THEORETICAL AND OBSERVED RELATIONSHIPS BETWEEN DEFOLIATION AND PARTITIONING IN GRASSES

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ABSTRACT

A model is presented that analyses the potential effect of vertebrate grazing on the partitioning of grasses. Its conclusions are: 1) When grazing is sufficiently frequent and severe, grasses can increase their net increase in biomass by partitioning growth to reserves. 2) Partitioning growth to reserves greatly reduces leaf growth between defoliations. After repeated clipping, dryland browntop (*Agrostis castellana*) and red fescue (*Festuca rubra*) allocated a smaller proportion of growth between defoliations to leaves than ryegrass (*Lolium perenne*) or rough meadow-grass (*Poa trivialis*). Browntop and fescue achieved less leaf growth than ryegrass and meadow-grass between defoliations, but their total biomass increased faster through a series of repeated weekly clippings.

KEYWORDS

Agrostis castellana, Festuca rubra, Lolium perenne, Poa trivialis, allocation, herbivory, tolerance, remobilization

INTRODUCTION

Remobilization of resources from reserves may be an important mechanism by which grasses tolerate herbivory (Richards, 1993; Thornton *et al.*, 1993). However, reserves may be gathered at the expense of other functions (Chapin *et al.*, 1990). In particular, partitioning of resources to reserves may reduce leaf production. Thus herbivory may apply a selective pressure on a sward favouring reserve formation and therefore against high leaf production. Here the trade-off between reserve formation and leaf production has been analysed mathematically in a model simple enough to allow comparison with an experiment in controlled conditions.

MODEL

A mathematical model was derived from seven assumptions:

1) A plant can be divided into two parts: an active part, analogous to the leaves, which contributes to growth in the short term, but is exposed to grazing, and a reserve, which is protected from grazing, but does not contribute to growth.
2) Shoot biomass rather than root biomass limits growth.
3) All active biomass makes an equal contribution to growth.
4) All defoliation occurs during brief events in which a large proportion of the plant is removed instantaneously.
5) Reserve biomass can only be reallocated to active biomass immediately after defoliation. This remobilization takes place instantaneously.
6) Between successive defoliations a constant proportion of the increase in biomass is partitioned to reserves.
7) The growth of each grass tiller between successive defoliations is not self-limited, but is determined by its environment in the sward, the length of time between the defoliations, and the partitioning between the active part and the reserve.

If the active biomass before and after defoliation are unrelated, the grass can only achieve net growth by accumulating reserves. The reserves accumulated between successive defoliations depend on the proportional partitioning to reserves, but also on the amount of active biomass. There is therefore an optimum partitioning to maximize the net increase of biomass from just after one defoliation to just after the next. This optimum varies with the amount of growth possible between successive defoliations. The model measures this potential for growth as the amount by which the active biomass would multiply if all growth was allocated to active biomass, "the potential growth multiple", *v*. The amount by which the active biomass actually multiplies is called the "active growth multiple", *m*. The multiple by which reserve biomass increases is determined by the active growth multiple and the proportional partitioning to reserves, *p*:

$$\text{multiplicative increase in reserve biomass} = \frac{p}{1 - p}\ (m - 1)$$

The active growth multiple is itself partly determined by *p*. To derive the optimum value of *p* to maximize the increase in reserve biomass, we should substitute the potential growth multiple *v* for the active growth multiple *m*:

$$m = v^{1-p}$$

Simple calculus allows us to calculate the optimum value of p to maximize the increase in reserve biomass and hence net growth (the first author can supply further details):

optimum

$$\text{optimum } p = \frac{1 - v^{1-p}}{(1 - p)\,1\mathrm{n}(v)} = \frac{1 - \frac{1}{m}}{1\mathrm{n}(m)}$$

The optimum partitioning to reserves can be a large proportion of growth (Fig. 1). If the potential growth multiple is less than c. 7.4, the optimum partitioning is 100% to reserves. The optimum partitioning to reserves is still over 30% even when the potential growth multiple is much higher (Fig. 1). When partitioning to reserves is optimum the active growth multiple, which is the plantís actual leaf growth multiple, is a fraction of the potential growth multiple (Fig. 1). Thus optimum partitioning to maximize net growth can greatly reduce leaf production.

However, if the active biomass before and after defoliation are significantly related, an increase in active biomass can contribute to net growth in addition to any increase in reserve biomass. Therefore, a strong relationship between active biomasses before and after defoliation reduces the optimum partitioning to reserves, and in the extreme can make the formation of any reserve disadvantageous.

EXPERIMENT

Four grass species were grown in pots and defoliated repeatedly to a constant height every week for 12 weeks, until the clippings taken each week were nearly constant (Thornton *et al.*, 1993). The pots were watered with a nutrient solution including 6 mol m^{-3} N. The plants in this study therefore satisfied the assumptions of the model, with the clippings being equivalent to the active part, while the roots and leaf base were equivalent to the reserve. For 4 weeks after the 12th defoliation samples of five pots of each species were harvested each week at the same time as the clipping, and another five pots 3 d later. This allowed calculation of the proportional allocation of growth to the roots and leaf base (the reserve) between 3 and 7 d after defoliation. (It was assumed that most remobilization took place in the first 3 d after defoliation (White, 1973).)

RESULTS AND DISCUSSION

Plants could only achieve limited growth in the week between successive defoliations, so the model predicted that plants that allocated the greatest proportion of growth to reserves would achieve the most net growth. Red fescue and dryland browntop allocated a higher proportion of growth to reserves than ryegrass and rough meadow-grass, and accumulated more biomass after 14 weeks of repeated clipping (Fig. 2). All other measures of growth confirmed that red fescue and dryland browntop were continuing to grow faster than ryegrass and rough meadow-grass at the end of the experiment. Red fescue and dryland browntop achieved greater net growth despite producing clippings more slowly than the other two species, as the model predicted.

Comparison with past studies of undefoliated grasses grown on generous nutrient solutions showed that ryegrass and rough meadow-grass allocated the same proportion of growth to leaves (clippings), with and without defoliation (Elias and Chadwick, 1979; Poorter and Remkes, 1990; Garnier, 1992). Red fescue and dryland browntop allocated a lower proportion of growth to leaves after repeated defoliation than when not defoliated. These observations suggest that red fescue and dryland browntop may be adapted to grazing regimes in which reserves can benefit recovery after defoliation, whereas recovery of ryegrass and rough meadow-grass may depend more on leaves that survive defoliation. This division between two different mechanisms by which grasses tolerate defoliation may be widespread.

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Figure 1

The relationship between the potential growth multiple and the optimum partitioning to reserves to maximize net growth. The active growth multiple for given potential growth multiple and optimum partitioning is also shown. The contrast between the two curves shows the cost to growth of active biomass due to the partitioning to reserves.

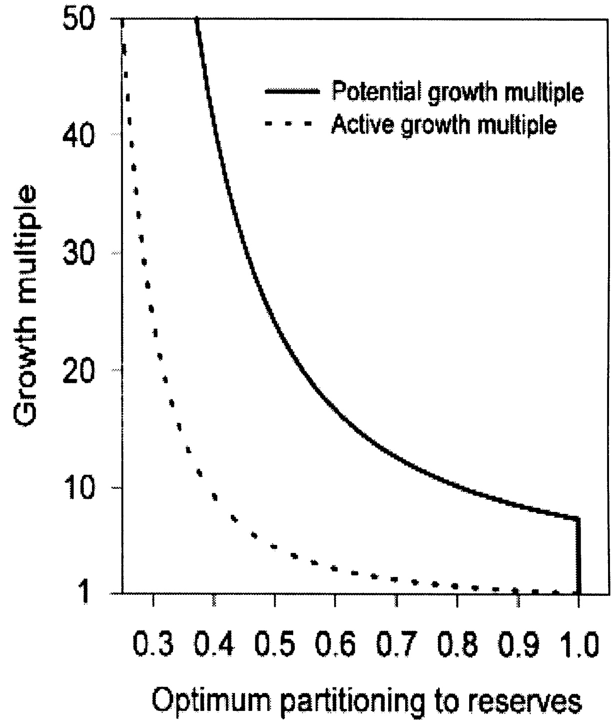

Figure 2

The proportional allocation of growth 3-7 days after defoliation to the leaf base and roots (LB + R) of four grass species, and the biomass of their leaf base and roots after 14 weeks of weekly clipping. The bars show 90% confidence intervals.