Regrowth Kinetics of *Dactylis glomerata* Following Root Excision

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The growth kinetics of *Dactylis glomerata* following a root excision were studied in order to characterize the process of partitioning of carbon assimilates between shoots and roots. Plants were grown hydroponically, in constant environments. The variations with time of shoot and root fresh weights during regrowth were measured using a non-destructive method. The effect of root excision on shoot and root water contents was also determined from complementary experiments. Immediately after cutting, the specific growth rate increased markedly for roots and decreased slightly for shoots, but this decrease can be at least partly accounted for by the variation of the shoot water content. At the end of the perturbed phase, the specific growth rates and the root fraction had almost returned to the values measured immediately before cutting.

The experimental regrowth kinetics were analysed in terms of a kinetic model which calculates shoot and root growth as the difference between the carbon provided by photosynthesis and carbon losses associated with respiration. A satisfactory description of the regrowth kinetics was obtained by assuming that the partitioning of carbon substrates between shoots and roots is not modified by cutting, and that the partitioning coefficient remains constant during regrowth. According to this analysis, the stimulation of root growth after cutting can be mainly attributed to the reduction in the part of carbon substrates utilized in roots for maintenance requirements.

Key words: *Dactylis glomerata* L., root excision, regrowth kinetics, shoot:root partitioning, maintenance requirements.

INTRODUCTION

Vegetative growth is usually discussed in terms of a functional equilibrium between the uptake of carbon by the shoots and the uptake of water and mineral nutrients by the roots (Brouwer, 1962; Davidson, 1969; Thornley, 1976). In response to a change in growth conditions, a plant adjusts its shoot or root growth in order to re-establish the initial nutritional equilibrium.

This description is essentially empirical. It accounts in general for experimental observations (Hunt and Burnett, 1973; Hunt, 1975; Richards and Rowe, 1977b), but it provides no information on the mechanism of the adaptive process (Bastow Wilson, 1988). A more mechanistic approach has been proposed by McMurtrie and Wolf (1983). Shoot and root growth are described using an energy-balance approach. In steady-state growth, there is an equilibrium between the two main utilizations of the carbon substrates supplied by photosynthesis, namely the maintenance of biomass and biomass production. A change in growth conditions perturbs the internal energy equilibrium (Szaniawski, 1983). This causes a change in the amount of photosynthetic substrates available in shoots or roots for biomass production and, consequently, a slowing or a stimulation of shoot or root growth.

This model has proved satisfactory in the analysis of the regrowth kinetics of *Dactylis glomerata* L. following defoliation (Caloin, Clément and Herrmann, 1990). It has been shown that shoot cutting increases the proportion of photosynthetic substrates utilized in roots for the purpose

of maintenance. The result is a slowing of root growth until the root:shoot ratio has almost recovered the value it had before cutting. The objective of the present study is to examine whether the same theoretical approach can equally describe the shoot and root growth following root excision. From an energy point of view, this perturbation should induce the opposite effect to that of defoliation since the level of maintenance should be reduced, due to the reduction in size of the root system. To test the validity of this approach, the kinetic behaviour predicted by the model was compared with experimental regrowth of *Dactylis glomerata* L. measured at 17 and 25 °C in controlled environments.

MCMURTRIE AND WOLF'S MODEL

In the theoretical approach presented by McMurtrie and Wolf (1983) and West (1987), the shoot and root growth is calculated as the difference between the input of carbon supplied by photosynthesis and the loss of carbon resulting from respiratory exchanges. Originally, the model included other factors such as animal grazing, litterfall and mortality which have not been taken into account in the present study.

At a given time of growth, the gross photosynthetic rate, P_G, defined as the rate of carbon assimilation by the shoots, dC/dt, can be expressed as

$$P_G = dC/dt = \sigma_c S, \qquad (1)$$

where σ_c is the specific activity of shoots with respect to carbon, and S is the shoot weight. These photosynthetic

substrates have two main utilizations, the maintenance of biomass which takes priority, and biomass production. As suggested by Pirt (1965), the maintenance requirements of a component will be considered proportional to the weight of this component, so that shoot and root maintenance requirements, M_S and M_R, are described by

$$M_S = m_S S \quad \text{and} \quad M_R = m_R R, \qquad (2)$$

where m_S and m_R are the shoot and root maintenance coefficients, and R is the root weight.

The biomass production in shoots and roots is calculated according to the following scheme. The carbon substrates supplied by photosynthesis first serve to satisfy shoot maintenance requirements. The excess is the net photosynthetic production, P_N, defined as

$$P_N = P_G - M_S = \sigma_N S, \qquad (3)$$

where $\sigma_N = \sigma_C - m_S$ is the net specific activity of shoots.

The net photosynthetic production is then partitioned between shoots and roots according to the partitioning coefficients, s_p and r_p with $s_p + r_p = 1$. The amounts of carbon substrates available for growth in shoots and roots per time unit are therefore given by

$$dC_S/dt = s_p \sigma_N S \qquad (4a)$$

and

$$dC_R/dt = r_p \sigma_N S - m_R R. \qquad (4b)$$

It is assumed that these carbon substrates are immediately converted into new shoot and root materials, which excludes the possibility of an accumulation of these substrates in the plant. The shoot and root growth are thus described by the following equations

$$dS/dt = Y_S s_p \sigma_N S \qquad (5a)$$

and

$$dR/dt = Y_R (r_p \sigma_N S - m_R R), \qquad (5b)$$

where Y_S and Y_R are the efficiencies of conversion of the carbon substrates into shoot and root materials.

Using these relationships, the shoot and root specific growth rates, k_S and k_R respectively, can be calculated as

$$k_S = (1/S)(dS/dt) = Y_S s_p \sigma_N \qquad (6a)$$

and

$$k_R = (1/R)(dR/dt) = Y_R[r_p \sigma_N(S/R) - m_R]. \qquad (6b)$$

The shoot specific growth rate, k_S, is independent of the size of the shoot or root system. On the contrary, k_R is a function of the S/R ratio.

The coefficients of eqns (5) and (6), namely Y_S, Y_R, s_p, r_p, σ_N, and m_R, cannot be considered to be constant with time, or independent of environmental parameters. Therefore, it is not possible to predict the plant response to a perturbation of growth conditions from these relationships alone. In the next sections, we present the main features of the regrowth kinetics following a root excision, and we attempt to analyse them on the basis of the model.

MATERIALS AND METHODS

A detailed description of the methods used has been previously reported by Caloin *et al.* (1990). Experiments were carried out in two culture rooms, at constant temperatures of 17 and 25 °C. Vegetative plants of *D. glomerata* were grown hydroponically under white illumination from fluorescent tubes providing an irradiance of 55 W m^{-2} at the plant level for 16 h d^{-1}. The nutrient solutions, maintained at a constant nitrate concentration (10 mM), were aerated for 10 min every 2 h.

The effects of temperature and plant age on regrowth were investigated from three sets of experiments. At 17 °C, plants were sampled at two stages of growth; the initial plant weights were, respectively, in the ranges 2–4 g and 20–40 g. At 25 °C, all plants were in the range 20–40 g. Three levels of cutting were performed, corresponding to 50, 70 and 80% of excised roots. At least six replicates were measured per treatment. Following root excision, no significant wilting effect was observed for shoots. However, a partial wilting cannot be excluded for excised roots which ceased elongating due to the removal of terminal apices (Biddington and Dearman, 1984).

The variations with time of the shoot f. wt, S_h, and of the total f. wt, W_h, were measured using a non-destructive method derived from Arnott, Brockington and Spedding (1974). The f. wt, W_h, measured after wiping the superficial water from roots, was determined with a coefficient of variation of about 3% for entire plants, and less than 1% when 80% of the root system was removed. The reliability of the S_h determination was regularly tested using plants which were dissected immediately after the non-destructive measurement. Throughout the course of all the experiments, the relative accuracy of S_h was within 5%, while the root f. wt, R_h, calculated by $R_h = W_h - S_h$, was accurate to 15–20% during unperturbed growth and to about 30% immediately after cutting. Figure 1 presents the accuracy of the shoot and root f. wt measurements before and after root excision, for a 25 °C treatment. The effect of successive non-destructive measurements on plant growth was not examined in this study, but it should not alter significantly the characteristics of growth kinetics (Causton, 1991).

Complementary determinations of shoot and root d. wts of plants dissected after non-destructive measurements were also performed in order to characterize the variation of the shoot and root water contents during regrowth.

RESULTS

The change in root fraction with time following an 80% root excision at 17 and 25 °C is illustrated in Fig. 2, for plants selected in the same weight range (20–40 g). During vegetative growth preceding excision (measured accurately only at 25 °C), the root fraction decreased slightly with time, as usually observed under non-limiting growth conditions (Bray, 1963; Troughton, 1967; Caloin and Yu, 1984). Immediately after cutting, the percentage of roots increased and attained a maximum close to its initial value (Brouwer, 1962; Biddington and Dearman, 1984). This maximum should indicate the end of the perturbed phase since, in the growth which followed, the root fraction again exhibited the decrease characteristic of unperturbed vegetative growth.

For these same plants, the variations with time of the shoot, root and total f. wts are shown in Fig. 3 on a
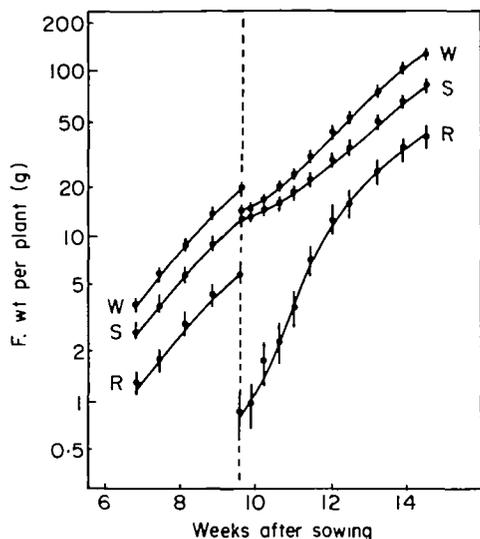
FIG. 1. Accuracy of f. wt measurements (vertical bars) before and after an 80% root excision for (S) shoot, (R) root and (W) total f. wts. The dashed line indicates the time when the cutting was carried out. The continuous lines are only guides.
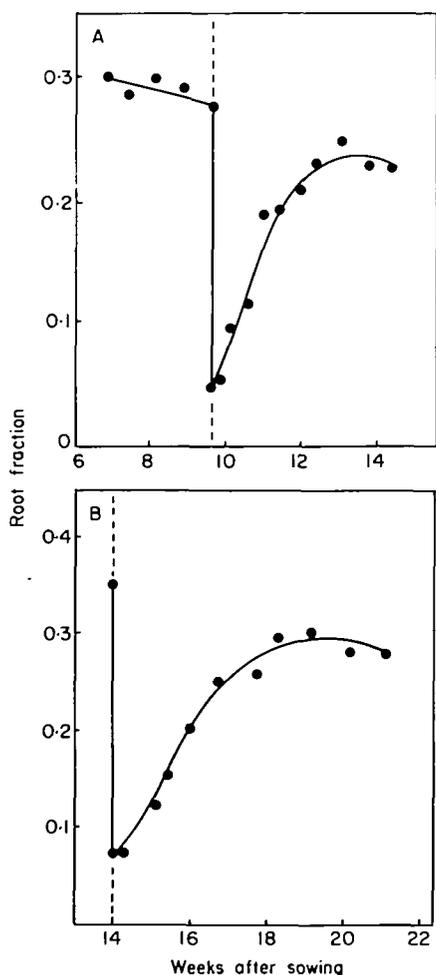
FIG. 2. Root fraction with time following an 80% root excision: (A) 25 °C; (B) 17 °C. The continuous line is only a guide.
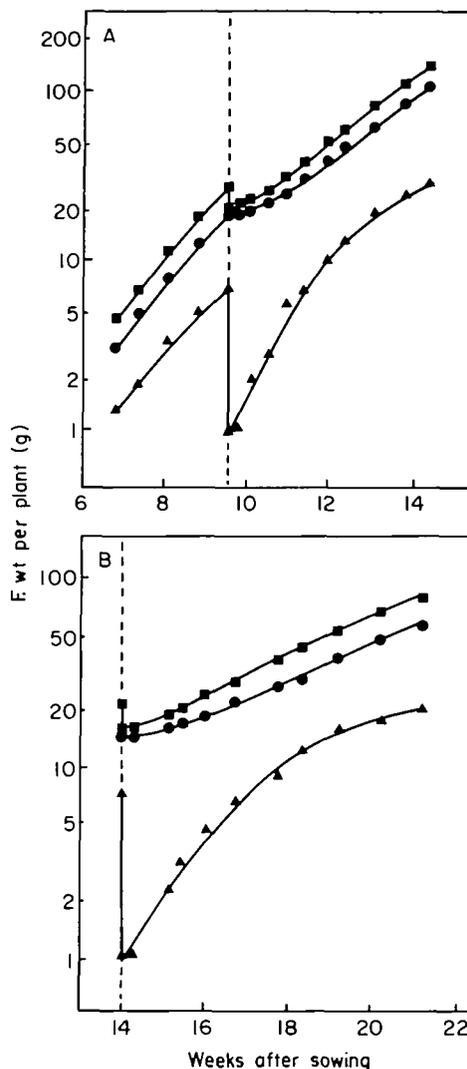
FIG. 3. Shoot, root and total f. wts with time following an 80% root excision at 25 °C (A) and 17 °C (B): (●) shoot, (▲) root, and (■) total f. wts. The continuous lines are only guides.

logarithmic scale. The regrowth process is qualitatively similar at both temperatures. As is apparent from Fig. 3A, which includes pre-cutting measurements, the specific growth rate (corresponding to the slope of the curves in Fig. 3) increased for roots in response to root excision, whereas it decreased slightly for shoots; but this decrease was only clearly apparent at the two most severe cutting levels. This behaviour, which agrees with previous reports (Humphries, 1958; Buttrose and Mullins, 1968; Richards and Rowe, 1977*a*; Biddington and Dearman, 1984), was observed whatever the initial plant weight. During the following time course, both specific growth rates approximately regained the values observed before cutting (Figs 1 and 3A). And it must be noted that, at the end of the perturbed phase, the root fraction and the specific growth rates were generally found to be 10–20% lower than their initial values, which should reflect a plant ageing effect since these two parameters decrease continuously with time during unperturbed vegetative growth.

TABLE 1. *Fresh weight to dry weight ratio following an 80% root excision*

	Temperature (°C)	Before cutting ($t = 0$)	F. wt to d. wt ratio
			Weeks after cutting
			0·5	1	1·5	2	3
Shoots	17	6·6	5·9	5·7	5·9	6·1	6·3
Roots	17	15·3	11·6	11·5	12·4	13·4	14·4
Shoots	25	6·8	6·0	5·7	5·8	6·0	6·3
Roots	25	15·8	11·7	11·5	12·8	14·0	15·1

Values are means of at least six replicates. The coefficient of variation is approximately 8%.
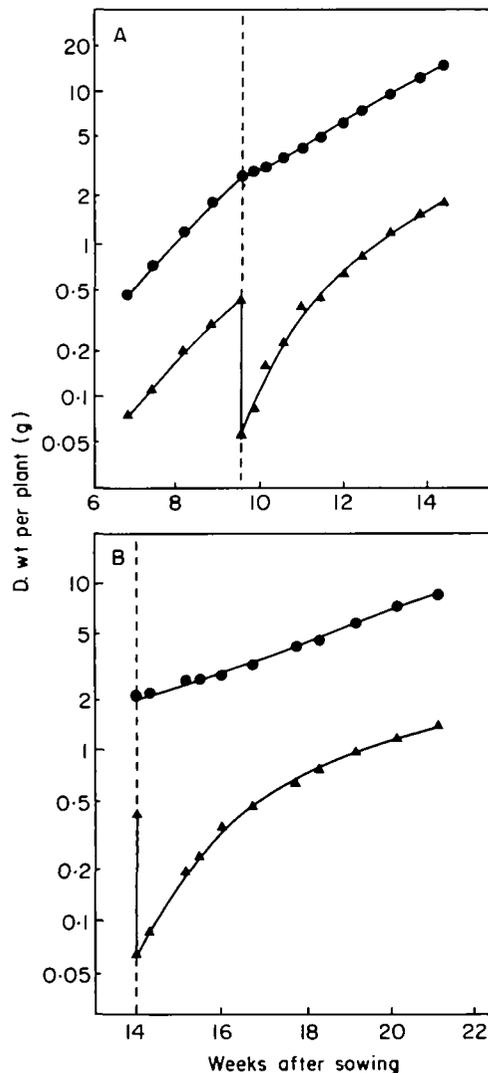
FIG. 4. Shoot and root d. wts with time following an 80% root excision, at 25 °C (A) and 17 °C (B): (●) shoot, and (▲) root d. wts. The continuous lines are only guides.

The variation with time of the f. wt to d. wt ratio during regrowth is given in Table 1. At both temperatures, this ratio decreased by about 15% for shoots and 25% for roots in the days following cutting, and had almost returned to its initial value three weeks later.

In order to analyse the shoot and root f. wt measurements in terms of the present model developed on the basis of a carbon budget, they must be converted into shoot and root d. wts (approximately proportional to shoot and root carbon contents). This conversion was performed using the f. wt to d. wt ratio values obtained at the different samplings. The variation of the root fraction, expressed in d. wt, is almost unchanged compared with that reported in Fig. 2, due to the similar variation of shoot and root water contents. However, in Fig. 4, it can be observed that the kinetic behaviour is slightly modified. The initial slowing of shoot growth (Fig. 3) is partly accounted for by the decrease in shoot water content, particularly for the 17 °C treatments. For roots, the regrowth kinetics are similar to those described in Fig. 3, but the stimulation of root growth after cutting is still accentuated.

DISCUSSION

The regrowth kinetics of *D. glomerata* following a root excision are mainly characterized by an initial increase in root specific growth rate, which contrasts with the approximately constant value of shoot specific growth rate. This behaviour can be discussed initially by assuming, as in the analysis of regrowth following a defoliation (Caloin *et al.*, 1990), that the values of the s_p and r_p coefficients, and more generally of all the coefficients of eqns (5) and (6), are not modified by cutting and remain constant during regrowth. In this case, according to eqn (6), the shoot specific growth rate is constant, and the increase in root specific growth rate, related to the increase in the S/R ratio, is explained by the reduction in root maintenance requirements. This assumption could not be entirely justified for the σ_N coefficient since σ_C, and thus σ_N, is expected to decrease during growth, as a result of an increase in the overlapping of shoots (Charles-Edwards and Thornley, 1973). We will not consider this effect, which should be relatively weak in the present experiments due to the short duration of the perturbed phase. Under this assumption, the regrowth kinetics can be calculated analytically and compared with experimental variations.

From eqn (5a), the growth of shoots is exponential and described by the relationship

$$S(t) = S_0 \exp(k_0 t),\qquad(7)$$

with

$$k_0 = Y_s s_p \sigma_N.\qquad(8)$$

TABLE 2. *Parameters of eqns (7) and (9) determined by non-linear regression analysis, for treatments presented in Fig. 4. The second set of values are related to the analyses which exclude the first shoot and root d. wt*

Temperature (°C)	k_0 (d^{-1})	α_R (d^{-1})	S_0 (g)	R_0 (g)	R_{F0} (g)	ϵ
17	0·028	0·025	2·03	0·051	0·41	0·061
	0·028	0·032	2·01	0·034	0·40	0·049
25	0·051	0·053	2·56	0·049	0·33	0·068
	0·052	0·064	2·43	0·031	0·31	0·056
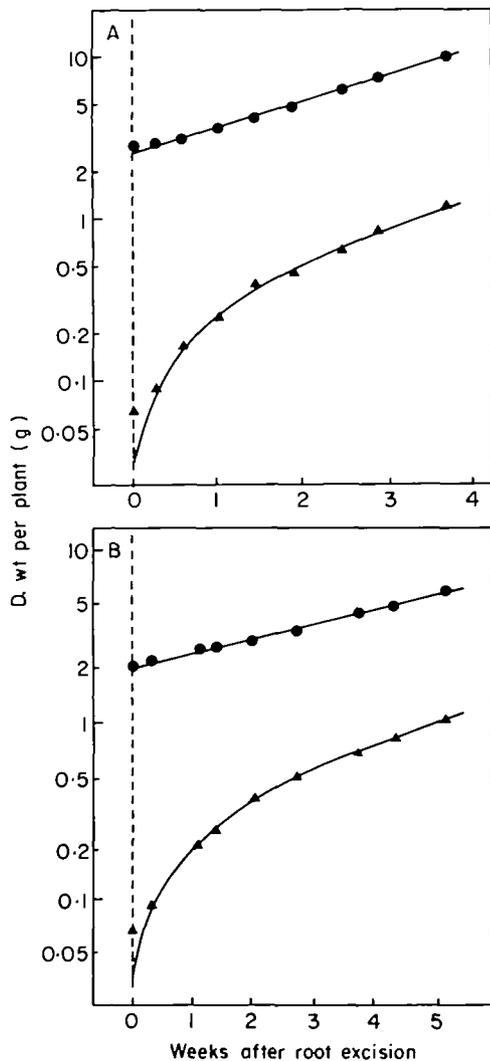
FIG. 5. Comparison between the experimental and theoretical growth kinetics following an 80% root excision. The theoretical trends were calculated from eqns (7) and (9) using the second set of coefficients in Table 2. (A) 25 °C; (B) 17 °C. Symbols as in Fig. 4.

By substituting eqn (7) in eqn (5*b*), this equation can be integrated, which leads to the $R(t)$ variations expressed as

$$R(t) = R_{F0}\exp(k_0 t) + (R_0 - R_{F0})\exp(-\alpha_R t), \quad (9)$$

with

$$\alpha_R = Y_R m_R \quad (10)$$

and

$$R_{F0} = Y_R r_p \sigma_N S_0/(k_0 + \alpha_R). \quad (11)$$

S_0 and R_0 are the initial shoot and root weights, and R_{F0} is the extrapolated value at time $t = 0$ of the final exponential root growth.

The five coefficients of eqns (7) and (9), S_0, R_0, R_{F0}, α_R and k_0 were determined simultaneously using a non-linear regression (Marquardt, 1963). The result of this analysis for the treatments presented in Fig. 4, is given in Table 2 (first set of data). The ϵ coefficient, defined as

$$\epsilon = (1/n)\Sigma|(X_{ci} - X_i)/X_i|, \quad (12)$$

characterized the quality of the fit between the calculated and the experimental d. wts, X_{ci} and X_i, respectively; n was the number of measurements lying in the perturbed phase. In all treatments, at both temperatures, the initial shoot and root specific growth rates predicted by the model were found to be greater than those measured experimentally. The difference was more accentuated for roots than for shoots. The divergence between experimental and theoretical values cannot reflect a change in the value of the partitioning coefficient which should modify shoot and root specific growth rates in an opposite manner [eqn (6)]. It could be attributed to a decrease in the σ_N coefficient, which should reduce both specific growth rates and could be explained by a transient deficiency in leaf nitrogen concentration (Carmi, 1986; Charles-Edwards, Doley and Rimmington, 1986). However, the most likely explanation is that irreversible wilting of a part of plant material occurs after cutting. The effect is larger for roots than for shoots due to the mortality of terminal parts of excised roots. The percentage of this dead component in total shoot and root weights should rapidly decline during regrowth. A better agreement with the model should therefore be expected if the first shoot and root d. wt is not taken into account in the analysis. The results of this analysis correspond to the second set of values in Table 2 and are illustrated by the continuous lines in Fig. 5. If we exclude the initial datum at time zero, the agreement between the experimental and calculated variations is satisfactory.

For each treatment, all the replicates of the most severe level of cutting were analysed according to the same fitting procedure (excluding the first measurement). Table 3 gives the variability of the values of the main parameters of the model among the different replicates. The k_0 and α_R coefficients increase with temperature, in agreement with the values derived from the analysis of defoliation experiments (Caloin *et al.*, 1990). However, due to the inaccuracy of root

TABLE 3. *Variability of the* k_0 *and* α_R *values among the different replicates for the three experiments*

Temperature (°C)	Initial weight (g)	k_0 (d^{-1})	α_R (d^{-1})
17	2–4	0·045–0·049	0·028–0·059
17	20–40	0·025–0·033	0·025–0·064
25	20–40	0·044–0·057	0·058–0·121

f. wt determination immediately after cutting and to the wilting effect mentioned above, the α_R values present a large dispersion and the variation of this coefficient with plant age cannot be deduced from these results.

According to the present study, it can be concluded that, as in the case of defoliation, the regrowth kinetics of *D. glomerata* following root excision can be described satisfactorily according to McMurtrie and Wolf's model (1983) by assuming that the partitioning of carbon substrates between shoots and roots is not modified by cutting, and that the partitioning coefficient remains constant during regrowth. In both cases, the perturbation induces a change in the proportions of carbon substrates utilized in roots for growth and maintenance requirements. This explains that the restoration of the balanced shoot and root growth predicted by the functional approach results essentially from a modification in root specific growth rate. The successful description of the plant response to these perturbations demonstrates the validity of the model which should constitute a useful framework in the quantitative analysis of vegetative growth.

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