Below-ground dynamics in a wet grassland ecosystem

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SUMMARY

1 Below-ground dynamics in a wet grassland ecosystem were investigated using four different parameters: total root dry weight; new root dry weight; species root dry weight; and species root activity.

2 In wetter conditions above- and below-ground dry weights were higher than in drier conditions (respectively, 800 and 1409 g m^{-2} *v.* 400 and 1199 g m^{-2}). The shoot : root ratio was highest in the wetter conditions. The total root dry weight was highest in September and lowest in December. The difference was used to get a minimum estimate of productivity: 1222 g m^{-2} year^{-1}.

3 The growth of new (lateral) roots was lower in wetter conditions (381 g m^{-2} year^{-1} *v.* 596 g m^{-2} year^{-1}). Taking into account the higher total root dry weight, this suggests a lower turnover rate in these conditions.

4 The species root dry weights, measured in pot experiments, showed a similar vertical distribution to that found in the field, although the vertical nutrient decrease was absent in the pots. The vertical root distribution in the field and in the pots of *Carex acuta* and *Phalaris arundinacea* was less pronounced when the water table was raised, while the vertical root distribution of *Glyceria maxima* stayed approximately equal.

5 While all root dry weights declined sharply between 5 and 15 cm depth, root activity by vigorous species remained relatively constant. From May to July the absorption intensity of *Carex acuta* increased slightly, while that of *Glyceria maxima* decreased.

INTRODUCTION

While the above-ground components of the dynamics of wet grassland have often been investigated (Verlinden 1985), below-ground data are scarce. The principal reasons for this lack of information are:

1 the inaccessibility and the variability of root material; this involves much work to obtain significant results;

2 the difficulty (impossibility?) of identifying the roots of different species and separating dead and live materials. Nevertheless, knowledge of below-ground dynamics is important (Böhm 1979; Dickinson & Polwart 1982; Ingham & Detling 1984). Spatial and temporal differences in rooting patterns may enhance the

possibilities of coexistence (Berendse 1979, 1981, 1982; Fitter 1982; Slydes & Grime 1984; Veresoglou & Fitter 1984). They may contribute to the survival mechanisms of species in extreme environmental conditions, e.g. in periods with high water tables (Crawford 1983). Also the regrowth after cutting and grazing merely depends on below-ground responses (Korte & Harris 1987). Ulehlova, Tesarova & Ostry (1970) described the soil as a subecosystem affected, in the course of the growing season, by the development, maturation and degradation of the vegetational cover. Root dynamics are the link between soil and vegetational cover.

Many estimates of below-ground dynamics and production have been based upon total root dry weights. These figures have many restrictions, as they neglect inactivity, mortality and decomposition of roots (Hansson & Andrén 1986). For a better understanding of the below-ground influences on ecosystem composition and structure, several parameters have to be combined. This paper presents a comparative study of four estimates of root dynamics which are useful in semi-natural or natural grassland ecosystems. Total root dry weight, the ingrowth of new roots and the root dry weight of selected species were measured. Root activity was investigated using absorption experiments. The effects of a high water table were assessed.

In these grasslands, the below-ground biomass consists of roots and rhizomes. When talking about root dry weight, rhizomes are also included. The term dry weight was preferred to biomass, because the amount of dead roots is not known.

STUDY SITE

The investigation was carried out in two hayfields in the nature reserve 'Bourgoyen-Ossemeersen' in the alluvial plains of the river Leie (51°6′N, 3°40′E). The water table varies between −60 and +20 cm in the wetter hayfield, which is flooded during several months each winter, while the water table in the drier hayfield fluctuates between −90 and 0 cm. The soil profiles show no profile development. The humuficious upper layer is restricted to ±10 cm, while the rest of the profile consists of homogeneous rich clay (Table 1). Important species in the wetter hayfield are *Carex acuta* (nomenclature follows De Langhe *et al.*), *Glyceria maxima, Ranunculus repens, Phalaris arundinacea, Poa trivialis, Cardamine pratensis, Lychnis flos-cuculi, Carex disticha*, etc. As conditions become drier they are less

TABLE 1. Vertical distribution (cm) of chemical characteristics (p.p.m.) and total root dry weight (g m^{-2}) in the upper soil layers

Depth	N	P	K	Ca	Mg	Na	pH	Roots
0–5	10 243	22	182	4 400	181	52	5·03	724
5–10	7 280	12	150	5 367	109	32	5·23	207
10–15	4 526	4	103	6 767	83	23	5·47	167
15–20	2 683	4	102	7 433	87	23	6·22	100

productive and accompanied by *Holcus lanatus, Anthoxantum odoratum, Festuca rubra*, etc. The hayfields are cut once a year during summer. Above-ground yields vary from ±800 g m^{-2} in the wetter hayfield to ±400 g m^{-2} in the drier hayfield.

METHODS AND MATERIALS

Total root dry weight

Total root dry weight was measured by taking three (at 2-monthly intervals, in a wet plot, 1984–85) or nine (in a wet and a dry plot, November 1987) random samples with a steel corer with a diameter of 8·2 cm. From each sample above-ground parts were cut at the soil surface. The cores were transported to the laboratory in polyethylene bags, divided into vertical sections of 5–10 cm and stored at 2 °C for a few days. From the November 1987 sample soil was removed for chemical analysis. Homogeneous clay samples were oven-dried (24 h; 90 °C) and then soaked in a 0·27% $Na_4P_2O_7$ solution for the dispersion of clay particles. Soil samples were washed with water and the roots captured on a 450 μm -sieve. Visual separation of living and dead roots was not possible, because of the density of the root network and the presence of a number of different species. Finally the washed roots were oven dried (24 h; 90 °C), weighed, ashed, and dissolved in 1 N HCl. This indicated a residual soil fraction of 16%, which was used as a correction factor.

New root dry weight

To obtain supplementary estimates of the production of new roots during 1 year, root-free soil samples ($\phi = 8{\cdot}2$ cm, H = 10 cm) were put into the ground (September 1986). Eighty soil cores were taken *at random* from both the wetter and drier plots, and roots were extracted manually. This seemed to be the best method, as wet sieving washes out the nutrients and dry sieving was too labour intensive. Some sandy soil was added to the remaining soil to obtain the original volume and conserve soil structure. The root-free soil was sterilized (8 h; 110 °C) and put back in the holes. The soil was compacted to a density similar to that of the surrounding soil. No resowing or replanting was done. One year later, in September 1987, the soil was removed and roots washed out and dried (see above).

Species root dry weight

Species root dry weights of *Carex acuta, Glyceria maxima* and *Phalaris arundinacea* were investigated in pot experiments. To evaluate root responses to water saturation three permanent water tables were established (−32, −16 and 0 cm). Eighty-one plants of each of the above species were dug out (±10 cm soil) from the field and transplanted into pots (22·5 × 24 × 48 cm deep) (March–April 1986). Each pot contained nine plants of the same species, so each water table–species combination was repeated three times. The soil was obtained from neighbouring agricultural land, which had not been treated with pesticides during the previous year. Its structure was loamy clay. Roots were extracted manually from the soil, which was sterilized (8 h; 110 °C). After 1 year (March–April 1987) soil from the middle of each pot (15 × 15 cm) was divided into vertical sections 5–10 cm long. Roots were washed out and dried (see above).

Species root activity

Measurements of root dry weight concentrate emphasis on the thick roots, while absorption mainly occurs in the fine roots. To investigate this aspect of root dynamics, a strontium absorption technique was used (Veresoglou & Fitter 1984). A strontium solution (3 mg ml^{-1}) was injected in three different 5 × 5 grids at a spacing of 5 cm. Each grid used a different injection depth: 5, 10 or 15 cm. Grids were sited where the species under investigation were abundant. Plants with similar intensities of flowering were chosen as preliminary measurements and showed that flowering shoots accumulated only approximately half of the concentrations of strontium in their leaves. One month after injection, the above-ground biomass was cut at the soil surface, separated by species, oven dried and weighed. After ashing, the strontium concentration was measured by atomic absorption. The experiment was repeated in May, June and July 1986.

RESULTS

Total root dry weight

The total root dry weight between 0 and 20 cm depth varied from 1199 g m^{-2} in the drier plot to 1409 g m^{-2} in the wetter plot. As above-ground dry weights were 400 g m^{-2} and 800 g m^{-2} respectively the shoot : root ratio varied from 0·3 to 0·6 respectively. As the above-ground biomass is removed each year, while some roots may stay for over 1 year, the actual shoot : root ratio for productivity may be higher. On the other hand, if the amount of decomposed roots is higher than the mean root dry weight then the ratio may be lower. The vertical root distribution is presented in Fig. 1. The root system under wetter conditions was shallower than under drier conditions but still penetrated up to 100 cm depth under conditions where the reduction boundary was at 70 cm depth.

Time variations in total root dry weight are presented in Fig. 2. The quantity of roots showed a peak in September (2383 g m^{-2}), while the amount was lowest in January (1161 g m^{-2}). This means that at least 1222 g m^{-2} new roots were produced between 0 and 40 cm during 1 year. As the curve is a result of productivity, mortality and decomposition, actual production could be higher.

New root dry weight

In the wet plots, 273 ± 187 g m^{-2} roots were formed between 0 and 5 cm, and 108 ± 89 g m^{-2} roots were produced between 5 and 10 cm depth. In the dry plots,

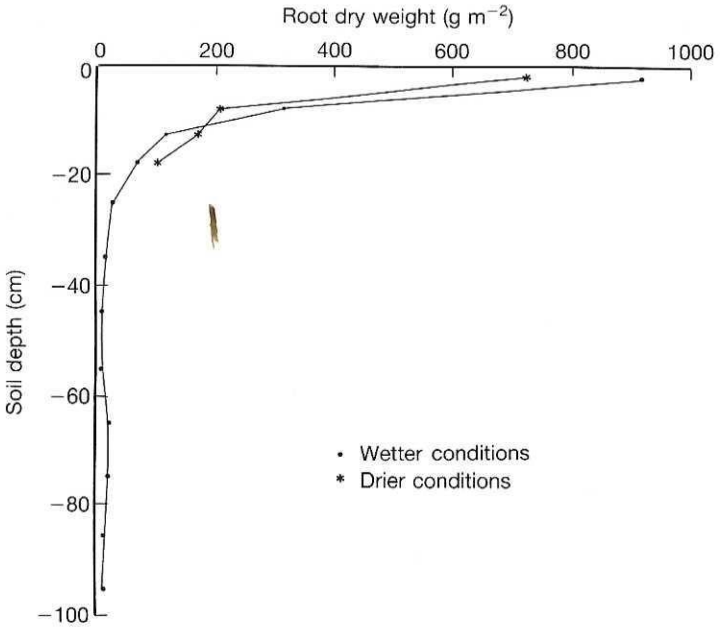

FIG. 1. Vertical root distributions.

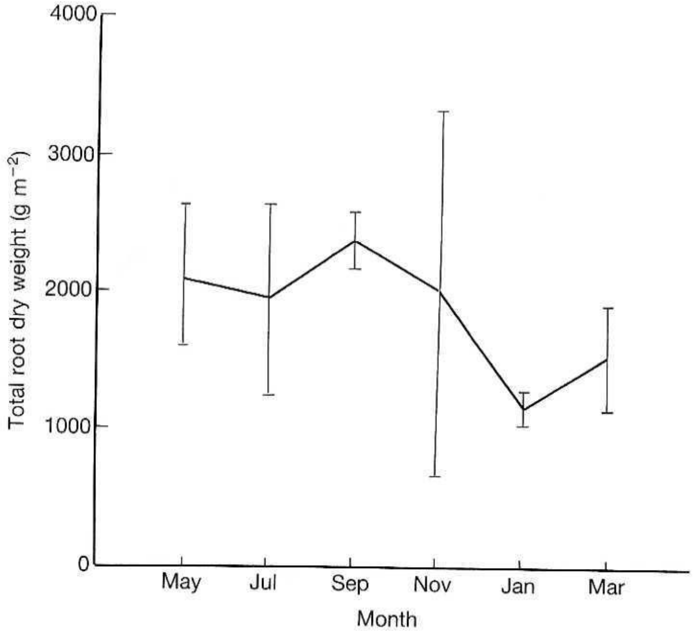

FIG. 2. Seasonal changes in total root dry weight (wet plot).

comparable values were 422 ± 184 and 174 ± 96 g m^{-2}. These quantities are much lower than the previous calculations which were considered an underestimate. The cause of this may be that when using root-free soil cores only lateral root growth is measured, while normal soil cores are regularly taken directly under the shoot. Other possible reasons for the lower estimate are that the experiment with the root-free soil cylinders was carried out in the extreme wet summer of 1987, that the soil conditions in the sterilized, slightly sandy clay are not exactly the same as in the surrounding soil, and surrounding roots are cut off or injured during installation which may influence the root production (Hansson & Andrén 1986).

New root production was higher in drier than under wetter conditions while the total root dry weight (between 0 and 10 cm) was lowest in drier conditions. This indicates a higher root-turnover in the drier plots and suggests that the difference in

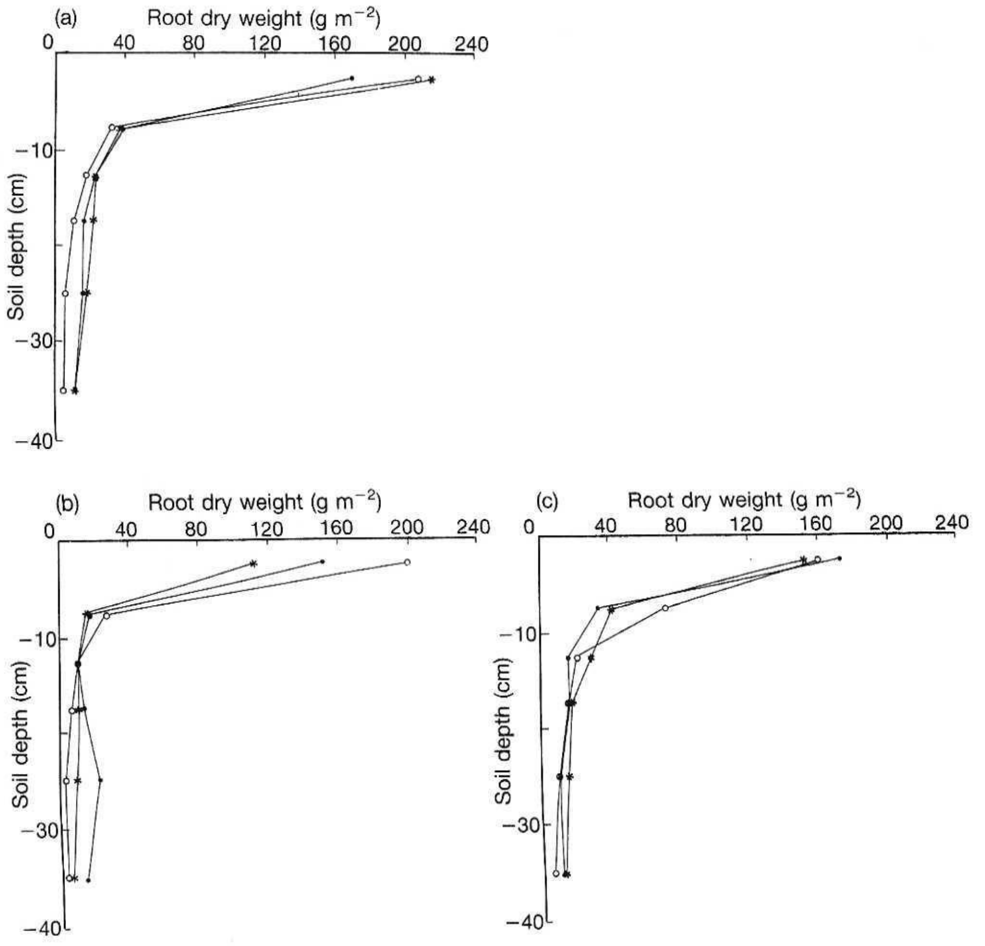

FIG. 3. Species vertical root distribution: (a) *Carex acuta*; (b) *Phalaris arundinacea*; (c) *Glyceria maxima*. ● = water table at −32 cm; * = water table at −16 cm; ○ = water table at 0 cm.

shoot : root ratio, indicated above, should be higher. The variability in root production was higher under wetter conditions.

Species root dry weight

Root dry weight between 0 and 40 cm was 295 g m^{-2} for *Carex acuta*, and 265 g m^{-2} for *Glyceria maxima* and 226 g m^{-2} for *Phalaris arundinacea*. This is less than determined with the root-free soil cylinders, although the roots immediately under the shoots were investigated in this experiment. The small quantity of roots recovered may be a consequence of transplantation, the absence of ecosystem interactions, the homogeneity of species composition etc. The vertical root distribution of the three species, in relation to the water table, is presented in Fig. 3. The global vertical root distribution was very similar to the root distribution found in the field, although the potplants got similar amounts of nutrients over all the soil profile. *Phalaris arundinacea* formed more roots with the high water table, although the roots were shallower. *Carex acuta* also formed shallower roots with a high water table although the total root mass stayed the same. *Glyceria maxima* formed slightly less roots with a high water table with little effect on vertical distribution.

Species root activity

The strontium absorption of *Carex acuta* is presented in Fig. 4. *Carex acuta* absorbed little strontium, analogous to its low calcium uptake (Soileau 1973). The strontium absorbed by *Glyceria maxima* decreased during the same period. While the quantities of root decreased sharply between 5 and 15 cm depth, activity was relatively constant. This was also the case for *Phalaris arundinacea* but not for all

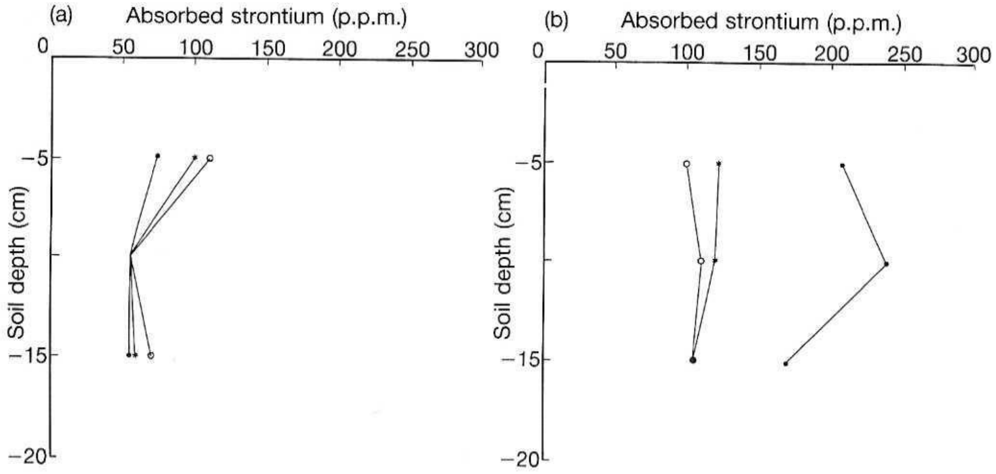

FIG. 4. Strontium absorbed by (a) *Carex acuta* and (b) *Glyceria maxima*. ● = May; * = June; ○ = July.

species. The absorption pattern of *Ranunculus repens* decreased between 5 and 15 cm depth. This also occurred with *Agrostis cappilaris*, *Holcus lanatus* and *Poa pratensis* (Veresoglou & Fitter 1984).

DISCUSSION

The estimates of below-ground root mass and production correspond with other figures from wet grassland ecosystems (Bradbury & Grace 1983). Marshes and swamps are amongst the most productive ecosystems, which is generally attributed to a plentiful supply of nutrients, due to flushing with nutrient-rich water, and sufficient water availability during most of the year (Bradbury & Grace 1983).

Some obvious differences between the wetter and the drier hayfield were observed. The shoot : root ratio was higher in wetter conditions and the root system was shallower. As the below-ground turnover was assumed to be lower, the percentage of dead root material has to be higher in these conditions. These observations mean that in spite of the stresses due to water-logged soil conditions, the remaining amounts of active roots are able to support higher shoot production. The capacity of some investigated species to survive in these extreme conditions was illustrated in pot experiments. The applied stagnant water table here resulted in a greater level of stress. The fluctuating water table in the field improves oxygen supply and reduces levels of toxic substances by sweeping them away. Some specific adaptations were described in Crawford (1983).

In the pot experiments mean vertical root distribution stayed similar to that found in the field. The homogeneous availability of nutrients over the soil profile did not result in a deeper rooting pattern. This suggests that nutrient availability is not important to root dynamics in these ecosystems.

The discordance between the vertical distribution of root weight and root activity for some of the species was remarkable. A possible explanation is the fact that some roots in the upper layer, which are generally thicker, function for the transport of water and nutrients, and do not (or only slightly) normally absorb. This hypothesis is supported by the fact that the more vigorous species continue to absorb with the same intensity in deeper soil layers. The ratio of 'transporting' roots : 'absorbing' roots declined with depth. Root dry weight, which is mainly dependent on the thick roots, declines sharply. The absorption, by the finer roots, which are relatively more abundant in the deeper layers, remains the same. Species with shallow root systems have little need for transport through the upper soil layer. The root dry weight is therefore mainly dependent on 'absorbing' fine roots, and consequently limited. Root dry weight, and absorption intensity, decline sharply with depth.

This discordance illustrates the necessity to apply different parameter types to understand ecosystem dynamics. This was also suggested by Veresoglou & Fitter (1984), who remarked that vegetative growth did not necessarily coincide with nutrient uptake.

The results of the absorption experiment demonstrated some seasonal changes in root activity. While the activity of *Glyceria maxima* obviously decreased between

May and July, the activity of *Carex acuta* increased slightly. Below-ground activity appeared to be lower during flowering. In addition different mowing dates, intervening in different stages of seasonal cycles, may have different consequences for ecosystem composition and structure. Below-ground reactions under different mowing regimes are currently under investigation.

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