The Effects of Nitrogen Fertilization and the Growing Season on Carbon Partitioning in a Sward of Tall Fescue (*Festuca arundinacea* Schreb)

G BÉLANGER*, F GASTAL* and F R WAREMBOURG†

* Station d'Ecophysiologie des Plantes Fourrageres INRA, Centre de Recherches de Lusignan, 86600 Lusignan and † Centre L. Emberger, CNRS, B P 5051, 34033, Montpellier Cedex, France

Accepted 18 March 1992

The effect of N fertilization on the relative carbon partitioning to the roots of tall fescue (*Festuca arundinacea* Schreb), grown under field conditions, was studied with a $^{14}$C-labelling technique on three regrowths representing contrasting growing seasons. Under non-limiting N growing conditions, the relative carbon partitioning to the roots averaged 17.0, 15.8, and 11.1% in the summer, autumn, and spring regrowths, respectively. The relative carbon partitioning to the roots increased during the summer and autumn regrowths but decreased during the spring regrowth. In the absence of N fertilization, the relative carbon partitioning to the roots averaged 31.3, 26.5, and 26.7% in the summer, autumn, and spring regrowths, respectively. The results were interpreted in terms of a functional equilibrium between the shoots and the roots. It was concluded that, for a dense canopy of a perennial grass growing under fluctuating conditions of solar radiation and temperature, the relative growth of the roots compared to the relative growth of the total biomass is primarily a function of the shoot biomass.

**Key words:** *Festuca arundinacea* Schreb, carbon, partitioning, nitrogen, root growth, fertilization, grass

**INTRODUCTION**

Carbon partitioning between the roots and the shoots is one of the main determinants of shoot growth along with solar radiation interception and the conversion of intercepted solar radiation into plant assimilates (Charles-Edwards, 1982). Most studies conducted under controlled conditions or on field-grown spaced plants have shown that a N deficiency resulted in an increase in the relative carbon partitioning to the roots (Barta, 1975, Powell and Ryle, 1978, Robson and Parsons, 1978, Caloin, Khodre and Atry, 1980, Gastal and Saugier, 1986, Jarvis and Macduff, 1989). To our knowledge, no field studies of the effect of N deficiency on carbon partitioning between the shoots and the roots in perennial grasses grown in a sward have been reported.

The growing season of perennial grasses is characterized by climatic variables such as temperature and incoming solar radiation (level and duration), and by the stage of plant development (vegetative or reproductive). Parsons and Robson (1981), working under high levels of N fertilization and at 90% light interception, reported that the relative carbon partitioning to the roots of perennial ryegrass (*Lolium perenne* L.) decreased during autumn and remained relatively low during winter. It increased early in the spring and then decreased during stem elongation. Warembourg and Shakiba (1987) reported that the carbon allocation to the roots of *Dactylis glomerata* L. grown under non-limiting N and water supplies was maximum in early spring and minimum during seed formation. Warembourg and Paul (1977) found that the relative carbon partitioning to the roots of a permanent grassland reached its minimum in the spring when the crop was actively growing.

The effect of one or two climatic variables on carbon partitioning has been studied under controlled conditions. The positive effect of low temperatures on the relative carbon partitioning to the roots has been reported on many species (Davidson, 1969, Pollock *et al.*, 1983, Szaniawski, 1983, Shishido *et al.*, 1989). The relative carbon partitioning to the roots was reduced by low light intensity under controlled conditions (Ryle, 1970, Ryle and Powell, 1976, Gastal and Saugier, 1986).

The study of carbon partitioning to roots of an established perennial grass cannot be achieved by measurements of the variation in root dry matter since this variation only represents the balance between growth, senescence and decomposition. The carbon partitioning to the roots should therefore be studied with a tracer technique.

The objective of this work was to determine, under field conditions and using a $^{14}$C-labelling technique, the effect of N fertilization on the carbon partitioning coefficients to the roots. The carbon partitioning coefficients were measured on three regrowths of tall fescue representing three contrasting growing seasons.

**MATERIALS AND METHODS**

The study was conducted at the Station d'Ecophysiologie des Plantes Fourrageres de l'Institut National de la Recherche Agronomique, located in Lusignan, France (lat
Carbon partitioning to the roots of an established tall fescue (*Festuca arundinacea* Schreb cv Clarene) sward was studied on three contrasting regrowths summer (4 Jul-16 Aug 1988), autumn (17 Oct-6 Dec 1988) and spring (20 Mar-3 May 1989) The experimental plots for each regrowth were treated uniformly prior to their use for the study and they received a relatively low rate of N fertilization A different field location was used for each regrowth The average daily global radiation was 19.8, 62, and 14.1 MJ m⁻² during the summer, autumn and spring regrowths, respectively The average daily temperature was respectively 18.1, 8.7, and 10.0 °C The experimental plots were irrigated during the summer regrowth The water received by rainfall and irrigation during the summer regrowth was approximately equal to the potential evapotranspiration

Three or four levels of N fertilization were used 0, 80, and 240 kg N ha⁻¹ in summer, 0, 40, and 160 kg N ha⁻¹ in autumn, 0, 60, 120, and 180 kg N ha⁻¹ in spring The N fertilization was done immediately after the defoliation preceding each regrowth period The highest levels of N fertilization in each regrowth were chosen so that the N content was not limiting shoot growth (Bélanger, 1990)

The carbon partitioning coefficients to the roots, also referred to as the relative carbon partitioning, were studied using a ¹⁴C-labelling method adapted for sward conditions (Warembourg and Paul, 1973) The sward labelling was conducted with a closed chamber (50 x 50 x 70 cm) in which the CO₂ concentration and temperature were maintained within ± 1 °C of the ambient temperature The sward was exposed to ¹⁴CO₂ for 1 d (photoperiod) The specific activity of the solution used to generate the ¹⁴CO₂ was 9.2, 18.5, and 46 MBq g⁻¹ C during the summer, autumn, and spring regrowths, respectively

For the summer and autumn regrowths, one level of N fertilization was applied on each side of an iron plate which was inserted vertically into the soil to a depth of 50 cm at least 3 weeks prior to the experimental period Swards grown with the two contrasting N levels were then labelled with ¹⁴C on the same day, the labelling chamber covering both sides of the iron plate The possibility of confounding the effect of N fertilization with an effect of the day of ¹⁴C labelling was therefore eliminated The ¹⁴C-labelled area for each N level was 50 x 25 cm ¹⁴C-labelling of the sward receiving no N fertilization was conducted on a different day using an area of 50 x 50 cm The results obtained in the summer and autumn regrowths indicated that the effect of the day of ¹⁴C-labelling on the relative carbon partitioning was negligible compared to the effect of N fertilization ¹⁴C-labelling during the spring regrowth was therefore conducted on an area of 50 x 50 cm and on separate days for experimental plots receiving different rates of N fertilization

The shoots, shoot bases left below ground and the roots were harvested 7 d after labelling. The shoots for each N level were harvested at ground level on an area of 15 x 40 cm Three soil cores of 8 cm in diameter were then taken to a depth of 60 cm The shoot bases left below ground were separated from the roots at their morphological connection after the roots had been washed free of soil. The shoots, roots and shoot bases left below ground were dried at 80 °C for 48 h, weighed and ground The ¹⁴C was counted at 80 °C for 48 h, weighed and ground The ¹⁴C was counted at 80 °C for 48 h, weighed and ground The ¹⁴C was counted at 80 °C for 48 h, weighed and ground The ¹⁴C was counted at 80 °C for 48 h, weighed and ground The ¹⁴C was counted at 80 °C for 48 h, weighed and ground The ¹⁴C was counted at 80 °C for 48 h, weighed and ground The ¹⁴C was counted at 80 °C for 48 h, weighed and ground The ¹⁴C was counted at 80 °C for 48 h, weighed and ground The ¹⁴C was counted at 80 °C for 48 h, weighed and ground

The coefficients of carbon partitioning to a plant compartment were calculated as

\[ C_x = \frac{CA_x}{CA} \]  

(1)

where \( C_x \) is the coefficient of carbon partitioning to a plant compartment \( k \), \( CA_x \) is ¹⁴C activity in a plant compartment \( k \), and \( CA \) is the ¹⁴C activity in the total biomass (roots, shoots and shoot bases left below-ground)

The ¹⁴C activity in a plant compartment and the total biomass were calculated by multiplying the specific activity of the plant compartment or the total biomass by their respective biomass Hence the coefficients of carbon partitioning to a plant compartment \( k \) can be expressed as

\[ C_x = \frac{SA_x \times B_k}{SA \times B} \]  

(2)

where \( SA_x \) is the specific activity of the plant compartment \( k \) (Bq mg C⁻¹), \( SA \) is specific activity of the total biomass (Bq mg C⁻¹), \( B_k \) is biomass of plant compartment \( k \) (mg C), and \( B \) is total biomass (mg C)

There were no replications of the experimental treatments since only one labelling chamber could be used. The variability of the carbon partitioning coefficients for each N fertilization level and each labelling day was assessed by calculating the standard error among the three soil cores in the summer and autumn regrowths, and the six soil cores in the spring regrowth

**RESULTS**

The growing season integrates both the vegetation status (vegetative or reproductive) and the combination of climatic...
variables typical of each season The effect of the growing season could be analysed only in situations for which the N status of the sward in the three regrowths was equivalent. This situation occurred only when N was not limiting shoot growth (Bélanger, 1990) Under N deficient growing conditions, the seasonal variations in soil N mineralization presumably resulted in swards having different N status even though similar amounts of N fertilization were applied.

Under non-limiting N growing conditions, obtained with the highest rate of N fertilization for each regrowth, the coefficients of carbon partitioning to the roots ranged from 10.9 to 24.6% with an average of 17.0% during the summer regrowth (Fig 1) In the autumn regrowth, the coefficients of carbon partitioning to the roots ranged from 11.1 to 19.2% with an average of 15.8%. The carbon partitioning coefficients ranged from 6.4 to 13.8% with an average of 11.1% during the spring regrowth. The coefficients of carbon partitioning to the roots, averaged over the entire regrowth, were therefore highest in the summer and lowest in the spring. The relative carbon partitioning to the shoot bases left below ground averaged 6.5, 12.9, and 4.6% during the summer, autumn, and spring regrowths, respectively.

The change in the carbon partitioning coefficients to the roots during regrowth also differed from one growing season to another. The proportion of assimilates exported to the root system increased during the summer and autumn regrowths. The increase was, however, greater during the summer regrowth than during the autumn regrowth since the proportion of assimilates exported to the root system reached a plateau during the autumn regrowth. The proportion of assimilates exported to the root system decreased during the spring regrowth.

The N deficiency resulted in an increase in the relative carbon partitioning to the roots in all three regrowths (Fig 2) The carbon partitioning coefficients to the roots in the absence of N fertilization averaged 3.1, 2.6, and 2.7% in the summer, autumn, and spring regrowths, respectively. The relative carbon partitioning to the roots was 1.8, 1.7, and 2.4 times greater (summer, autumn, spring) in the absence of N fertilization than under non-limiting N growing conditions. The carbon partitioning coefficients to the shoot bases left below ground in the absence of N fertilization were 7.3, 19.3, and 10.3% in the summer, autumn, and spring regrowths, respectively.

DISCUSSION

Results from studies conducted under controlled conditions indicated that 14C-labelled assimilates required a maximum of approximately 5 d to reach their final destination as structural carbon and long-term storage (Michulinas et al., 1985, Danckwerts and Gordon, 1987, Bélanger, 1990) Hence, since there was a period of 7 d between 14C-labelling and sampling, the relative carbon partitioning measured in this study refers to the carbon used for growth and long-term storage but it does not include the carbon lost by respiration.

Non-limiting N growing conditions

The range of carbon partitioning coefficients obtained under non-limiting N growing conditions in the autumn and spring regrowths was similar to those published by Parsons.
and Robson (1981) on perennial ryegrass and by Warembourg and Shakiba (1987) on orchardgrass. The carbon partitioning coefficients were also within the order of magnitude of the ratio of root biomass to total biomass measured on relatively young tall fescue plants grown under controlled conditions (Gastal and Saugier, 1986).

The priority given to the shoots immediately after a defoliation has been interpreted in terms of a functional equilibrium between the roots and the shoots, and their respective activities (Brouwer, 1962). This functional equilibrium implies that the carbon assimilation rate is proportional to the N absorption rate, and that the plant reaches this equilibrium by adjusting the relative dimensions of the shoot and the root biomass (Wilson, 1988). During the summer and autumn regrowths, the shoots received a high proportion of carbon when the carbon assimilation of the sward was reduced following defoliation.

The decrease in the relative carbon partitioning to the roots during the spring regrowth was also reported for perennial ryegrass by Parsons and Robson (1981) and for orchardgrass by Warembourg and Shakiba (1987). In the present study, the average height of the growth apex was 10 cm 30 d after the start of the regrowth, indicating that stem elongation was under way. The decrease in the relative carbon partitioning to the roots at the end of the spring regrowth period can therefore be ascribed to the increased shoot requirements for assimilates associated with stem elongation.

Many studies have indicated that low air temperature increased the proportion of assimilates allocated to the root system (Davidson, 1969; Pollock et al., 1983; Belanger, 1990). Our results, however, indicated that the relative carbon partitioning to the roots was less or equal in the autumn regrowth (average air temperature of 8.7 °C) than in the summer regrowth (average air temperature of 18.1 °C). The relative carbon partitioning to both the roots and the shoot bases left below ground averaged over the entire regrowth was greater in the autumn regrowth (28.7%) than in the summer regrowth (23.5%). This result emphasizes the importance of the shoot bases as a compartment for carbon allocation during the autumn regrowth, presumably originating from fructan storage in existing tillers and the production of new tillers. The relative tillering rate was higher during the autumn regrowth than during the spring and summer regrowths (data not shown).

Relative specific activity of the shoots

From eqn (2), the carbon partitioning coefficient to a plant compartment $k$ can be seen as the product of the relative specific activity ($RSA_k$) of that plant compartment and the ratio between the biomass of plant compartment $k$ and the total biomass:

$$C_s = \frac{SA_k \times B_k}{SA \times B} = RSA_k \times \frac{B_k}{B}$$ (3)

The relative specific activity is the ratio between the specific activity of a plant compartment and the specific activity of the total biomass. It is a dimensionless number used to compare the $^{14}$C concentration of a specific sink or plant compartment with that in the total biomass on a unit mass basis (Cradde and Heichel, 1988). The relative specific activity therefore represents the strength of a sink or a plant compartment relative to the total biomass.

In terms of dry matter change, the carbon partitioning coefficient can be expressed as

$$C_s = \frac{\Delta B_s}{\Delta B}$$ (4)

By combining eqns (3) and (4), it is shown that the relative specific activity is equal to the ratio of the relative growth of a plant compartment and the relative growth of the total biomass:

$$RSA_k = \frac{\Delta B_k}{\Delta B_k / B}$$ (5)

When the data obtained over the three regrowths were pooled, it was found that the shoot relative specific activity ($RSA_s$) decreased with an increase in the shoot biomass ($B_s$) (Fig 3). Fitting allometric equations to the data gave the following relationships:

$$RSA_s = 114.8(B_s)^{-0.78} \quad r^2 = 0.70 \quad \text{for no N}, \quad (6)$$

$$RSA_s = 61.6(B_s)^{-0.62} \quad r^2 = 0.76 \quad \text{for non-limiting N} \quad (7)$$

Compared to the total biomass and per unit of carbon, the shoots used a decreasing proportion of the newly assimilated carbon when the existing amount of carbon in the shoot increased. In terms of relative growth, those relationships indicate that the ratio of the shoot relative growth to the total biomass relative growth decreased as the shoot biomass increased.

The decrease of the shoot relative specific activity with an increase in shoot biomass is described by an allometric model similar to the one used to describe the decrease in N content with an increase in shoot biomass (Lemaire and Salette, 1984; Greenwood et al., 1990). The average leaf age increases during regrowth and the average radiation level received by the leaves decreases. Hence the physiological activity of the shoots relative to that of the total biomass decreases with an increase in shoot biomass during regrowth.

It was found that the decrease in shoot relative specific activity was slightly greater in the absence of N fertilization than when N was not limiting growth. Hence, the ratio of the relative growth of the shoots to the relative growth of the total biomass decreased faster during regrowth when N
as shoot biomass accumulates, the shoot relative specific activity decreases for all N fertilization but it decreases faster when N is limiting growth.

**LITERATURE CITED**


Parsons AJ, Robson MJ. 1981. Seasonal changes in the physiology of S24 perennial ryegrass (Lolium perenne L.) III Partition of assimilates between root and shoot during the transition from the vegetative to reproductive growth. Annales de Botanique 48: 733–744.


**Fig. 3** The relationship between the shoot relative specific activity and the shoot biomass for non-limiting N growing conditions (•) and no N fertilization (O) (curves represent the allometric equations and their 95% confidence intervals).


