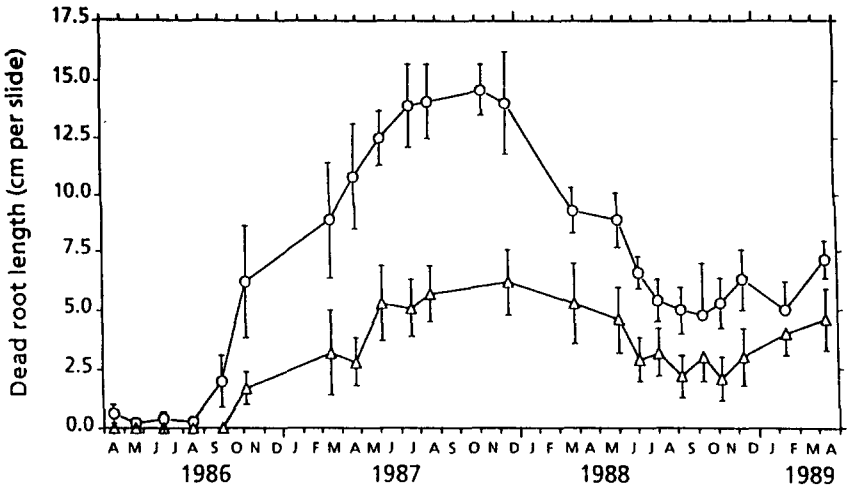

Fig. 4. Dead root length (cm per slide) of *Deschampsia flexuosa* (triangles) and *Molinia caerulea* (circles) in a dry heathland from April 1986 until April 1989 as determined by minirhizotron observations. Vertical bars indicate 1 S.E. ($n = 5$).

were 0.64 (yr^{-1}), 0.96 and 1.68, respectively (Table 2). Root length turnover estimates based on minirhizotron observations were lower than the core sampling turnover estimates and amounted to 0.75 yr^{-1} and 0.77 yr^{-1} for *Deschampsia* and 1.49 yr^{-1} and 1.17 yr^{-1} for *Molinia* (Table 2). In both years of the study the RLTR of *Molinia* significantly exceeded that of *Deschampsia* (1987—1988: $P < 0.05$; 1988—1989: $P < 0.05$).

Nutrient concentrations and nutrient input into the soil

Analysis of variance on root nitrogen and phosphorus concentration showed significant differences between species and sampling dates ($P < 0.0001$ for both variables for both nutrients). Average root N- and P-concentrations in *Calluna* roots were not significantly different from those in *Molinia* roots, but for both species they were higher than in *Deschampsia* roots ($P < 0.05$ for both N and P).

Root nitrogen and phosphorus concentrations showed significant seasonal changes for all three species under study ($P < 0.0001$ for both N and P) (Figs 5a, b, c).

In the split-root experiment, nutrient concentrations in dead roots were not significantly different from those in living roots in all three species (*Calluna*: nitrogen: $P < 0.12$, phosphorus: $P < 0.13$; *Deschampsia*: nitrogen: $P < 0.69$, phosphorus: $P < 0.21$; *Molinia*: nitrogen: $P < 0.33$, phosphorus: $P < 0.09$). So there was no significant resorption of N and P

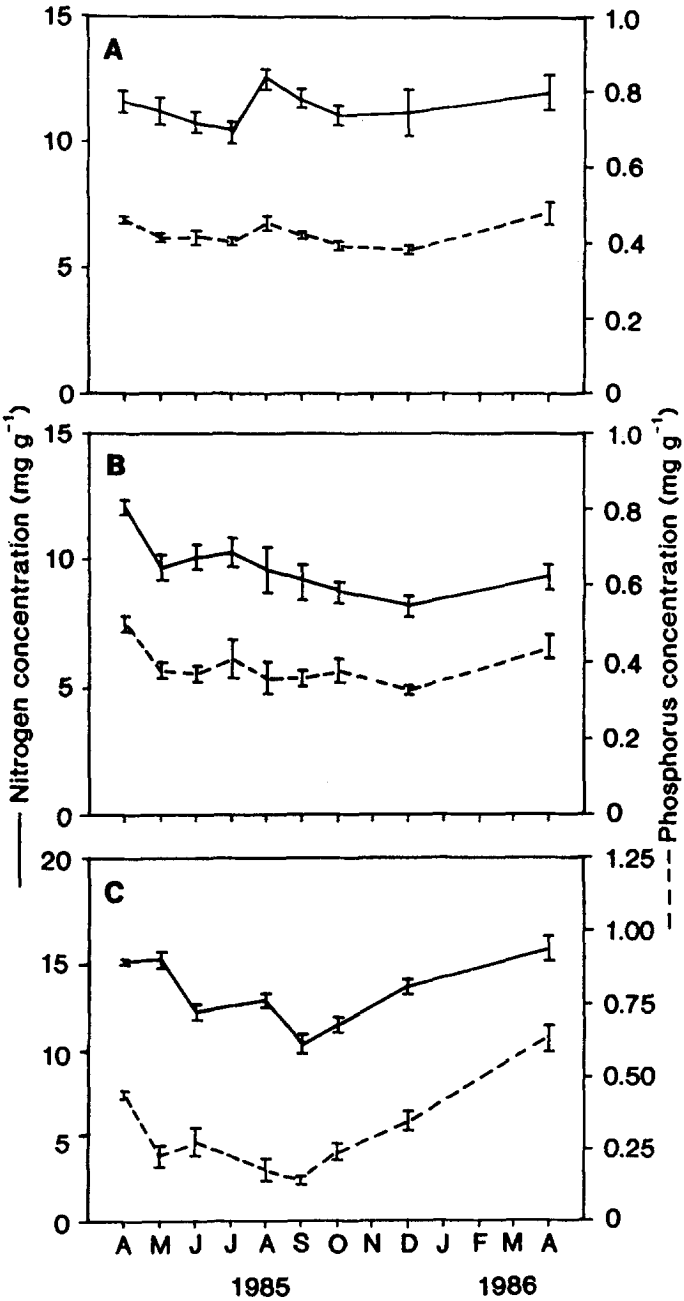

Fig. 5. Nitrogen (solid lines) and phosphorus (broken lines) concentrations (mg g^{-1}) in living roots of *Calluna vulgaris* (A), *Deschampsia flexuosa* (B) and *Molinia caerulea* (C) in a dry heathland from April 1985 until April 1986. Means ± 1 S.E. are given ($n = 5$).

from senescing roots in either of the three species under study. Nutrient input into the soil by root turnover was therefore calculated as the product of root turnover (expressed in g m^{-2} yr^{-1}) and the annual average of the nutrient concentration of the living roots.

The nitrogen and phosphorus inputs into the soil due to root turnover are given in Table 3. The inputs were calculated using both the core sampling turnover estimates and the minirhizotron turnover estimates (Table 2). The N and P input into the soil due to turnover of *Molinia* roots exceeded that of *Calluna* and *Deschampsia* considerably. As root length turnover rates were lower than root biomass turnover rates, the estimates of nutrient input into the soil based on the minirhizotron data were lower than those based on the core sampling data.

Table 3. Organic nitrogen and phosphorus input into the soil (g m^{-2} yr^{-1}) due to root turnover of *Calluna vulgaris, Deschampsia flexuosa* and *Molinia caerulea* in a dry heathland.

	nitrogen	phosphorus
Calluna	1.8^{a}/—	0.05^{a}/—
Deschampsia	1.7^{a}/$1.3^{b.1}$	0.07^{a}/$0.05^{b.1}$
	$1.3^{b.2}$	$0.05^{b.2}$
Molinia	19.7^{a}/$17.5^{b.1}$	0.55^{a}/$0.49^{b.1}$
	$13.8^{b.2}$	$0.39^{b.2}$

[a] using core sampling turnover estimates
[b] using minirhizotron turnover estimates
[1] measured in 1987—1988
[2] measured in 1988—1989

Discussion

Root production and turnover

Root production showed clear differences between the species under study. Both *Calluna* and *Deschampsia*, species with a low potential growth rate (Aerts et al. 1990; Robinson & Rorison 1983, 1988), had a low rate of root production, which contributed only 25% (*Calluna*) or 35% (*Deschampsia*) to total stand productivity (Aerts 1989; Aerts unpublished). On the other hand, root production of the *Molinia* population comprised 67% of total stand productivity (Aerts 1989). Thus, the between-species differences in belowground productivity (Table 2) are the

result of differences in allocation of assimilated carbon to shoots and roots and of differences in total productivity.

Data from the literature on belowground productivity of *Calluna* and *Molinia* stands are summarized in Table 4. No data were found for field populations of *Deschampsia* in the literature. Although there are relatively many data on belowground productivity of *Calluna* stands, reliable data are scarce, because most of the productivity estimates are based on statistically unreliable calculation methods (i.e. Forrest 1971; Chapman 1979; Tinhout & Werger 1988). Only Persson's (1978, 1979) data from a boreal pine-heath are statistically sound. He found a much lower root production than reported in this study. This is probably caused by a lower nutrient availability in the pine-heath and by a lower relative contribution of *Calluna* to total ecosystem plant biomass than in this study. The root production estimates for the *Molinia* stands, which are all located in the Netherlands, are very similar.

Table 4. Root production (g dry weight m^{-2} yr^{-1}) of *Calluna vulgaris* and *Molinia caerulea* as reported in different studies.

Study	Vegetation type	Root production
(a) *Calluna*		
Persson (1978)	pine-heath	38
Persson (1979)	pine-heath	65
This study	dry heathland	160
(b) *Molinia*		
Berendse et al. (1987)	wet heathland	1251
Aerts et al. (1989)	wet heathland	1080
This study	dry heathland	1380

The root turnover estimates based on the core sampling method corresponded rather well with those based on the minirhizotron observations (Table 2). Turnover estimates based on the latter method were 20—22% (*Deschampsia*) and 11—30% (*Molinia*) lower. This suggests that the turnover estimates from this study are reliable. However, in a wet heathland we found substantial differences between both types of turnover measurements (Aerts et al. 1989). So, a combination of both methods seems to be a useful check of the reliability of turnover measurements.

The root turnover rates found in this study (between 0.64 and 1.68 yr^{-1}) are in the range of other published turnover estimates (see Vogt & Bloomfield (1991) and references therein). Unfortunately, there are no data available for the species we studied.

The rank order of the root biomass turnover rates was similar to the rank order of belowground productivity. The low rate of root turnover of *Calluna*, which is the dominant species in low-nutrient heathlands, can be explained as a nutrient conservation mechanism (Grime 1979; Chapin 1980; Aerts 1990). In contrast, *Molinia*, a species with a high potential growth rate which dominates high-nutrient heathlands (Aerts et al. 1990), has a very high rate of root turnover (Table 2). An even higher root turnover rate (2.28 yr^{-1}) of *Molinia* was found in a wet heathland (Aerts et al. 1989). *Deschampsia* occupies an intermediate position. The high rate of root turnover as observed in the *Molinia* populations is a common feature of productive species from fertile habitats (Chapin 1980). Thus, the observed pattern of root turnover is consistent with the theories of Grime (1979), Chapin (1980) and Aerts (1990) about the adaptations of perennials to habitats with different levels of nutrient availability.

The importance of root turnover in ecosystem carbon and nutrient cycling

Nutrient input into the soil due to root turnover was substantial and differed clearly between species (Table 3). To assess the relative importance of root turnover in ecosystem carbon and nutrient cycling the percentage contribution of root turnover to ecosystem litter production and litter nitrogen and phosphorus loss was calculated (Table 5). These data show that 1) Root turnover comprises a substantial part of ecosystem litter production and ecosystem litter nutrient losses; and that 2) The relative contribution of root turnover in these processes differs between species.

The very high organic N- and P-input into the soil in the *Molinia* stand depends heavily on the fact that we did not measure any nutrient resorption from senescing roots. So, the results may be biassed due to the fact that we measured nutrient resorption from senescing roots under rather

Table 5. Percentage contribution of root turnover to total litter production (g m^{-2} yr^{-1}) and litter nitrogen and phosphorus losses (g m^{-2} yr^{-1}) in *Calluna vulgaris, Deschampsia flexuosa* and *Molinia caerulea* in a dry heathland.*

	litter	nitrogen	phosphorus
Calluna	22	23	21
Deschampsia	42	40	35
Molinia	67	87	84

* Calculated using the core sampling data of this study and aboveground data from Aerts (1989) and Aerts (unpublished data).

artificial conditions. If nutrient resorption from senescing roots would occur, this would affect the data for *Molinia* the most, because organic N- and P-input into the soil due to root turnover comprised for this species more than 80% of total litter N- and P-losses. Nevertheless, even if 50% resorption of N and P from senescing *Molinia* roots would occur, root turnover would still contribute 77% to total litter N-loss and 73% to total litter P-loss.

It should be noticed that the calculated values of nutrient input into the soil due to root turnover refer to organic N and P contained in the litter. The litter must be decomposed and the nutrients must be remineralized to be available for plant uptake again. There are substantial between-species differences in the mineralization rates of nutrients which are lost by litter production. French (1988) reported that *Calluna* stem litter decomposed at a much lower rate than did *Molinia* leaf litter. Berendse et al. (1989) studied the decomposition of several litter fractions, including roots, of the evergreen dwarfshrub *Erica tetralix* (closely related to *Calluna*) and of *Molinia*. They found a higher net release of nitrogen and phosphorus from decomposing *Molinia* roots as compared with *Erica* roots. Thus, the between-species differences in the rates of nutrient mineralization from root litter probably reinforce the between-species differences in nutrient input into the soil due to root turnover. This emphasizes once again the importance of the dominant plant species in the regulation of ecosystem carbon and nutrient cycling.

Acknowledgements

An earlier draft of the manuscript was critically commented by S. Bakker, W. Koerselman and C. Mesters. We thank G. de Mari and E. van der Veen for their skilled construction of the root endoscope and the observation tubes. M. Kortbeek-Smithuis is acknowledged for the preparation of the figures. The investigations were supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by the Netherlands Organization for Scientific Research (NWO).

References

Aber JD, Melillo JM, Nadelhoffer KJ, McClaugherty CA & Pastor J (1985) Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. Oecologia 66: 317–321

Aerts R (1989) Aboveground biomass and nutrient dynamics of *Calluna vulgaris* and *Molinia caerulea* in a dry heathland. Oikos 56: 31–38

Aerts R (1990) Nutrient use efficiency in evergreen and deciduous species from heathlands. Oecologia 84: 391–397

Aerts R, Berendse F, Klerk NM & Bakker C (1989) Root production and root turnover in two dominant species of wet heathlands. Oecologia 81: 374–378

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, Beltman B, Bobbink R, Kwant R & Schmitz M (1987) Primary production and nutrient availability in wet heathland ecosystems. Acta Oecol. /Oecol. Plant. 8(22): 265–279

Berendse F, Bobbink R & Rouwenhorst G (1989) A comparative study on nutrient cycling in wet heathland ecosystems II. Litter decomposition and nutrient mineralization. Oecologia 78: 338–348

Böhm W (1979) Methods of studying root systems. Springer-Verlag, Berlin

Caldwell MM (1979) Root structure: the considerable cost of belowground function. In: Solbrig OT, Jain S, Johnson GB & Raven PH (Eds) Topics in plant population biology (pp 408–427). Columbia University Press, New York

Chapman SB (1979) Some interrelationships between soil and root respiration in lowland *Calluna* heathland in southern England. J. Ecol. 67: 1–20

Cheng W, Coleman DC & Box Jr. JE (1990) Root dynamics, production and distribution in agroecosystems on the Georgia Piedmont using minirhizotrons. J. Appl. Ecol. 27: 592–604

Chapin FS (1980) The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11: 233–260

De Smidt JT (1977) Heathland vegetation in the Netherlands. Phytocoenologia 4: 258–316

Forrest GI (1971) Structure and production of North Pennine blanket bog vegetation. J. Ecol. 59: 453–479

French DD (1988) Some effects of changing soil chemistry on decomposition of plant litters and cellulose on a Scottish moor. Oecologia 75: 608–618

Frissel MJ (1981) The definition of residence time in ecological models. In: Clark FE & Rosswall T (Eds) Terrestrial Nitrogen Cycles (pp 117–122). Ecol. Bull. (Stockholm) 33

Grime JP (1979) Plant strategies and vegetation processes. John Wiley and Sons, New York

Kubiena WL (1953). The soils of Europe. Murby, London

McClaugherty CA, Aber JD & Melillo JM (1982) The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63: 1481–1490

Persson H (1978) Root dynamics in a young Scots pine stand in Central Sweden. Oikos 30: 508–519

Persson H (1979) Fine-root production, mortality and decomposition in forest ecosystems. Vegetatio 41: 101–109

Raich JW & Nadelholffer KJ (1989) Belowground carbon allocation in forest ecosystems: global trends. Ecology 70: 1346–1354

Robinson D & Rorison IH (1983) A comparison of the responses of *Lolium perenne* L., *Holcus lanatus* L. and *Deschampsia flexuosa* (L.) Trin. to a localized supply of nitrogen. New Phytol. 94: 263–273

Robinson D & Rorison IH (1988) Plasticity in grass species in relation to nitrogen supply. Funct. Ecol. 2: 249–257

SAS Institute Inc. (1985) SAS/STAT Guide for personal computers, Version 6 edition. Cary, N.C.

Singh JS, Lauenroth WK, Hunt HW & Swift DM (1984) Bias and random errors in estimates of net root production: a simulation approach. Ecology 65: 1760–1764

Taylor HM (1987) Minirhizotron observation tubes: Methods and applications for measuring rhizosphere dynamics. ASA Special Publication 50. ASA/CSSA/SSSA, Madison, 143 pp

Tennant D (1975) A test of a modified line intersect method of estimating root length. J. Ecol. 63: 995–1001

Tinhout A & Werger MJA (1988) Fine roots in a dry *Calluna* heathland. Acta Bot. Neerl. 37: 225–230

Vogt KA & Bloomfield J (1991) Tree root turnover and senescence. In: Waisel Y, Eschel A & Kafkafi U (Eds) Plant roots, the hidden half (pp 287–306). Marcel Dekker Inc, New York

Vogt KA, Grier CC, Vogt DJ (1986) Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Adv. Ecol. Res. 15: 303–377

Vogt KA, Grier CC, Meier CE & Keyes MR (1983) Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington, as affected by fine root input. Ecological Monographs 53: 139–157

Vos J & Groenwold J (1983) Estimation of root densities by observation tubes and endoscope. Plant Soil 74: 295–300