INTRASPECIFIC COMPETITION IN LUCERNE AND RELATIONSHIPS WITH RESERVE AVAILABILITY

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ABSTRACT

Below-ground reserves are thought to provide an indication of a forage potential for shoot regrowth after defoliation. The aim of this work was to re-evaluate the causal relationships existing between organic reserves (non-structural carbohydrates and N reserves) and shoot regrowth of alfalfa. The variations brought about by cultivar differences (cv Lodi or Europe), length of the previous regrowth period (30 or 45 d), or by intraspecific competition for light within a dense canopy, were studied. Field grown plants were harvested at weekly intervals, and separated as dominant, intermediate and suppressed plants. Shoot regrowth yield was determined and taproot were analyzed for starch, N, soluble proteins and vegetative storage proteins. Results showed that taproot starch and N contents were modified by the length of the previous regrowth but not by the position of the plant within the canopy. Soluble protein or VSP concentrations increased with the length of the previous regrowth, and with a higher position of the plant within the canopy. Shoot regrowth yield was linearly related to taproot soluble protein and VSP contents on day of defoliation, but relationships were not found with initial starch or N contents. These results suggest that root protein and VSP are key organic nutrient for alfalfa shoot regrowth after harvest.

KEY WORDS

Defoliation, Lucerne, *Medicago sativa*, Nitrogen, Reserve, Starch, Tap roots, Vegetative storage proteins.

INTRODUCTION

Although it is well admitted that carbon reserves are needed to sustain regrowth after defoliation of forage species, numerous experimental evidences show that the role of N reserves may be more important than often believed (see Richards, 1993 for a review). Nitrogen flows from source tissues remaining after defoliation to regrowing sink tissues of lucerne have been quantified using ^{15}N labelling, demonstrating that a significant amount of N in regrowing shoot of lucerne may be derived from reserve mobilization (Kim et al., 1993). Furthermore, it has been shown that N reserve availability rather than starch may limit regrowth potential of isolated, hydroponic-grown lucerne plants (Ourry et al., 1994), and this can be explained by the fact that root carbohydrates are predominantly used for root respiration (61% of the stored C) while only a small proportion (5%) was recovered in regrowing shoots (Avice et al., 1996a). Similarly, for *Lolium temulentum* L. (Ourry et al., 1996), greater storage of N prior to defoliation significantly increased leaf regrowth rate.

Protein-N constitutes the largest reserve pool, and amino acid-N the most readily mobilized from source to sink tissues (Hendershot and Volenec, 1993a,b ; Volenec et al., 1996). In *Medicago sativa* taproots, specific proteins of molecular masses of 15, 19 and 32 kD are believed to act as vegetative storage proteins. These abundant proteins exhibit a cyclic pattern of synthesis/mobilization induced either by defoliation (Hendershot and Volenec, 1993b) or spring growth (Hendershot and Volenec, 1993a), are localized primarily in vacuoles, with smaller amounts found associated with amyloplasts (Avice et al., 1996c) and their degradation during regrowth is concomitant with N mobilization from source to sink tissues (Kim et al., 1993).

These previously cited studies were conducted with isolated plants grown under controlled conditions without resource (light, water, nutrients) limitation. Competition for such resources in a dense canopy affects growth of individual plants, and consequently plant survival. It can be hypothetized that differential C and N storage during regrowth under light competition is a factor contributing to differences in shoot yield and plant mortality. Therefore, the aim of this work was to study intraspecific competition within a lucerne canopy in order to evaluate the causal implication of root organic reserves, i.e. nonstructural carbohydrates or N reserves as N, soluble protein and vegetative storage protein (VSP) contents on regrowth potential of plants situated at different depth in the canopy.

MATERIAL AND METHODS

Alfalfa stands (cv. Europe, or cv. Lodi) were sown (16.5 cm between rows) in April 1993 at Lusignan (46.26°N ; 0.07°E) and harvested three times (July, August and November) in 1993. In February 1994, they received 80 kg $P.ha^{-1}$ and 90 kg K ha^{-1}. Plants were then subjected to a frequent defoliation regime (first cut on 5 May 1994 and then harvested at 30 day intervals) or an infrequent defoliation regime (first cut on 24 May 1994 followed by a 45 days regrowth interval). All plants allowed to regrow for 30 or 45 days were defoliated on 6 July 1994. Regrowth of the different plants was then followed by successive weekly samplings for 35 days.

In order to sample plants whose shoots have been located in different positions (from suppressed to dominant) in the canopy during the previous regrowth, a preliminary study was conducted to relate taproot diameter to the position of plants within the canopy. Taproot diameter was found to be highly significantly and linearly correlated with the length of the longest stem. After defoliation, plants were then sampled according to their taproot diameter, in order to separate plants which were either dominant, intermediate and suppressed during the previous regrowth. Plants were harvested firstly by removing the taproots of all plants from the first 20 cm of soil along 2 m of row and then sorted according to taproot diameter. The taproot fresh weights were determined and the sample was immediately frozen in liquid N2. After freeze-drying, samples were analyzed for N, starch, protein and VSP concentrations (Avice et al., 1996b). Shoots were harvested and separated into stem, leaves, and crown.

RESULTS AND DISCUSSION

Lengthening the previous regrowth from 30 to 45 d increased shoot yield during the following regrowth (Table 1), as well as taproot and crown dry weight. Similarly, N, starch, soluble proteins and vegetative storage protein concentrations of taproots were positively affected. Shoot yield after 35 d of regrowth was similar for the two cultivars Lodi and Europe, but it should be pointed out that initial regrowth rates were faster for Lodi than for Europe during the first 3 weeks of regrowth (data not shown), while N, starch, soluble protein (significant only for suppressed plants) concentrations were higher in Lodi than in Europe cultivar. Shoot regrowth yield, taproot and crown dry weights (Table 1) were affected according to plant position within the canopy (dominant, intermediate or suppressed). More surprisingly, the position of the plant within the canopy had no effect on N or little on starch concentrations in taproots : only plants with a suppressed position had a lower starch concentration than dominant or intermediate plants (Table 1). Taproot soluble protein and VSP concentrations in taproots were significantly decreased with the depth of the plant within the canopy, being the lowest for suppressed plants, and higher for dominant than for intermediate plants.

When data from both cultivars, defoliation frequencies, and all plants irrespective of position in the canopy, were pooled and regressed together against shoot dry matter production after 35 days of regrowth, there was no relationship to either N or starch concentrations of taproots measured on the day of defoliation (Fig. 1A and 1B). In contrast, highly significant linear relationships were found between shoot dry matter production and soluble protein or VSP concentrations in taproots on day of defoliation (Fig. 1C and 1D). Increased VSP levels or soluble protein concentrations were found in plants with a larger root biomass which correspond to dominant plants, i.e. to plants having a greater access to high resources as they also produced greater shoot dry matter during regrowth. Soluble protein concentrations were significantly related to VSP concentrations while, more surprisingly, root N concentration was independent of soluble protein and VSP concentrations (regressions not shown).

Results showed that taproot starch was not affected markedly by genotypic effects, harvest frequency, and more surprisingly, by plant size resulting from its position within the canopy (Table 1). Shoot regrowth was not associated with initial starch accumulation in taproots (Fig. 1B), a conclusion supported by other studies (see for example, Volenec, 1988; Boyce and Volenec, 1992; Ourry et al., 1994). The functional role of non-structural carbohydrates during regrowth was assessed in labeling experiments which demonstrated that most root C was used for root respiration and therefore, is an energy source rather than a source of C skeletons for regrowth of shoot tissues (Ta et al., 1990 ; Avice et al., 1996a).

The rapidity of alfalfa shoot regrowth is largely determined by availability of the taproot N reserves, so that the survival of an individual plant within a dense canopy may heavily rely on its capacity for a more rapid shoot regrowth than nearby competitors. Multiple cuttings within a season would amplify the importance of possessing a faster ability to store/mobilize and store again, N reserves in taproots. Taproot soluble protein or VSP rather than N or starch, may provide reliable estimates of shoot regrowth potential although these contents are subjected to variations resulting from numerous biotic (cultivar, competition effects) and abiotic factors (harvest frequency, availability of resources).

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Table 1

Effects of the length of the previous regrowth period (30 or 45 d), the cultivar used (Lodi or Europe) and the position of the plant within the canopy (D: dominant, I: intermediate, and S: suppressed position) on shoot, crown and taproots dry weight and taproot N, starch, soluble proteins and vegetative storage proteins (VSP) concentration. Data obtained from weekly harvests during 35 days of regrowth were averaged and pooled together for comparisons. Significantly higher (>) or not significantly different (=) for P=0.05.

	on dry matter of:			on taproot concentration of:			
Effects of:	Taproots	Crown	Shoot	N	Starch	Soluble proteins	VSP
Length of the previous regrowth (45d>30d)	45d>30d	45d>30d	45d>30d	45d>30d	45d>30d	45d>30d	45d>30d
Cultivars (Lodi or Europe)	L=EL=E	L=E	L>E	L>E	L>E for S	L>E plants only	
Plant position within the canopy (D, I or S)	D>I>S	D>I>S	D>I>S	D=I=S	D=I>S	D>I>S	D>I>S

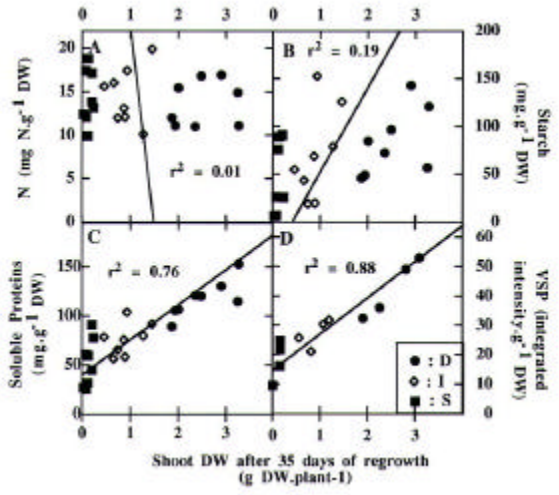

Figure 1

Relationships between lucerne shoot dry matter production after 35 d of regrowth and initial (Day 0) nitrogen (A), starch (B), soluble protein (C) and VSP (D) concentrations in taproots, the day of defoliation in two *Medicago sativa* L. cultivars (Europe or Lodi) previously subjected to a harvest frequency of 30 or 45 d and for dominant (D), intermediate (I) and suppressed (S) plants. Regressions were highly significant at $P < 0.01$ (**) or not significant (NS) at $P > 0.05$.