Fine roots in a dry *Calluna* heathland

A. TINHOUT and M. J. A. WERGER

Department of Plant Ecology, University of Utrecht, Lange Nieuwstraat 106, 3512 PN Utrecht, The Netherlands

SUMMARY

The fine roots in a dry *Calluna vulgaris* heathland are concentrated in the top soil. Over a 21-month period their dry mass varied from 303 to 612 gm^{-2} , or from 15.7 to 55.2% of the total root mass in the top 5 cm of soil. In early summer and in late autumn to early winter there appeared to be peaks in fine root mass. Data suggest that fine root mass is correlated with moisture availability in the top soil. Nitrogen concentration of the fine roots averaged 17.3 mg g^{-1} and showed seasonal variation; Phosphorus concentration averaged 0.56 mg g^{-1} and did not show such variation.

Key-words: Calluna vulgaris, fine roots, nitrogen concentration.

INTRODUCTION

Northwest European heathlands have shown dramatic shifts in species composition during the past few decades. The predominant dwarfshrubs Calluna vulgaris and Erica tetralix have been largely, in some areas even fully, replaced by the grasses Molinia caerulea and Deschampsia flexuosa, and in a few instances by some other grasses. This has strongly contributed to a rapid disappearance of the vast purple-coloured heathlands that were so typical of the sandy parts of northwestern Europe. The replacement of heath by grasses has been particularly prevalent in the zone from Belgium through The Netherlands and northwest Germany to Denmark (Gimingham & De Smidt 1983). It has stimulated a great number of studies focused on the phenomenon of heath replacement. Studies included phytosociological investigations (De Smidt 1977, 1979), pattern analyses of the replacement (Berdowski 1987a, b; Berdowski & Zeilinga 1987), investigations into the effects of nutrient availability on the competitive relationships between heathland species (Heil & Diemont 1983; Berendse & Aerts 1984; Brunsting & Heil 1985; Heil & Bruggink 1987), the effects of damage by the heather beetle Lochmaea suturalis on the ecophysiology of Calluna vulgaris (Brunsting 1982; Berdowski 1987a), seedling establishment and regeneration of Calluna vulgaris after sod cutting (Helsper et al. 1983; Werger et al, 1985), and phytomass and nutrient budget studies in heathlands (Berendse & Aerts 1987).

In this paper we address one aspect of phytomass build-up: in our budget studies in dry *Calluna* heathland we found strong fluctuations in the fine root fraction in the top soil, especially in and near the humus layer. We quantified this fraction through the course of several seasons.

STUDY AREA AND METHODS

We sampled a dry heathland vegetation in the National Park Hoge Veluwe, The Netherlands. The vegetation was classified as a Genisto-Callunctum (De Smidt

1977). To the eye the vegetation was floristically and structurally homogeneous. Calluna vulgaris (L.) Hull covered between 80 and 90%, and was 40–50 cm tall. Deschampsia flexuosa (L.) Trin., Dicranum scoparium Hedw., Pohlia nutans (Hedw.) Lindb. or Cladonia portentosa (Duf.) Zahlbr. all occurred occasionally, with a cover of less than 1%. The above-ground standing phytomass was about 1800 g m⁻² and the root mass 800 g m⁻² dry weight at the start of the measuring period.

The soil was a nutrient-poor sand without clear horizons ('duinvaaggrond', De Bakker & Schelling 1973): there was a layer of humus a few centimetres thick, but there was no B-horizon. The water table was always several metres below the surface.

The stand was sampled monthly from October 1983 till June 1985 (21 months). One *Calluna* plant was marked at the beginning of the sampling period and served as a reference plant to facilitate the selection of similar plants for sampling throughout this period. At each sampling date a similar *Calluna* plant was selected. Raw, loose litter was blown away and 20 core samples were taken from a circle of radius 20 cm around the plant's centre. Samples were cut with a soil gouge of 2.5 cm diameter. All cores sampled the soil from 0 to 7 cm deep. Each sample core was wrapped in plastic and stored the same day at -20° C (cf. Persson 1978).

After defrosting, each sample was rinsed in tap water above a metal sieve with mesh size 0.355 mm and later carefully washed in a large petri-dish. In the petri-dish humus and dead roots float and heavy soil particles sink, while live roots remain suspended. Frequent checks by bending the roots and by microscopic examination confirmed the precision of this way of distinction between live and dead roots (see also Singh & Coleman 1973 and Persson 1980a). Only Calluna roots were collected and only roots thinner than 2 mm in diameter were considered to be fine roots. Live fine roots were oven-dried at 70°C and weighed. At each sampling date subsamples were taken and mixed. From this mixture two samples of about 0.3 g were taken and heated to 850°C for 2 h to determine the ash weight in the samples. Dry weights were corrected for the ash weights. Weight values were averaged per sample date and calculated on a m² basis. In another, more comprehensive, study undertaken in the same stand total biomass of the above-ground and below-ground plant parts in the *Calluna* vegetation were sampled for three years in plots of 30×30 cm. Full data will be published elsewhere (J. van Rheenen et al., personal communication); part of the data is used to calculate the amount of fine roots as a percentage of total root mass in the top 5 cm of soil and humus.

A subsample of about 0.2 g was taken from each sample and, after destruction (Kjeldal, H_2SO_4 and H_2O_2), analysed for N and P in a continuous flow analyser (Skalar). Values were calculated in mg g⁻¹ of fine root. Potassium was not measured as too high a proportion was leached from the roots during rinsing (cf. Boehm 1979).

Measured root values were correlated with meteorological data integrated over various time intervals prior to sampling dates. Differences in root mass and N and P concentrations between sample dates were tested using a *t*-test (Sokal & Rohlf 1969).

RESULTS

Over the sampling period the amount of fine roots varied between 303 ± 122 g m⁻² and 612 ± 196 g m⁻². Recalculated as a percentage of the total root mass of *Calluna* in the top 5 cm of the soil, the fine roots fraction varies between 15.7% (July 1984) and 55.2% (December 1983), and is usually about 30% (Fig. 1). This confirms the suggestion that fine roots probably make up a very considerable part of the total plant biomass (Wallen 1983).



Fig. 1. Dynamics in fine root mass in a dry *Calluna vulgaris* heathland. Top: Fine root mass $(g m^{-2})$ in the top 7 cm of soil plus humus; bottom: Fine root mass in the top 5 cm of soil plus humus as a percentage of total root mass of *Calluna* in those top 5 cm. The x-axis represents the time scale on a monthly basis.

While the data appear to show an increase in the total amount of fine roots over the course of the sampling period, the proportion of fine roots does not show such a trend. Therefore, the proportional values were compared and correlated with meteorological data. In both early summer seasons (April–June) the percentage of fine roots of the total root mass was significantly higher (P < 0.005) than in the full summer periods, and also in late autumn–early winter there appeared to be peaks in the proportion of fine roots.

Kendall's rank correlation between percentage of fine roots and sum of precipitation over a 2-week period prior to sampling date revealed a significant positive relationship at the 10% level. Summation of precipitation values or of average temperatures over 1, 3 or 4 week periods did not give significant correlations with percentage fine roots. In addition, when integrated over a 3-month period, data did not show significant correlations.

The sum of all increases in fine roots mass between successive sampling dates may be considered to be a rough measure of fine root production, although it does not take into account stochastic variation in the data. In our study this averaged at 804.8 ± 97.4 g m⁻² year⁻¹.



Fig. 2. N and P concentration (mg g^{-1} fine root) in the fine roots of *Calluna vulgaris*. The x-axis represents the time scale on a monthly basis.

The N concentration of the fine root fraction varied between $11.8 \pm 1.9 \text{ mg g}^{-1}$ and $24 \cdot 1 \pm 3 \cdot 4 \text{ mg g}^{-1}$ with an average $17 \cdot 3 \text{ mg g}^{-1}$. The P concentration of the fine root fraction varied between $0.36 \pm 0.19 \text{ mg g}^{-1}$ and $0.77 \pm 0.26 \text{ mg g}^{-1}$, with an average value of 0.56 mg g^{-1} (Fig. 2). These values are considerably higher than those for N concentration ($6 \cdot 3 \text{ mg g}^{-1}$) and P concentration (0.38 mg g^{-1}) for the total root mass (J. van Rheenen *et al.*, personal communication). The variation in N and P concentrations was not correlated significantly with the amount of fine roots present.

DISCUSSION

Few quantitative data about root mass and root growth in *Calluna vulgaris* exist (Gimingham *et al.* 1979; Woolhouse & Kwolek 1981). Prospective investigations had shown that about three quarters of the total root mass in the investigated dry *Calluna* vegetation were concentrated in the top 5 cm of soil. Also Heath & Luckwill (1938), Chapman (1970) and Persson (1980a) reported a very high concentration of *Calluna* roots in the top soil. Therefore, we restricted our fine root sampling to the top soil. The fairly high standard deviations in our fine root mass data probably largely result from the considerable spatial heterogeneity in root distribution around an individual dwarfshrub and not from the method of separating live fine roots from the soil. Schuurman & Goedewagen (1979) reported that such a method gave reliable estimates with a loss of less than 5% of the true fine root mass. It is possible that, had we followed a fully random sampling strategy, the standard deviations in root mass might have been somewhat larger. This could result from a possible below-ground patchiness even when the above-ground vegetation appears homogeneous. However, the magnitudes of the seasonal peaks in fine root mass are such that they would also have been detected with such a sampling strategy.

The apparent increase in total fine root mass over the sampling period suggests that the heathland stand was not at a steady-state equilibrium. Total above-ground and below-ground phytomass over the period also show a similar trend and reinforce the suggestion that the *Calluna* stand is still in its building phase (J. van Rheenen *et al.*, personal communication).

Our data showed seasonal fluctuations in the fine root mass fraction, with minima in full summer and, less clearly, in full winter. In full summer the sandy soil is repeatedly very dry. The significant correlation of percentage of fine root mass with the sums of the precipitation in the 2-week period before the sampling dates also points to available moisture as a factor stimulating fine root growth. The full winter low cannot be expected to be regulated by moisture availability. It is possible that low soil temperatures hamper fine root growth in this period, while fine root mortality is maintained at an equal rate; together this could result in a low in live fine root mass. Stimulation of fine root growth by moisture availability has been shown elsewhere in interruptedly dry, nutrient-poor ecosystems (Kummerow 1981; Kummerow *et al.* 1978; Caldwell 1979; Haines in Specht 1981; Dell & Wallace 1983), while the reported higher density of fine roots below plant crowns as against unshaded areas in such ecosystems may be regarded as additional indirect evidence. On the other hand, a number of studies have shown adverse results (Lyr & Hoffmann 1967; Rutherford 1983). For *Calluna*, Persson (1980b) also reported increased fine root growth in moist periods of the year and Wallen (1983) found that spring and autumn roots were a principal sink of photosynthates in *Calluna* growing on peat, which indicates fine root growth. Favourable soil temperatures have been reported to stimulate fine root growth in trees (Lyr & Hoffmann 1967). This effect may also be expected in *Calluna* heathland. We could not find a significant correlation with average air temperature in the period before sampling dates, however, and we did not measure soil temperature.

The amount of fine root production measured by us seems high. It is possible that our method is too simple and results in an overestimation of real production (Persson 1978). Apart from that, in considering our values it should be kept in mind that this heathland stand appeared to be in a building stage.

In the winter and early spring period, the N concentration is significantly higher than in other periods. This is especially apparent in winter and early spring of 1984-1985. Our values compare well with the early spring and late autumn highs as well as summer lows in N concentration measured by Steen (1983) in ingrown grass roots. The high values may possibly result from a temporary increased availability of N originating from the temporary high amount of litter a few months earlier (J. van Rheenen et al., personal communication). Wallen (1983) found similarly rapid uptake in spring and autumn of nutrients by the uppermost layers of fine roots of Calluna growing on peat, and Steen (1983) found that N concentration in grass roots increased to similar levels after fertilization. In that case, however, one would expect to find a higher percentage of fine roots at the same time (cf. Vogt et al. 1987). This is not the case. An additional possible explanation (M.A.P.A. Aerts, personal communication) might be that the C content of the roots gradually reduces in autumn and winter as a result of respiration and in summer because the above-ground phytomass acts as a sink, thus causing the peaks in N concentration on a dry weight basis in these periods. However, one would expect parallel peaks in P concentration if this explanation was valid; but in our measurements the variation in P concentration does not show significant changes over time.

REFERENCES

- Berdowski, J.J.M. (1987a): Catastrophic death of Calluna vulgaris in Dutch heathlands. Thesis Univ. Utrecht.
- (1987b): Transition from heathland to grassland initiated by the heather beetle. Vegetatio 72: 167-173.
- & Zeilinga, R. (1987): Transition from heathland to grassland: damaging effects of the heather beetle.
 J. Ecol. 75: 159-175.
- Berendse, F. & Aerts, R. (1984): Competition between Erica tetralix L. and Molinia caerulea (L.) Moench as affected by the availability of nutrients. Acta Oecol. Oecol. Plant. 5: 3-14.
- & Aerts, R. (1987): Nitrogen use efficiency: a biologically meaningful parameter? *Funct. Ecol.* 1: 293-296.
- Boehm, W. (1979): Methods of studying root systems. Ecol. Stud. Vol. 33. Springer, Berlin, New York.
- Brunsting, A.M.H. (1982): The influence of the dynamics of a population of herbivorous beetles on the development of the vegetational patterns in a heathland system. Proc. 5th Int. Symp. Insect-Plant Relationships, Wageningen pp. 215-223. Pudoc, Wageningen.
- & Heil, G.W. (1985): The role of nutrients in the interactions between a herbivorous beetle and some

competing plant species in heathlands. Oikos 44: 23-26.

- Caldwell, M.M. (1979): Root structure: the considerable cost of belowground function. In: O. Solbrig et al. (eds.): Topics in Plant Population Biology. pp. 408-427. MacMillan, London.
- Chapman, S. B. (1970): The nutrient content of the soil and root system of a dry heath ecosystem. J. Ecol. 58: 445-452.
- De Bakker, H. & Schelling, J. (1973): Systeem van bodemclassificatie voor Nederland. Pudoc, Wageningen.
- Dell, B. & Wallace, B.M. (1983): Periodicity of fine root growth in jarrah (Eucalyptus marginata Don ex. Sm.). Aust. J. Bot. 31: 247–254.
- De Smidt, J.T. (1977): Heathland vegetation in the Netherlands. *Phytocoenologia* 4: 258-316.
- (1979): Origin and destruction of northwest European heath vegetation. In: O. Wilmanns & R. Tuxen (eds.): Werden und Vergehen von Pflanzengesellschaften. pp. 411-433. Cramer, Vaduz.
- Gimingham, C.H. & De Smidt, J.T. (1983): Heaths as natural and semi-natural vegetation. In: W. Holzner, M.J.A. Werger & I. Ikusima (eds): Man's Impact on Vegetation. pp. 185-199. Junk, The Hague, Boston.
- —, Chapman, S.B. & Webb, N.R. (1979): European heathlands. In: R.L. Specht (ed.): Heathlands and Related Shrublands. Ecosystems of the World. Vol. 9A: 365-413. Elsevier, Amsterdam.
- Heath, G.H. & Luckwill, L.C. (1938): The rooting system of heathplants. J. Ecol. 26: 331-352.
- Heil, G.W. & Bruggink, M. (1987): Competition for nutrients between *Calluna vulgaris* (L.) Hull and Molinia caerulea (L.) Moench. *Oecologia* 73: 105–107.
- & Diemont, W.H. (1983): Raised nutrient levels change heathland into grassland. Vegetatio 53: 113-120.
- Helsper, H.P.G., Glenn-Lewin, D.C. & Werger, M.J.A. (1983): Early regeneration of Calluna heathland under various fertilization treatments. *Oecologia* 58: 208-214.
- Kummerow, J. (1981): Structure of roots and root systems. In: F. di Castri, D.W. Goodall & R.L. Specht (eds): Mediterranean-type Shrublands. Ecosystems of the World, Vol. 11: 269–288. Elsevier, Amsterdam.
- Kummerow, J., Krause, D. & Jow, W. (1978): Seasonal changes in fine root density in the southern Californian chaparral. *Oecologia* 37: 201–212.

- Lyr, H. & Hoffmann, G. (1967): Growth rates and growth periodicity of tree roots. *Int. Rev. Forest Res. N.Y.* 2: 181–236.
- Persson, H. (1978): Root dynamics in a young Scots pine stand in central Sweden. Oikos 30: 508-519.
- (1980a): Spatial distribution of fine root growth, mortality and decomposition in a young Scots pine stand in central Sweden. Oikos 34: 77–87.
- (1980b): Fine root production, mortality and decomposition in forest ecosystems. Vegetatio 41: 101-109.
- Rutherford, M.C. (1983): Growth rates, biomass and distribution of selected woody plant roots in Burkea africana-Ochna pulchra savanna. *Vegetatio* **52:** 45–63.
- Schuurman, J.J. & Goedewagen, M.A.J. (1971): Methods for the Examination of Root Systems and Roots. Pudoc, Wageningen.
- Singh, J.S. & Coleman, D.C. (1973): A technique for evaluating functional root biomass in grassland ecosystems. *Can. J. Bot.* 51: 1867–1870.
- Sokal, R.R. & Rohlf, F.J. (1969): *Biometry*. Freeman, San Francisco.
- Specht, R.L. (1981): The water relations of heathlands: morphological adaptations to drought. In : R. L. Specht (ed.): *Heathlands and Related Shrublands. Ecosystems of the World*, Vol. 9B: 123-129. Elsevier, Amsterdam.
- Steen, E. (1983): The net stocking method for studying quantitative and qualitative variation with time of grass roots. In: W. Boehm, L. Kutschera & E. Lichtenegger (eds): Root Ecology and its Practical Application. pp. 63-74. Bundesanstalt Alp. Landw. Irdning, Austria.
- Vogt, K.A., Vogt, D.J., Moore, E.E., Fatuga, B.A., Redlin, M.R. & Edmonds, R.L. (1987): Conifer and angiosperm fine-root biomass in relation to stand age and site productivity in Douglas-fir forests. J. Ecol. 75: 857–870.
- Wallen, B. (1983): Translocation of ¹⁴C in adventitiously rooting Calluna vulgaris on peat. Oikos 40: 241–248.
- Werger, M.J.A., Prentice, I.C. & Helsper, H.P.G. (1985): The effect of sod-cutting to different depths on Calluna heathland regeneration. J. Environ. Managem. 20: 181–188.
- Woolhouse, H.W. & Kwolek, A.V.A. (1981): Seasonal growth and flowering rhythms in European heathlands. In: R.L. Specht (ed.): Heathlands and Related Shrublands. Ecosystems of the World, Vol. 9B: 29-38: Elsevier, Amsterdam.