ALLOCATION OF CARBON-14 TO ROOTS OF DIFFERENT AGES IN PERENNIAL RYEGRASS (*Lolium perenne L.*)

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ABSTRACT

The objective of this study was to provide information on how current photosynthate allocated to the root system in perennial ryegrass (*Lolium perenne L.*) is distributed among individual roots at differing nodal positions. Mature single ryegrass tillers were transplanted in September 1993 to glass house pots and three months later four of the plants were supplied with $^{14}CO_2$. Individual roots from these radioactively-labeled plants were identified according to their nodal position on the tiller axis and amount of radiocarbon in each root quantified for root tip segments and for the remainder of the root axis. Similar plants were destructively harvested and the number of roots, and mean weight and mean length of individual roots at each node recorded. Counting basipetally from the node of the first fully expanded leaf, root initiation occurred by node two, and final root mass and length was attained by node six. Of the total radiocarbon recovered from the root system, approximately 70% was found in roots attached to the first five nodes. The greatest allocation to root tips was at node one (17.7% of radiocarbon recovered) while the greatest allocation to root axes was at node three (12.1% of radiocarbon recovered). Implications for understanding of timing of root development in relation to nodal position on the tiller axis are discussed.

KEYWORDS

Radiocarbon, perennial ryegrass, roots, nodal distribution

INTRODUCTION

Perennial ryegrass was classified by Stuckey (1941) as having an annual root system, and an annual replacement cycle of ryegrass roots has been described conceptually by Jacques (1956) and from field observations by Caradus and Evans (1977). However, other evidence (Gibbs and Reid, 1992; Matthew, 1992) suggests that root formation in ryegrass is a more continuous process than is implied by the early studies and can be best understood by considering the segmental morphology of the grass tiller. Under the segmental development hypothesis, successive segments formed on the tiller axis may each produce their quota of roots at a particular point in the segmental life cycle, regardless of the time of year. To test this hypothesis, roots from perennial ryegrass plants were individually identified by nodal position of attachment, and measurement made of number of roots, and weight and length of roots at successive nodes. Radiocarbon allocation of current photosynthate to individual roots was also determined.

EXPERIMENTAL

The experiment was conducted at the Institute of Grassland and Environmental Research, Aberystwyth. Single tillers of a perennial ryegrass natural ecotype known as ìP4î were transplanted in September, 1993 to pipes approximately 0.09 m in diameter and 1.0 m high. A horticultural silica sand was used as a rooting medium to facilitate recovery of roots at harvest. Approximately 75 g slow release fertiliser per pipe was added. In December, by which time some ten to twenty primary and secondary daughter tillers were present, the original parent tillers of four of the plants were fed approximately 185 kBq $^{14}CO_2$, released by application of lactic acid to ^{14}C $NaHCO_3$ as described by Matthew (1992). Labeled tillers were destructively harvested 24 hours later. At harvest, tops were discarded, the root system washed out from the sand, and individual roots carefully extricated by floating the root mass in water and teasing out each root. Roots were collected in basipetal order of nodal attachment to the tiller axis, counting the node of the first fully expanded leaf as node one. Recovered roots were first dissected into two segments, tips (the distal 50 mm from the tiller axis), and axes (the remainder of the root axis with attached laterals), then dried and weighed. Radiocarbon was recovered by combustion of root samples in a Harvey OX400 biological sample oxidiser, and entrapment of CO_2 in Oxysol scintillation liquid. Radioactivity was counted as disintegrations per minute (dpm) in a LKB Wallac scintillation counter. A further four plants to which radiocarbon had not been applied were destructively harvested in the same way. For these roots, main axis length was measured with a ruler, total length including lateral branches determined by the grid intersect method (Tennant, 1975) and roots dried and weighed.

RESULTS AND DISCUSSION

The observed distribution of radiocarbon is consistent with allocation being proportional to strength and size of the sink, and inversely proportional to distance from the photosynthetic source. For root tips, the specific activity (Fig. 1a) and percentage of total radiocarbon recovered (Fig. 1b) were greatest at node 1, and decreased more or less logarithmically at successive nodes. This indicated that root elongation activity constitutes a very strong sink and that roots higher on the tiller axis have priority in drawing substrate (Fig 1a & b). For root axes, specific activity was higher at node 3 than at node 2 (Fig. 1a) and total allocation was higher at node three than at any other node (Fig 1b). It seems probable that this reflects both larger sink size at this node as a result of increase in root mass, and high sink strength associated with onset of lateral branching. Between nodes two and three, root mass increased by 77% and root length by 315%, the axis length: total length ratio decreasing from 0.68 to 0.37 (Table 1). It appears that roots reach their final mass and length by node five or six. During the experiment insolation declined with the onset of winter. The fact that roots at nodes nine and ten would have formed during the period of highest light levels, shortly after transplanting in September, may explain the somewhat higher mass and length observed for these roots.

The implication of the preferential allocation to younger roots higher on the tiller axis is that older roots lower on the tiller axis are no longer supported, and this may well be the factor which governs the final length and later death of grass roots. This suggests that root turnover should be a nodally organised, more or less continuous process, rather than an annual replacement event. It would be valuable to conduct a more extensive series of experiments to determine the effect on this root turnover process of seasonal factors such as variation in light level and temperature, to determine nodal position of acquisition and loss of particular physiological functions of roots, and to determine the extent to which nitrogen, carbon and other elements are recycled from senescing roots to younger roots or to the shoot system.

ACKNOWLEDGMENTS

We thank Dr H. Thomas for helpful comment and access to glass house facilities, Drs A. J. Gordon and J. MacDuff for assisting with radiocarbon labeling, and Dr C. Marshall, University College of North Wales for access to facilities for radiocarbon quantification. The

award of an IGER fellowship to the senior author while on sabbatical leave from Massey University is gratefully acknowledged .

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Figure 1
Recovery of radiocarbon from roots at successive nodal positions in perennial ryegrass. Node 1 is the node of the first fully expanded leaf; (a) specific activity, disintegrations per minute per mg dry weight; (b) expressed as a percentage of total radiocarbon recovered from the root system. ⇔ Root tips; ▼ Root axes. Percentages total to less than 100% because some plants had roots beyond node 10.

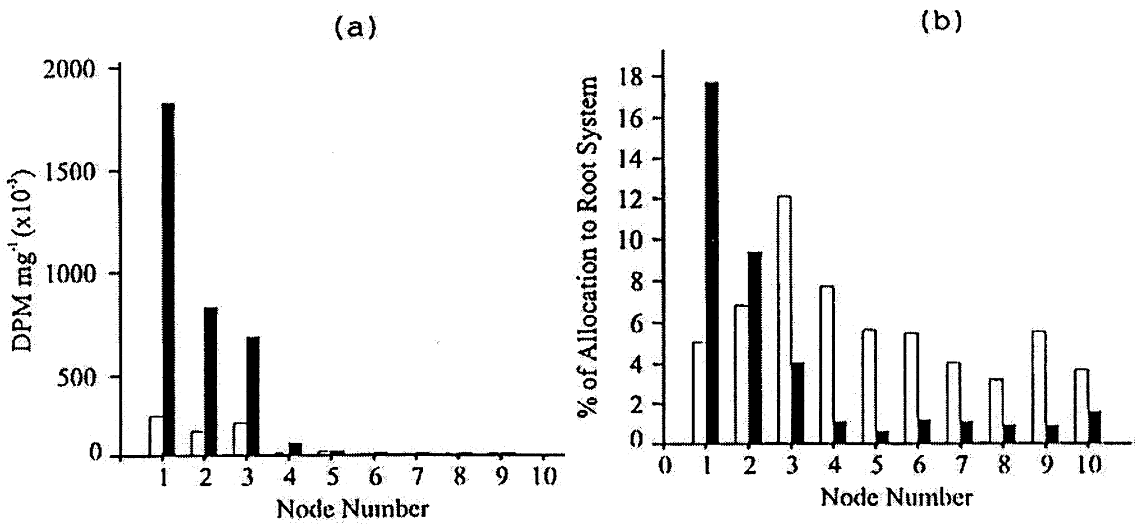

Table 1
Number of roots, and mean weight and length of roots by nodal position on the tiller axis in perennial ryegrass

Measurement	Nodal position on the tiller axis (counting basipetally from the first fully expanded leaf) 1	2	3	4	5	6	7	8	9	10	SEM (%)[1]
Number of roots[2]	1.67	2.25	2.00	2.00	2.75	1.75	1.75	2.00	2.67	2.33	n.d.[3]
Individual root mass (mg)	2.8	5.2	9.2	10.1	16.3	18.6	16.7	19.9	22.4	20.9	15
Main axis length (m)	0.06	0.13	0.22	0.25	0.30	0.36	0.30	0.32	0.35	0.30	12
Total length including laterals (m)	0.07	0.19	0.60	0.80	1.95	2.27	2.44	2.80	2.68	3.30	18
Main axis:total length ratio	0.84	0.68	0.37	0.31	0.15	0.16	0.12	0.11	0.13	0.09	n.d

1. SEM expressed as a % to account for increase in variance with increasing root size at lower nodal positions.
2. This statistic is analogous to F_{rl} of Hunt and Thomas (1985), and was designated P_r by Matthew (1992).
3. Standard deviation not determined for number of roots per node and main axis:total length ratio.