NITROGEN AND CO2 EFFECTS ON REMOBILIZATION OF ROOT AND CROWN RESERVES FOR REGROWTH FOLLOWING DEFOLIATION

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ABSTRACT
The effect of carbohydrate and nitrogen reserve remobilization during the first 4 d following defoliation on subsequent regrowth was studied under different soil nitrogen and atmospheric CO_2 conditions. On a structural dry matter basis, elevated CO_2 increased carbohydrate concentration without affecting total nitrogen in roots and crowns. High soil nitrogen had the opposite effect, increasing nitrogen concentration with no effect on nonstructural carbohydrates. Regrowth was significantly correlated with total nitrogen concentration at the time of defoliation. Carbohydrate concentration was not related to subsequent regrowth, nor was there a consistent correlation between carbohydrate or nitrogen remobilization and regrowth. No nitrogen remobilization was detected in Low N treatments, which maintained greater nitrogen uptake rates immediately following defoliation than did High N treatments. Regrowth was most closely correlated with reduced whole plant relative growth rate during the first 4 d after cutting.

KEYWORDS
reserve remobilization, defoliation, nitrogen, carbon dioxide

INTRODUCTION
Defoliation greatly reduces photosynthesis and nitrogen uptake. The importance of stored carbohydrates for regrowth following defoliation has long been assumed, although regrowth ability is often not associated with reserve carbohydrate status (Boyce & Volenec 1992). Recently, the importance of reserve nitrogen has received increasing attention (Ourry et al. 1994). Increased atmospheric CO_2 affects plant carbohydrate and nitrogen concentrations (Hunt et al. 1996; Korner & Miglietta 1994) such that carbohydrates become relatively abundant while nitrogen becomes relatively scarce (Luo et al. 1994). These changes could affect the relative influence of carbon and nitrogen reserves on regrowth following defoliation. Little is known, however, about how elevated CO_2 affects defoliated plants. We studied the effects of soil nitrogen and atmospheric CO_2 on regrowth of three forage species, and examined how carbon and nitrogen remobilization during the first 4 d following defoliation affected subsequent regrowth.

MATERIALS AND METHODS
Seeds from a legume (alfalfa, *Medicago sativa* L.), C_3 grass (western wheatgrass, *Pascopyrum smithii* (Rydb) A. Love), and C_4 grass (blue grama, *Bouteloua gracilis* (H.B.K.) Lag ex Steud.) were planted in 15 cm diameter by 46 cm deep pots containing a 50:50 prairie soil/ sand mixture. Seedlings grew for 6 wk at ambient CO_2 in a greenhouse, then were cut to 5 cm and transferred to a walk-in growth chamber set at either ambient (350 ppm) or elevated (700 ppm) CO2. The chamber had a 14 h photoperiod, 28/17° C day/night temperature, and 50% relative humidity. Nutrient treatments were initiated 1 wk after planting and consisted of half strength Hoaglandís solution containing either 0 or 400 ppm N applied twice weekly. After transfer to the growth chamber, plants were allowed to acclimate for 3 wk then were again cut to 5 cm. With alfalfa, all partially- and fully-unfolded leaves below 5 cm were also removed. Sequential harvests were made at 0, 4, 7, 10, 14, and 20 d after cutting. Plants were separated into root, crown, and regrowth, immediately immersed in liquid nitrogen, and freeze dried. Dry matter was partitioned into structural dry matter, nonstructural carbohydrates and nitrogen containing compounds. Nitrogen compounds were then partitioned into buffer-soluble (N_s) and buffer-insoluble (N_i) structural nitrogen (proteins, chlorophyll, nucleic acids, etc.) and low molecular weight (N_l) compounds (amino acids, NO_3, etc.).

RESULTS AND DISCUSSION
Combined across species, whole plant relative growth rates (RGR, g g^{-1} d^{-1}) increased 12% with elevated CO_2 and 46% under N fertilization with significant species by treatment interactions. Elevated CO_2 increased alfalfa RGR in the Low N but not in the High N treatment. Even though alfalfa was not inoculated with Rhizobium, nodules were observed on roots from all treatments. Nodules appeared to be particularly large and healthy in the Low N-Elevated CO_2 treatment, consistent with reports that CO_2 enrichment increases N_2 fixation (Ryle & Powell 1992; Stulen & den Hertog 1993). Elevated CO_2 apparently reduced nitrogen limitations in the Low N treatment, so that increased RGR was actually a response to increased nitrogen rather than to elevated CO_2. Blue grama RGR was also unaffected by CO_2 concentration at High N, and decreased 29% in the Low N-Elevated CO_2 treatment. Western wheatgrass was the only species to respond positively to elevated CO_2 in both the High and Low N treatments, increasing 21 and 24%, respectively.

Elevated CO_2 increased root and crown total nonstructural carbohydrate (TNC) concentration but had no effect on total N at the time of defoliation (Table 1). High nitrogen increased N concentrations without affecting TNC. High N and elevated CO_2 increased TNC remobilization during the first 4 d after cutting. Significant N remobilization ($P < 0.10$) only occurred in the high N - elevated CO_2 treatment. However, in all cases there was a trend for N pools to increase with low N and decrease with high N treatments. No consistent relationship existed between C or N remobilization and subsequent regrowth rates. Regrowth was correlated, however, with total N concentration immediately after defoliation ($r = 0.77$, $P < 0.05$).

The best predictor of root or shoot RGR from 4 to 20 d after defoliation was whole plant RGR between 0 to 4 d (Fig. 1). Caldwell et al. (1981) suggested that curtailment of root growth was important for allowing rapid reestablishment of photosynthetic tissue following defoliation since reduced root growth should allow diversion of plant resources to regrowing shoots. We found, however, that later regrowth was negatively correlated with both root ($r = -0.57$, $P=0.05$) and shoot ($r = -0.73$, $P<0.01$) dry matter production from 0 to 4 d after defoliation. Regrowth following defoliation involved two processes: 1) reduced partitioning to existing roots and crowns and 2) reestablishment of leaf tissue. The ability to rapidly shut down root and crown dry matter accumulation appeared to be initially more important than the reestablishment of leaf area.

Rangeland ecosystems are currently nitrogen limited and elevated CO_2 could further reduce soil inorganic N concentrations (Hunt et al. 1996). In our Low N treatments, nitrogen remobilization had no effect on regrowth following defoliation, especially at elevated CO_2. Nitrogen remobilization would not be expected, therefore, to influence regrowth under rangeland conditions.

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Table 1

Effect of nitrogen and CO2 on root and crown carbohydrate and nitrogen pools at the time of defoliation, and on reserve remobilization during the first 4 d after cutting. Data are averaged across species, n = 36.

	Ambient CO_2		Elevated CO_2	
Pool	Low N	High N	Low N	High N
	Initial pool size (% structural dry weight)			
N_i	1.22[bc]	1.35[ab]	1.05[c]	1.53[a]
N_s	0.56[b]	0.70[a]	0.44[c]	0.54[b]
N_l	0.74[c]	1.15[a]	0.77[c]	0.95[b]
Total N	2.52[b]	3.20[a]	2.26[b]	3.02[a]
Starch	12[b]	9[b]	22[a]	21[a]
Labile CHO	25[bc]	22[c]	33[a]	29[ab]
TNC	37[b]	31[b]	55[a]	50[a]
	Change in pool size (%)			
N_i	32	-7[ns]	28[ns]	-3[ns]
N_s	-2[ns]	-25	4[ns]	-33
N_l	39	-10[ns]	20[ns]	-20[ns]
Total Soluble N	23ns	-14[ns]	14[ns]	-25
Starch	18[ns]	0[ns]	-42	-70
Labile CHO	-50	-58	-46	-58
TNC	-25[ns]	-41	-44	-64

[a,bc] Entries within a row followed by the same superscript are not significantly different at P = 0.05.

[ns] The change in pool size between 0 and 4 d was not significant at P = 0.10.

Figure 1

Relationship between whole plant relative growth rate (RGR) during the first 4 d following defoliation and subsequent root (open symbols) or shoot (closed symbols) RGR for three species, alfalfa (circles), blue grama (squares) and western wheatgrass (triangles). Root and shoot regressions are significant at P < 0.01.