

Carbon and nitrogen allocation patterns of Douglas-fir seedlings fertilized with nitrogen in autumn. II. Field performance¹

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October-fertilized and unfertilized 2-0 Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings were outplanted the following February. Half of each planting block was seeded with grass to induce water stress during the typical summer drought. Sucrose was applied to soil around each seedling to limit availability of nitrogen to tree roots. Fertilized seedlings broke bud 9–10 days earlier, produced more shoot growth, and, as shown in later harvests, had higher relative growth rates than unfertilized seedlings. However, initial differences in growth response were due primarily to the earlier budbreak. Seedlings growing with grass had predawn water potentials of -1.5 MPa by early August; by September 3, unfertilized seedlings growing with grass were significantly more stressed than any others. Although free amino acid and total nitrogen concentrations were higher in fertilized than unfertilized seedlings when planted, they became equal by the end of one growing season. However, fertilized seedlings contained more free amino acids and nitrogen because of their greater size. Grass competition affected both seedling nitrogen and carbohydrate chemistry. After one growing season, fertilized seedlings had greater height increment, shoot growth, leaf area, relative growth rate, and production per unit nitrogen. Although autumn fertilization benefited these Douglas-fir seedlings, negative effects could result from carbohydrate depletion because of increased respiration or from frost damage because of earlier budbreak.

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Des semis 2-0 de sapin de Douglas (*Pseudotsuga menziesii* Mirb.) Franco fertilisés en octobre en non fertilisés furent mis en terre au mois de février suivant. La moitié de chacune des parcelles plantées fut ensemencée avec de l'herbe en vue d'amorcer un stress hydrique typique d'une sécheresse estivale. On a appliqué du sucrose au sol entourant chaque semis pour limiter la disponibilité de l'azote aux racines des semis. Les semis fertilisés ont débouffé 9 à 10 jours plus tôt que ceux qui ne le furent pas, ont eu une meilleure croissance des tiges et, comme il fut démontré plus tard, de meilleurs taux de croissance relatifs. Toutefois, les différences initiales dans la réponse de croissance furent provoquées essentiellement par le débouffage plus hâtif. Les semis qui ont crû parmi l'herbe ont montré des capacités de rétention d'eau de $-1,5$ MPa au début d'août; au 3 septembre, les semis non fertilisés ayant crû avec l'herbe étaient sensiblement plus stressés que les autres. Bien que les concentrations d'acide aminé libre et d'azote total fussent plus élevées dans les semis fertilisés que dans ceux qui ne l'étaient pas au moment de la mise en terre, le tout devint équivalent au bout d'une saison de croissance. Cependant, les semis fertilisés renfermaient plus d'acide aminé libre et d'azote par suite de leurs plus grandes dimensions. La compétition de l'herbe affecta autant l'azote des semis que la chimie des hydrates de carbone. Après une saison de croissance, les semis fertilisés montraient une meilleure croissance de la hauteur et des pousses, une surface foliaire plus élevée, un taux de croissance relatif plus fort et une production accrue par unité d'azote. Bien que la fertilisation d'automne puisse bénéficier aux semis de douglas, il pourrait survenir des effets négatifs à cause des pertes d'hydrates de carbone consécutifs à une augmentation de la respiration ou à des dommages par le gel provoqués par un débouffage hâtif.

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Introduction

Fertilizing tree seedlings in plantations can be inefficient because it may stimulate growth of competing vegetation. Because crop trees may experience intense competition in the early stages of stand establishment, there has been much interest in developing cultural procedures to grow nursery seedlings of high physiological vigor that are capable of rapid early growth (Wakely 1954; Duryea and Landis 1984). In the Pacific Northwest, however, standard nursery practice includes withholding water and nitrogen in midsummer to induce dormancy and protect seedlings from frost injury (Cleary *et al.* 1978). For this reason, late-season nitrogen applications have been avoided.

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In general, field performance of nursery seedlings receiving late-season nitrogen fertilization has not proven beneficial with pines (*Pinus* spp.) in the southeastern United States (Ursic 1956; Gilmore *et al.* 1959; Shoulders 1959), has been inconclusive with a variety of conifers in Great Britain (Benzian *et al.* 1974), and has been favorable with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Pacific Northwest (Anderson and Gessel 1966). However, most of these field experiments have only involved relatively simple correlations of the fertilization treatment with height growth and survival. To our knowledge, only van den Driessche's (1985) recent greenhouse study has explored any of the mechanisms behind the observed growth response. Apparently, no investigators have conducted a detailed examination of the mechanisms behind this growth response under field conditions.

Consequently, we chose to outplant 2-0 Douglas-fir seedlings whose internal nutrition had been altered by October fertilization with ammonium nitrated in the nursery (Margolis and Waring 1986). One half of each planting block was seeded with a heavy grass cover to induce water stress during the summer drought (Hedrick and Keniston 1966; Newton 1967; Larson and

Schubert 1969; Preest 1977; Eissenstat and Mitchell 1983). This combination of treatments allowed us to study the interaction between seedling nutrition and water stress and assess effects on seedling biochemistry, physiology, morphology, and growth.

Materials and methods

Treatments

Douglas-fir seedlings at a western Oregon nursery were fertilized in October 1983 with 112 kgN/ha as ammonium nitrate (two applications of 56 kg/ha each, 9 days apart). Both the fertilized and unfertilized (control) seedlings were lifted on February 2, 1984, and placed in cold storage at 2°C. All the seedlings were outplanted by February 11, 1984, at an elevation 110 m above sea level near Corvallis, OR (44°30' N, 123°15' W). This area has considerable rainfall throughout autumn, winter, and spring, but typically has a substantial dry period during summer (Franklin and Dyrness 1973). The planting site has a gently sloping, south-facing aspect on a deep, well-drained Jory series clay (U.S. Soil Conservation Service 1975). The surface soil is about 50 cm deep and friable.

In a split-plot design with three blocks, nearly 900 seedlings were carefully planted with a shovel in a ~0.2-ha area that had been disked and planted with annual rye grass (*Lolium multiflorum* L.) the previous autumn. The main treatment, the presence or lack of grass competition, was intended to place the seedlings under different degrees of water stress during the droughty summer months. Within each main treatment, the previously fertilized and unfertilized seedlings (the secondary treatment) were randomly planted. Subplots (3 blocks × 2 grass treatments × 2 fertilized treatments) totaled 12.

In March, when the grass was already several centimetres tall, one half of each of the three blocks was randomly selected to have the grass removed. Atrazine was applied on these plots at 3.4 kg/ha on March 2, 1984, and at 1.3 kg/ha on March 16, 1984; applications resulted in nearly total removal of the rye grass cover. In mid-July, any grass that had become established since the atrazine treatment was spot sprayed with glyphosate. Grass on the untreated plots grew ~0.75 m tall and did not seem to significantly shade the tree seedlings.

On March 9 and 21, 1984, about 29 g of sucrose was placed in a 30 cm radius around each seedling; this was equivalent to about 1000 kg/ha on each date. The sucrose provides a readily available carbon substrate to soil microbes; their subsequent rapid growth immobilizes much of the nitrogen in microbial biomass, creating a condition of nitrogen stress (Johnson and Edwards 1979; Waring 1982). Applying sucrose maximized our chance of detecting the response of outplanted seedlings to the nursery fertilization treatment.

Measurements and analyses

To determine budbreak, a survey was conducted every 2 days on 341 fertilized and 341 unfertilized seedlings between March 21 and May 9, 1984. A seedling was considered to have broken bud if two buds on the upper half had new leaves extending out of the bud. On May 17 and 18, black-tailed deer caused considerable damage to seedlings by browsing the terminal leaders. On May 19, a small amount of BGR Big Game Repellent® was applied to every terminal leader; no additional deer damage was observed. All browsed seedlings were removed from the experiment. Of the remaining seedlings, less than 2% died during the first growing season.

Five seedlings were removed from each of the 12 subplots on both May 15 and June 15, 1984, and the dry weights of new shoot growth, old leaves, and stems were determined. Growth analyses, not including roots or secondary stem growth, were performed.

Mean relative growth rates (RGRs) were calculated as follows

$$\text{RGR} = \ln(W_2) - \ln(W_1)/\text{days}$$

where W_2 is the dry weight of the total aboveground portion of the seedling at harvest, W_1 is the dry weight of the stem and old leaves only, and "days" represent the number of days since budbreak.

Mean net assimilation rates (NARs) were calculated as follows:

$$\text{NAR} = \frac{(W_2 - W_1)}{\text{days}} \times \frac{(\ln LA_2 - \ln LA_1)}{LA_2 - LA_1}$$

where LA_2 is the leaf area of both old and new needles and LA_1 is the leaf area of old needles only. This equation assumes that LA and W are linearly related over time (Radford 1967).

Leaf area ratios (LARs) were calculated as follows:

$$\text{LAR} = LA_2/W_2$$

Since both RGR and NAR are average values over significant periods of time, the relationship $\text{RGR} = \text{NAR} \times \text{LAR}$ does not apply. This relationship is valid only if the values are calculated instantaneously (Radford 1967).

On July 11, August 2 and 18, and September 3, 1984, predawn water potentials were measured on three seedlings per subplot (36 seedlings in total) with a pressure chamber (Scholander *et al.* 1965; Ritchie and Hinkley 1975). Once a seedling was sampled, it was removed from the experiment. On August 7 and 8, diurnal water potentials were measured approximately every 3 h throughout a 24-h period on two seedlings per subplot (24 seedlings in total).

On September 3, two composites of five whole seedlings each were taken from each subplot. From each of these 24 composites, samples of new shoot growth, old leaves, stems, and fine roots were extracted and analyzed for free amino acids (FAAs), total Kjeldahl nitrogen, total phosphorus, sugars, and starch according to procedures described in Margolis and Waring (1986).

On September 4, the length of the terminal leader and total seedling height were measured on 25 seedlings from each subplot (300 seedlings in total). Only seedlings with an easily identifiable terminal leader were sampled. The final harvest occurred on September 5, 1 day before the first autumn rain. The aboveground portions of these 300 seedlings were harvested, dry weights of the new shoot growth, old needles, and stems were determined, and growth analyses were performed as described previously. However, since significant portions of old needles were shed during the summer drought, Radford's (1967) equation for NAR could not be used. Consequently, NAR for the September harvest was estimated on the basis of the seedlings' original leaf area:

$$\text{NAR} = (W_2 - W_1)/(LA_1 \cdot \text{days})$$

To assure that nitrogen analyses expressed on a dry-weight basis were not confounded by differences in nonstructural carbohydrates (NSCs), we corrected for different NSC levels. Since this correction did not significantly affect the results, nitrogen concentrations were expressed on a simple, dry-weight basis. The number of stem units (needles plus buds) on the terminal leader also was measured for each seedling.

A sample of leaves equivalent to about 10 cm² was collected and the projected area was determined with a LiCor model 3100 area meter. The leaves were then dried in a forced-air oven at 70°C and weighed. Specific leaf area was calculated by dividing leaf area by the dry weight.

Data were subjected to analyses of variance for a split-plot design; grass competition was the main treatment and nursery fertilization was the secondary treatment. Seasonal predawn and diurnal water potential data were subjected to analyses of variance for a split-split plot design; time was the main treatment, grass competition was the secondary treatment, and nursery fertilization was the tertiary treatment. The statistical package for the social sciences (SPSS) was used to calculate the analyses of variance and descriptive statistics (Nie *et al.* 1975; Hull and Nie 1981). For multiple comparisons of more than two means, Tukey's honestly significant difference test was used to compute least significant differences (LSDs) at the 90 and 95% levels (Harter 1960; Steel and Torrie 1980). For single comparisons of two means, the *t*-test was used (Snedecor and Cochran 1980).

Results

The analyses of variance indicated that all the variables measured before August showed only fertilizer effects. The effects of grass treatment and interactions between grass and fertilizer treatments were not apparent until after the summer drought had begun.

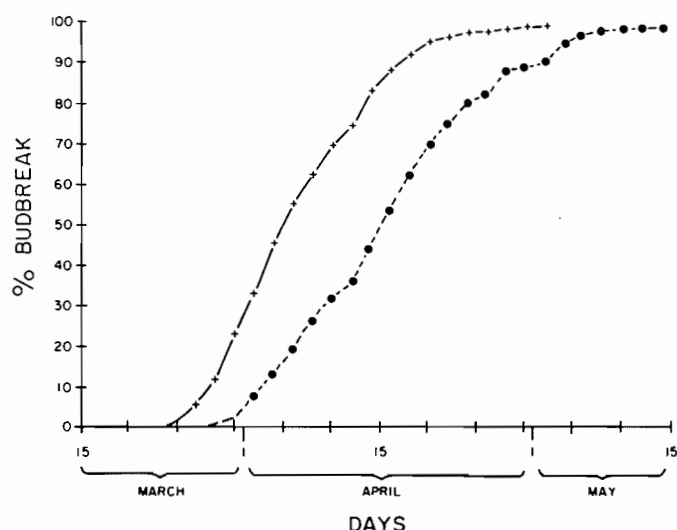


FIG. 1. Cumulative frequency of budbreak for Douglas-fir seedlings fertilized (+ — +) or unfertilized (• - - •) in the nursery in October and outplanted the following February with and without grass competition. Budbreak surveys were conducted every 2 days on 341 fertilized and 341 unfertilized seedlings. A seedling was considered to have broken bud if two buds on the upper half had new leaves extending out the bud.

Budbreak and growth

Applying nitrogen fertilizer to nursery beds in early October resulted in significantly ($p < 0.01$) earlier budbreak of outplanted seedlings (Fig. 1). Mean budbreak date shifted from April 16 for the unfertilized seedlings to April 7 for the fertilized seedlings; 50% budbreak date was April 15 and April 5 for unfertilized and fertilized seedlings, respectively.

The fertilized seedlings not only broke bud earlier but had significantly greater amounts of new shoot tissue when sampled on May 15, June 15, and September 5 (Table 1). RGRs of fertilized and unfertilized seedlings did not differ significantly on the May 15 harvest but were higher for fertilized seedlings on the June 15 and September 5 harvests. NARs and LARs showed a pattern similar to that for RGRs (Table 1).

The deer damage, although not a planned part of this experiment, revealed an interesting trend. Out of the 55 seedlings browsed on May 17 and 18, 43 (78%) had been October-fertilized in the nursery. Of the 12 unfertilized seedlings browsed, 7 (13%) had been growing adjacent to fertilized seedlings also damaged by deer.

Water stress

The month of June had a record high 110 mm of rain. From June 29 to September 6, however, summer drought was severe; during this 9-week period, the only measurable rain fell on the evening of July 25.

Grass competition did not significantly affect predawn water potential until sometime between mid-July and early August (Fig. 2A). Although the grass treatment clearly caused a significant amount of water stress, both fertilized and unfertilized seedlings had similar predawn values until the final September 3 measurement, when unfertilized seedlings growing with grass were significantly more stressed than those in any of the other three treatments.

At both 0900 and 1200 on August 7–8, 1984, unfertilized seedlings growing with grass were more stressed ($p < 0.10$) than fertilized seedlings growing without grass (Fig. 2B). The other three treatments did not differ significantly from each

TABLE 1. Growth and assimilation on three harvest dates for Douglas-fir seedlings fertilized or unfertilized in the nursery in October and outplanted the following February

Characteristic	Unfertilized	Fertilized	Δ (%)
New shoot growth (g)			
May 15	0.8 (0.1)	1.3 (0.1)***	+63
June 15	3.1 (0.5)	5.0 (0.6)**	+61
Sept. 5	4.5 (0.3)	6.5 (0.4)***	+44
Relative growth (g/g)			
May 15	0.08 (0.01)	0.12 (0.01)***	+50
June 15	0.25 (0.02)	0.39 (0.03)***	+56
Sept. 5	0.42 (0.01)	0.55 (0.02)***	+31
Relative growth rate (mg/g per day)			
May 15	3.3 (0.2)	3.2 (0.4)NS	
June 15	3.9 (0.3)	5.1 (0.3)**	+31
Sept. 5	2.5 (0.1)	3.3 (0.1)***	+32
Net assimilation rate (mg/cm ² per day)			
May 15	0.12 (0.02)	0.13 (0.01)NS	
June 15	0.12 (0.01)	0.16 (0.01)*	+24
Sept. 5 ^b	0.16 (0.05)	0.23 (0.05)***	+44
Leaf area ratio (cm ² /g)			
May 15	29.8 (0.9)	31.4 (0.7)NS	
June 15	39.3 (1.1)	45.1 (1.2)***	+15
Sept. 5	36.7 (0.8)	43.0 (1.2)***	+17

NOTE: Each value is the mean of six subplots with SE in parentheses; the effect of the grass treatment was not significant, so values were pooled. NS, not significant; **, $p < 0.05$; ***, $p < 0.01$.

^bCalculated on the basis of initial leaf area (see Materials and methods).

other in the morning and none of the treatments differed in the afternoon. After sundown, however, seedlings growing without grass recovered more quickly from the daytime water stress than those growing with grass.

Seedling biochemistry

The analyses of variance showed that only grass competition significantly affected the concentration of seedling biochemical components. The effects of fertilizer treatment and the interactions between fertilizer and grass treatments were not significant. Regardless of fertilization, by September the grass treatment had resulted in higher FAA concentrations in the new shoot growth, higher nitrogen:phosphorus ratios in the old leaves, and higher FAA : total nitrogen ratios in the stems (Table 2). The fine roots of seedlings growing with grass had similar responses to those observed in the aboveground tissues (higher FAA concentrations, higher nitrogen:phosphorus ratios, and higher FAA : total nitrogen ratios).

The analyses of variance showed that regardless of fertilization, grass competition had significantly affected NSC concentrations by September (Table 3). With regard to carbohydrate status, none of the fertilizer \times grass interactions were significant. New shoot growth and old leaves had higher sugar, lower starch, and lower total NSC (sugar + starch) concentrations in seedlings growing with than without grass. Stems and fine roots also had higher sugar and lower starch concentrations in seedlings growing with than without grass. But total NSC concentrations were higher in fine roots for seedlings growing with than without grass (Table 3).

Although the nitrogen and NSC concentration data showed primarily grass effects (Tables 2 and 3), the total seedling nitrogen and NSC contents (concentration times biomass)

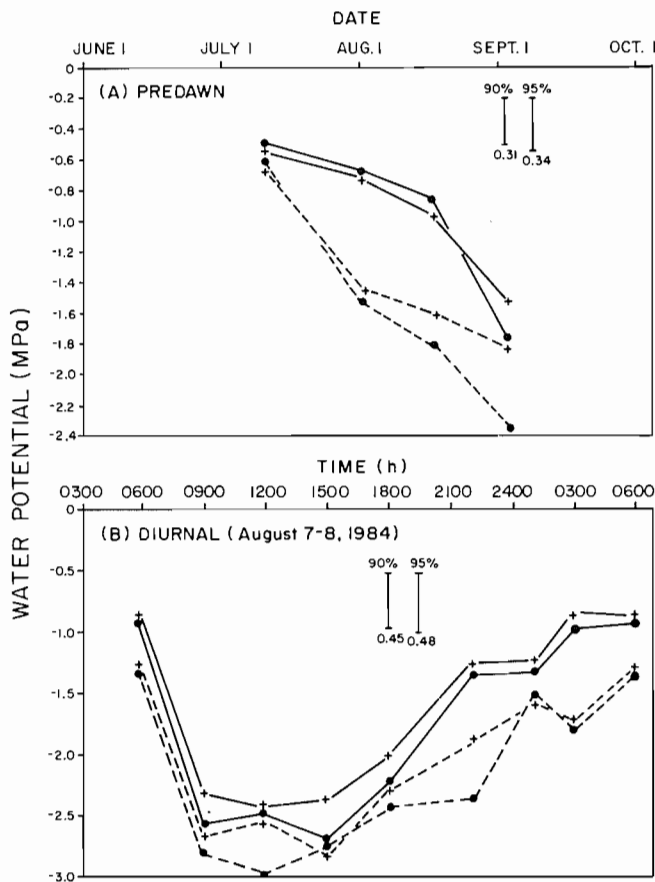


FIG. 2. (A) Predawn and (B) diurnal water potentials for Douglas-fir seedlings fertilized (+) or unfertilized (●) in the nursery in October and outplanted the following February with (---) and without (—) grass competition. Each point is the mean of nine seedlings. Tukey's honestly significant difference test was used to compute LSDs at the 90 and 95% levels (bars.)

showed pronounced fertilizer effects (Table 4). Fertilized seedlings had greater FAA, total nitrogen, sugar, and total NSC contents than unfertilized seedlings.

Seedling growth and morphology were variously affected by fertilization (Table 5). Height, stem units, new shoot growth, RGR, NAR, and LAR were all positively affected by the fertilization treatment. However, none of the growth or morphological traits were significantly affected by grass competition. The specific leaf areas of seedlings growing with grass increased significantly from 78 to 84 cm²/g in new needles and from 58 to 65 cm²/g in old needles. Fertilization did not affect specific leaf areas. Fertilized seedlings growing with grass shed significantly more of their old needles (40%) than seedlings in any of the other three treatments: grass, unfertilized, 27%; no grass, fertilized, 20%; no grass, unfertilized, 18%.

Discussion

Improved nitrogen nutrition of treated seedlings advanced budbreak and increased growth. Three samples taken throughout the growing season showed that growth differences were initially influenced by earlier budbreak. On May 15, no difference in RGRs could be discerned and 51% of the variation in the amount of new shoot growth could be explained by budbreak date. In contrast, by June 15 and throughout the remainder of the growing season, the differences in RGRs were also responsible for the greater growth of the fertilized seed-

lings. By June 15, only 13% of the variation in new shoot growth could be explained by budbreak date, yet RGR was 36% higher in the fertilized seedlings. The higher NAR and LAR in fertilized seedlings indicate that higher RGRs were due to both greater photosynthetic efficiency and a larger photosynthetic surface area.

The carbon:nitrogen ratio in foliage is thought to influence the relative allocation of resources between roots and shoots (Chapin 1980; Novoa and Loomis 1981; Lanson and Thornley 1982; Reynolds and Thornley 1982). Consequently, increasing nitrogen concentrations in our experimental seedlings may have shifted the relative allocation of dry matter production away from roots to stems and leaves. Thompson (1983) and van den Driessche (1985) showed greater root growth potential in fall-fertilized seedlings, but whether a greater fraction of carbon was allocated to shoots was not reported.

A shift in carbon allocation away from roots toward shoots could increase the susceptibility of fertilized seedlings to drought. The predawn water potentials (Fig. 2A), however, showed that the fertilized Douglas-fir seedlings were not significantly more stressed than the unfertilized. In fact, the September 3 sample indicated that fertilized seedlings growing with grass may have been somewhat less stressed than unfertilized seedlings growing with grass. Conceivably, a larger and more established root system gave fertilized seedlings a greater ability to exploit the soil for water. The diurnal water stress pattern (Fig. 2B) also suggests a tendency for fertilized seedlings to be less stressed than unfertilized. It is important to keep in mind, however, that although the seedlings had different internal nitrogen concentrations, the soil in which they were planted was equally fertile. This is distinctly different from the more common type of experiment in which seedlings are grown in both fertilized and unfertilized soils.

Although the fertilized seedlings had greater nitrogen concentrations at lifting, after one growing season in the field the nitrogen concentrations of fertilized and unfertilized seedlings were not statistically different (Table 2). The total nitrogen and FAA contents of fertilized seedlings, however, were greater than those of the unfertilized because of the greater size of the fertilized seedlings. Although RGRs of both fertilized and unfertilized seedlings would probably be the same in future years, the initial differences in seedlings size might result in substantially larger trees throughout the rotation.

We thought that many of the variables measured would show interactions between the grass and fertilizer treatments and were surprised to discover that by and larger, these interactions did not occur. The nitrogen and carbon chemistry, when expressed on a concentration basis, almost exclusively showed simple grass effects. Some evidence suggested that the grass competed with the seedlings for nitrogen and that it also altered seedling nitrogen chemistry by inducing a substantial water stress (Table 2).

As expected, the grass competition resulted in higher sugar and lower starch concentrations, supporting previous work with sugar maple (*Acer saccharum* Marsh.) (Parker 1970) and black oak (*Quercus velutina* Lam.) (Parker and Patton 1975). Interestingly, however, although the grass caused significant decreases in total NSC concentrations, the differences did not exceed 20 mg/g. The seedlings growing with grass, while experiencing significant water stress for much of the summer, were not in danger of dying from exhaustion of carbohydrate reserves. Consistent with the expected shift of carbon resources from shoots to roots as a result of water stress, the fine roots of

TABLE 2. Nitrogen chemistry in September of Douglas-fir seedlings fertilized or unfertilized in the nursery the previous October, outplanted in February, and grown for one season with or without grass competition

Biochemical component, by plant part	Without grass	With grass	Δ (%)
New shoot growth			
FAA ($\mu\text{mol}/\text{dry g}$)	26.4 (1.0)	30.4 (0.1)**	+15
Total N (mg/g)	12.4 (1.0)	9.3 (0.3)NS	
Total N : total P ratio (mg/mg)	8.2 (0.6)	7.0 (0.3)NS	
FAA : total N ratio ($\mu\text{mol}/\text{g}$)	2.6 (0.2)	2.9 (0.2)NS	
Old leaves			
FAA	26.4 (0.8)	27.7 (1.5)NS	
Total N	10.4 (0.5)	9.1 (0.2)NS	
Total N : total P ratio	8.2 (0.7)	6.5 (0.4)*	-21
FAA : total N ratio	2.5 (0.1)	3.0 (0.2)NS	
Stems			
FAA	17.2 (1.2)	19.5 (1.1)NS	
Total N	2.7 (0.3)	2.2 (0.2)NS	
Total N : total P ratio	4.8 (0.2)	4.7 (0.3)NS	
FAA : total N ratio	6.5 (0.7)	9.5 (0.8)**	+46
Fine roots			
FAA	25.0 (1.0)	35.0 (0.9)**	+40
Total N	7.5 (0.3)	7.2 (0.3)NS	
Total N : total P ratio	7.1 (0.2)	6.7 (0.1)**	-6
FAA : total N ratio	3.4 (0.2)	5.0 (0.3)*	+47

NOTE: Each value is the mean of three main plots with SE in parentheses; the effect of the fertilizer treatment was not significant, so values were pooled. NS, not significant; *, $p < 0.01$; **, $p < 0.05$.

TABLE 3. Carbohydrate chemistry (mg/dry g) in September of Douglas-fir seedlings fertilized or unfertilized in the nursery the previous October, outplanted in February, and grown for one season with or without grass competition

Carbohydrate component, by plant part	Without grass	With grass	Δ (%)
New shoot growth			
Sugars	113.9 (1.5)	131.9 (5.3)*	+16
Starch	56.0 (6.1)	18.5 (3.4)**	-67
Total NSC	169.9 (6.2)	150.3 (4.5)**	-12
Old leaves			
Sugars	124.5 (2.6)	149.4 (3.8)**	+20
Starch	41.6 (6.8)	0.0 (0.6)**	-100
Total NSC	166.1 (6.6)	149.4 (3.8)***	-10
Stems			
Sugars	53.5 (2.3)	60.7 (3.1)*	+13
Starch	23.3 (3.4)	8.1 (0.7)*	-65
Total NSC	76.8 (5.2)	68.8 (3.0)NS	
Fine roots			
Sugars	49.5 (2.5)	66.9 (4.2)***	+35
Starch	15.6 (2.0)	7.1 (1.4)**	-54
Total NSC	65.1 (3.9)	74.0 (5.1)*	+14

NOTE: Each value is the mean of three main plots with SE in parentheses; the effect of the fertilizer treatment was not significant, so values were pooled. NS, not significant; *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$.

the seedlings growing with grass had greater NSC concentrations.

Fertilized seedlings showed greater shoot growth after outplanting than unfertilized whether grown with grass competition or not (Table 5). Most of the morphological traits measured showed only fertilizer effects. The grass treatment,

TABLE 4. Total content of biochemical components in September of the aboveground portions of Douglas-fir seedlings fertilized or unfertilized in the nursery the previous October, outplanted in February, and grown for one season with or without grass competition

Biochemical component	Unfertilized	Fertilized	Δ (%)
FAA (μmol)	366.1 (12.6)	403.7 (30.9)**	+10
Total N (mg)	102.7 (10.8)	120.8 (14.7)**	+18
Sugars (mg)	1462.7 (46.2)	1642.8 (79.9)*	+12
Starch (mg)	350.7 (111.2)	438.4 (117.4)NS	
Total NSC (mg)	1813.4 (109.6)	2081.2 (134.8)*	+15

NOTE: Each value is the mean of six subplots with SE in parentheses; the effect of the grass treatment was not significant, so values were pooled. NS, not significant; *, $p < 0.10$; **, $p < 0.05$.

though definitely influencing seedling water relations and carbohydrate status, did not appear to affect seedling height increment, dry weight gain, leaf area, stem units, or RGR. This may be because moisture stress was not significant until late July or early August, after much of the growing season had been completed. Eissenstat and Mitchell (1983), on the other hand, found that Douglas-fir in Idaho had reduced shoot and height growth in areas seeded with grass and clover. Of all the traits measured, only biomass and leaf area of old needles were significantly affected by the interaction between grass and fertilizer treatments. The fertilized seedlings growing with grass shed significantly more old needles than those in the other three treatments.

The increased nitrogen productivity⁴ indicated that the

⁴Milligrams of new shoot growth in September per milligram of nitrogen in the entire seedling the previous November.

TABLE 5. Growth and morphological characteristics in September of Douglas-fir seedlings fertilized or unfertilized in the nursery the previous October, outplanted in February, and grown for one season with or without grass competition

Characteristic	Unfertilized	Fertilized	Δ (%)
Height growth (cm)	8.2 (0.3)	11.2 (0.4)***	+37
Relative height growth (cm/cm)	51.5 (1.1)	54.4 (0.7)***	+6
Stem units on terminal leader (no.)	217 (6.1)	281 (10.9)***	+37
Stem units per length of leader (no./cm)	29.2 (1.0)	25.2 (0.8)***	-14
New aboveground growth (g)	4.5 (0.3)	6.5 (0.4)***	+44
Leaf area of new growth (cm ²)	362 (19)	522 (30)***	+44
Leaf area of total seedling (cm ²)	574 (16)	715 (30)***	+25
Relative growth rate (mg/g per day)	2.5 (0.1)	3.3 (0.1)***	+32
Leaf area ratio (cm ² /g)	36.7 (0.8)	43.0 (1.2)***	+17
Nitrogen productivity ^a	43.4 (2.7)	49.5 (3.1)***	+14

NOTE: Each value is the mean of six subplots (25 seedlings per subplot) with SE in parentheses; the effect of the grass treatment was not significant, so values were pooled. *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$.

^aMilligrams of new growth per milligram of nitrogen in the entire seedling the previous November.

fertilized seedlings were able to use their nitrogen more efficiently. However, because nitrogen productivity increased only 14%, whereas the amount of new shoot growth increased 44%, the greater amount of nitrogen within fertilized seedlings was more important than the efficiency with which it was used.

Increasing the nitrogen concentration of 2-0 Douglas-fir the October before lifting resulted in a considerably greater growth response the year after outplanting. However, this was possible only because serious carbohydrate depletion from increased winter respiration rates and frost damage from early budbreak were avoided. Furthermore, because the site had been treated with sucrose to decrease nitrogen availability, these results probably approach the maximum differences that can be expected for seedlings with nitrogen values similar to those in this experiment. On planting sites with greater nitrogen availability, the treatment effect would probably be less dramatic. Moreover, to what extent the results reported here apply to other seed zones is not known at this time.

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