ECOPHYSIOLOGICAL STUDIES OF RED ALDER (*ALNUS RUBRA* BONG.) SEEDLINGS GROWN IN PURE AND MIXED PLANTINGS OF DIFFERENT DENSITY

by

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ABSTRACT

Seasonal changes in growth, nitrogen fixation, apparent photosynthesis (APS) and dark respiration (RS) were followed in first-year seedlings of red alder (Alnus rubra Bong.). Following this initial study, density stress factors were examined by growing second-year red alder seedlings at densities 2, 4, 8 and 16 plants dm^{-2} in pure and mixed culture with Douglas-fir. By combining techniques of growth and CO_2 exchange rate analysis, it was possible to examine ecophysiological characteristics of red alder with regard to its high growth rates, shade intolerance, nitrogen fixation abilities and its role in vegetation succession.

Nodulated alder seedlings grown without a soil nitrogen source attained a mean nitrogen content of 63 mg by the end of the growing season, undoubtedly due to nitrogen fixation in root nodules. Non-nodulated control plants showed relatively little gain in total nitrogen, exhibited symptoms of nitrogen deficiency and eventually died.

Similar seasonal APS and nitrogen fixation patterns suggested a close relationship between nodules and leaves. Highest APS, dark RS and nitrogen fixation rates per plant occurred in late August - early September. Photochemical capacity and nodule efficiency were highest early in the season (June) and then decreased. Decreased nitrogen fixation at the end of the season was probably a direct result of curtailment of essential substrates to the nodules resulting from a corresponding reduction in APS rates.

Alder's potential for rapid growth was revealed by its high maximum APS rates at light saturation (ranging from 7.46 - 26.38 mg CO_2 h^{-1} dm^{-2}), light saturation level (4000 - 5000 ft-c) and leaf weight ratio (approx.

0.45 - 0.60 mg leaf mg^{-1} plant) during the growing season.

The major effect of density stress on alder was to reduce the relative growth rate (RGR) and net assimilation rate (NAR) due to low light intensities within the crop canopies. The reduction in NAR mainly resulted from a corresponding reduction in crop APS rates as there was no consistent change in dark RS rates. Density stress also resulted in decreased leaf weight ratios (LWR) in most cases, but this was frequently offset by an increase in the leaf area ratio (LAR) and the specific leaf area (SLA). Marked increases in alder nodule weight ratios occurred at the higher densities suggesting that (1) nitrogen levels were reduced at the higher densities, and (2) nitrogen fixation in root nodules compensated for these reduced nitrogen levels.

In fir seedlings, density effects were similar to those shown for alder except that fir seedlings usually (1) exhibited an increase in LWR at the higher densities, and (2) showed less marked differences in growth response than alder to the degree of density stress. Photochemical capacity and maximum APS rates also increased in fir seedlings after growth at the higher densities. Alder seedlings showed an opposite response, exhibiting lower shade adaptability than fir.

Alder's shade intolerance could not be explained in this study either on the basis of photosynthetic efficiency or with respect to leaf production. Alder usually had higher RGR, NAR, APS and dark RS rates, higher photochemical capacity, LWR, LAR and SLA and lower root weight ratio (RWR) than the more shade tolerant Douglas-fir. Alder's shade intolerance may therefore arise in later stages of growth or be related to the initial stages of seed germination and seedling establishment on

a shaded forest floor.

Theoretical changes in alder growth with stand development (increased shading and soil nitrogen levels) are discussed.

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PROLOGUE

Red alder (Alnus rubra Bong.) is one of the most important hardwood species of the Pacific Northwest and coastal areas of Alaska from an ecological point of view. In British Columbia, it is associated with commercially important tree species including Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), western hemlock (Tsuga heterophylla (Raf.) Sarg.), Sitka spruce (Picea sitchensis (Bong.) Carr.) and western red-cedar (Thuja plicata Donn.). Under natural conditions, alder is one of the initial species to invade exposed moist habitats. Growth of the seedlings under these conditions is usually rapid and in later stages of succession, even-aged stands of alder are formed (Bernsten 1961). In most cases, alder seedling establishment and growth under shaded conditions does not occur and eventually more shade tolerant species outgrow and replace alder in the forest stand.

The presence of root nodules in alder species has been associated with fixation of atmospheric nitrogen which, in turn, has led to increased soil nitrogen content, nitrogen content of Douglas-fir foliage, and growth rate of the fir under natural conditions (Tarrant 1961). However, little information is available on the rate and efficiency of nitrogen

fixation in red alder root nodules during the growing season, on ecophysiological characteristics of alder with regard to shade tolerance or on seedling interactions with coniferous species under experimental conditions of different plant density.

The objectives of this study were 1) to determine the seasonal pattern of growth and the apparent photosynthetic (APS), dark respiration and nitrogen fixation rates of red alder seedlings (Part I of this thesis), and 2) to determine the modification, if any, of these responses due to intraspecific and interspecific interaction of seedlings at different densities (Part II). For the interaction studies, pure and mixed plantings of red alder and Douglas-fir seedlings were used.

The basic approach employed in the study combined growth analysis measurements with measurements of apparent photosynthesis and dark respiration of the seedlings. Nitrogen content of the leaves, stems, roots and nodules of the alder seedlings was determined and provided the basis for calculation of the rate and efficiency of nitrogen fixation between harvest periods (see Stewart 1962) for Part I of this study.

PART 1

SEASONAL GROWTH, CARBON DIOXIDE EXCHANGE AND NITROGEN FIXATION PATTERNS IN RED ALDER SEEDLINGS

INTRODUCTION

From nitrogen fixation studies on Alnus glutinosa (L.) Gaertn. (Stewart, 1962) and Alnus rugosa (Du Roi) Spreng. (Daly 1966), a marked seasonal pattern of nitrogen fixation and nodule efficiency is evident. In these studies, reduction in both nitrogen fixation and nodule efficiency occurred at the end of the growing season. Stewart (1962) suggested that this coincided with decreased late-season plant photosynthesis, and a possible curtailment of essential metabolites to the nodules. He found that nitrogen fixation was attuned more to the growth requirements of the plant than to requirements of the nodule endophyte. This suggests that the seasonal patterns of nitrogen fixation and growth are coincident and that a corresponding relationship between carbon dioxide exchange (ie. photosynthesis and dark respiration) and nitrogen fixation patterns should occur throughout the growing season.

As no concurrent measurements of the seasonal pattern of growth,

nitrogen fixation and photosynthesis have been made for Alnus rubra (Bong.), these relationships were examined in this study using first-year seedlings. Apparent photosynthetic and dark respiration rates have been reported previously for red alder seedlings grown to mid-season under different levels of shade (Krueger and Ruth 1969) and, more recently for nodulated alder seedlings grown under three different light treatments at several measurement periods during the growing season (Littel 1972). However, no concurrent data are available on the nitrogen fixation pattern of red alder under controlled experimental conditions.

METHODS

Plant Material and Establishment

Nodulated and non-nodulated first-year seedlings of red alder at the single-leaf stage were collected in mid-May 1969 from an exposed habitat on Burnaby Mountain, British Columbia (elevation 350 m). Approximately 200 seedlings of similar size were selected and transplanted into 600 ml Nalgene pots containing vermiculite. Holes were placed in the bottom of the pots to provide free drainage. Nodulated and non-nodulated plants were placed in separate pots; each pot initially contained 4 seedlings.

Potted seedlings were arranged randomly in the field on a raised bench under a shelter of fibreglass screening (mesh size 2 mm) and clear plastic (0.6 mm) which prevented rain from reaching the seedlings. Sides of the shelter were covered with similar screening and plastic to prevent the entry of rain and side light edge effects. Ample space between the sides of the shelter and the raised bench permitted relatively free air circulation around the seedlings. Periodic light intensity measurements made with a Brockway Sekonic Exposure Meter, Model S, throughout the growing season indicated that light intensity was reduced approximately 40 percent beneath the shelter on both clear and cloudy days. Air temperatures representing the pattern experienced by the experimental seedlings were obtained from the nearby Burnaby Mountain

climatic station (Fig. 1).

The alder plants were watered every three days throughout the growing season with 250 mls of Crone's nitrogen-free nutrient solution containing a micronutrient supplement (Table 1).

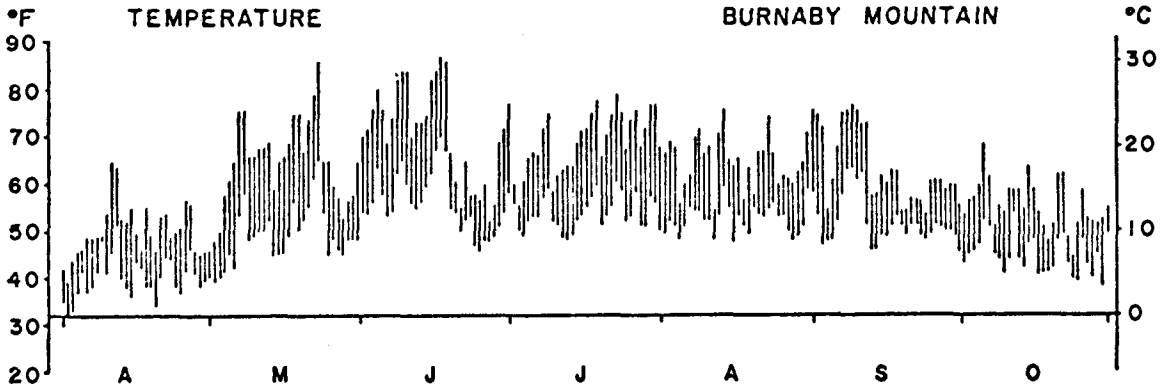


Figure 1. Daily temperature pattern on Burnaby Mountain (elev.350m) during the 1969 growing season (Canada Dept. Transport, Meteorological Branch 1969).

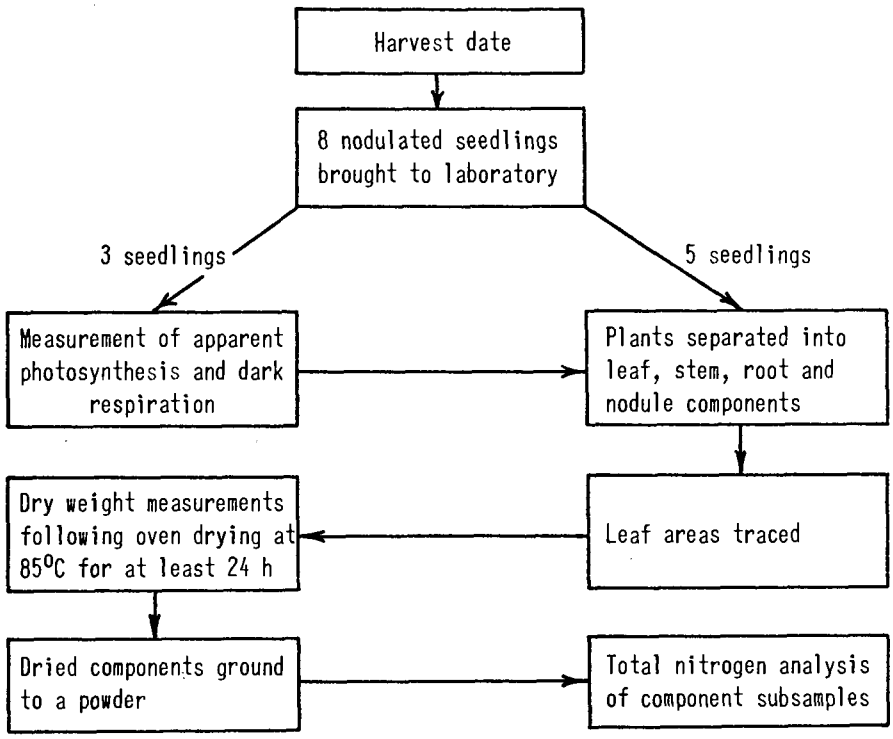
Table 1. Components of the nutrient solutions provided the alder seedlings (g liter^{-1} distilled water).

Crone's nitrogen-free nutrient solution *		Micronutrient supplement **	
KCl	1.00	H_3BO_3	2.86
$MgSO_4.7H_2O$	0.50	$MnCl_2.4H_2O$	1.81
$CaSO_4.2H_2O$	0.50	$ZnSO_4.7H_2O$	0.22
$Ca_3(PO_4)_2$	0.25	$CuSO_4.5H_2O$	0.08
$Fe_3(PO_4)_2.8H_2O$	0.25	$H_2MoO_4.H_2O$	0.02

* from Bond (1951)

** from Hoagland and Arnon (1938). One cc of the micronutrient supplement was added per liter of Crone's nitrogen-free solution.

Two weeks after transplanting, each pot was thinned to 2 seedlings of similar size. At approximately 14-day intervals within the growing season (June 2 to October 6), eight nodulated seedlings were selected, measured and harvested as follows:



Non-nodulated control plants were also measured and harvested as above at the beginning of the experimental sequence, but after 8 weeks on an N-free nutrient solution, most of these seedlings died from an apparent nitrogen deficiency. Measurements were made on a few non-nodulated seedlings provided with nitrogen part way through the harvest period.

Measurements

Growth characteristics and total nitrogen content

At each harvest date, measurement of the seedlings included physical characteristics such as leaf number, leaf area, stem height, and dry weight and total nitrogen content of the plant components. Leaf areas were determined by tracing the leaf outline on to mm graph paper and counting squares covered by the leaf surface.

For dry weight and total nitrogen determination, seedlings were washed to remove vermiculite from the roots and separated into leaf, stem, root and nodule components. Nodules were removed under a dissecting microscope. Each component was dried at 85^{o}C for at least 24 hours before weighing. Following weighing, each component was ground to a powder and total nitrogen content of a subsample was determined with a Perkin Elmer Model 240 elemental analyzer.

Apparent photosynthesis and dark respiration

Carbon dioxide exchange measurements were made with a URAS-11 infrared gas analyzer (0-600 ppm v/v range) in a closed system (Fig.2). The measuring air circuit consisted of a cylindrical brass plant chamber, a dessicator (anhydrous $CaSO_4$), the URAS-II analyzer, a mercury manometer, flowmeter and a diaphragm pump interconnected with Tygon tubing. Air was circulated throughout the system at a flow rate of 1 liter min^{-1} in the pneumatic line, and signal output from the analyzer was recorded on a Moseley 7100B strip chart recorder (Hewlett Packard). Volume of the measuring system was approximately 530 ml excluding the plant chamber.

Chamber volumes ranged from 45 to 3800 ml depending on size of the plant being measured.

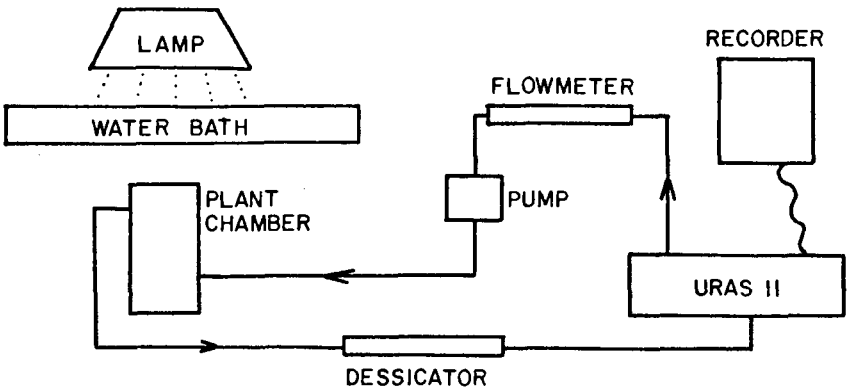


Figure 2. Principal components of the closed system used for the carbon dioxide exchange measurements.

The plant chambers were brass cylinders fitted with a clear 3mm plexiglass closure plate at one end (Fig.3). The cylinder was fitted with an air inlet and outlet. Base plates were grooved to accept the cylinder and the plate slotted to receive the plant stem. Plants were sealed in the chamber with Apiezon Q for the apparent photosynthesis (APS) and dark respiration (RS) measurements.

For the APS measurements, plants received light from two 500 watt Dicrolite quartz-iodine lamps (color temp. 3300^{o}K) positioned above the

plant chamber. Light was filtered through a 5 cm deep water bath to reduce the infra-red component. Light intensity was varied by changing the distance between the light source and the plant chamber. For low light intensities, neutral gray fibreglass screening was placed over the chamber. Light intensity was measured at the chamber top with a Brockway Sekonic exposure meter and spectral intensity (μ watts cm^{-2}) 400 to 750 nm for each light intensity was measured with an ISCO Model SRR spectroradiometer (Fig. 4; Appendix 1, Table 1).

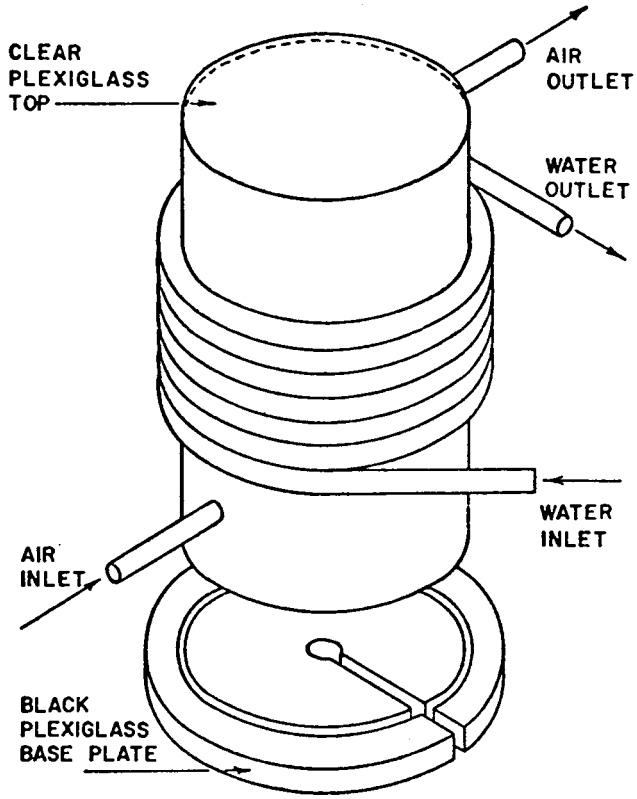
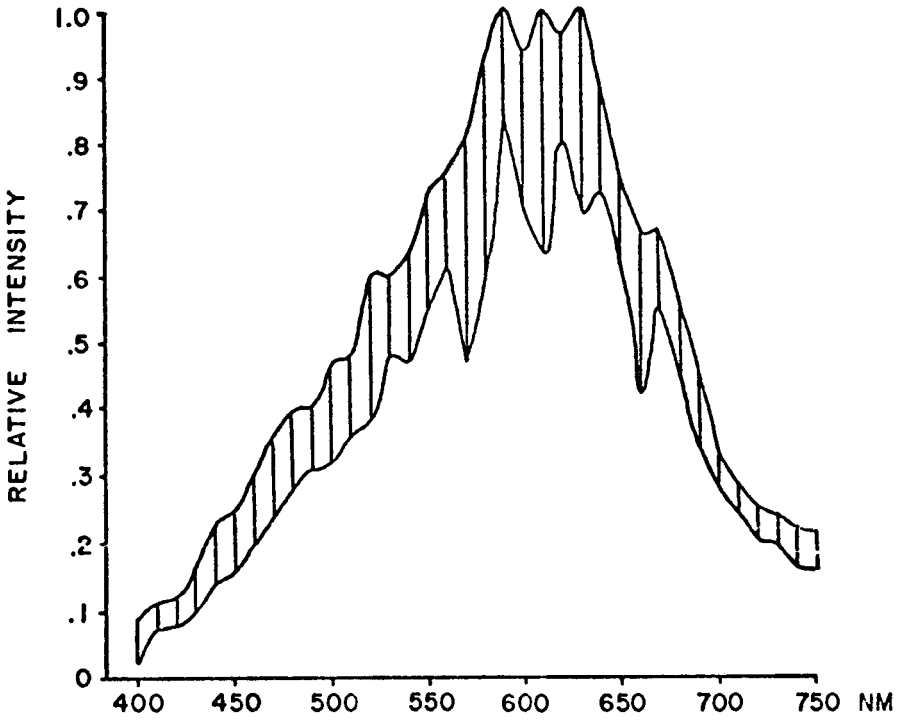


Figure 3. Diagram of the cylindrical plant chamber used for enclosing the plant during CO_2 exchange measurements. The inside of the chamber was painted white to increase reflection.



Total energy (μ watts cm^{-2}) provided by the Dicrolite lamps at light intensities used for the apparent photosynthesis measurements. Energy was measured at the top of the plant chamber.

	Spectral region (nm)								
Light (ft-c)	V 400-420	B 420-490	G 490-580	Y 580-590	O 590-650	R 650-700	FR 700-750	Total	0.5 λ (nm)*
5000	184.2	1813.3	5508.3	948.4	5580.5	2840.3	1292.2	18167.7	606.9
4000	139.7	1363.9	4389.3	756.1	4515.4	2326.0	1043.4	14533.8	608.3
3000	89.8	895.8	2717.6	474.5	2730.0	1379.3	641.1	8928.2	606.2
2500	74.8	754.4	2441.4	439.8	2466.2	1228.9	579.9	7985.4	606.9
2000	55.5	568.3	1781.0	349.8	1937.3	981.9	448.7	6122.4	608.4
1500	46.0	464.3	1479.6	264.1	1487.0	735.2	331.7	4808.0	606.0
1000	28.2	318.5	946.1	172.4	975.9	477.6	205.4	3124.2	605.9
750	35.3	324.0	924.6	151.0	892.4	416.1	187.5	2930.9	602.0
500**	20.7	222.4	620.7	106.0	611.2	290.4	132.0	2003.5	603.1

* Wavelength in nm at midpoint of the total energy distribution

** 500 ft-c measurement made with 1 fibreglas screen over sensor

Figure 4. Relative spectral distribution of energy (400 - 750 nm) received by the plant under experimental conditions for APS measurements. Graph shows absolute range in relative energy between light intensities of 5000 and 500 ft-c. The computer program of Bulley (1969) was used for the calculation of total energy.

Air temperature in the plant chamber was measured with a shielded 24-gauge copper-constantan thermocouple held just below the underside of a leaf. Temperature within the plant chamber was maintained at 21° ± 1°C for all measurements with a Lauda K-2R temperature controlled water bath which forced cool water through copper tubing coiled around the chamber.

Measurement of apparent photosynthesis (APS) was made over a range of light intensities from 5000 to 500 ft-c. Approximately twenty minutes was allowed for plant stabilization at each light intensity change before a new sequence of measurements was commenced. Three separate APS 'runs' were made at each light intensity within an ambient [CO_2] of 375 to 225 ppm v/v. Dark respiration was measured at the end of the day when photosynthesis measurements were completed. Following the CO_2 exchange measurements, the leaf area was determined and the plant harvested.

The infra-red gas analyzer was calibrated at the start and end of each day's measurements. Dry nitrogen was used as the zero reference standard and circulated through both reference and sample cells of the analyzer at a flow rate of 1 liter min^{-1}. The upscale standard (350 ppm CO_2 v/v in air, Matheson of Canada Ltd. calibration standard) was circulated through the sample cell (flow rate 1 liter min^{-1}) while dry nitrogen was 'trickled' at a lower flow rate through the reference cell. The zero standard was trickled continuously through the reference cell during the CO_2 exchange measurements.

Given the volume of the measuring circuit, the rate of apparent photosynthesis can be calculated from the measured rate of decrease in

$[CO_2]$ from the fixed volume when the plant is placed in light. Conversely, the rate of dark respiration can be calculated from the measured rate of increase in $[CO_2]$ from the fixed volume when the plant is placed in complete darkness.

Data analysis

The computer program of Bulley (1969) was used for determination of APS and dark respiration rates from the curves of $[CO_2]$ versus time recorded. Data input for the program consisted of $[CO_2]$ ppm read at one minute intervals along the measured curve of each 'run' spanning the air stream $[CO_2]$ of 325 ppm v/v. From the values of $[CO_2]$ ppm versus time, the computer program calculates a polynomial equation for the curve which yields rate values at specified ambient $[CO_2]$ as output. From the computer output, rate values at 325 ppm ambient $[CO_2]$ were standardized for pressure and temperature differences and expressed on a leaf area basis as:

$$\text{mg } CO_2 \text{ hr}^{-1} \text{ dm}^{-2} \text{ (single surface of leaf)}$$

From the dry weight and leaf area data, the rate of dry matter production (Rdmp), the relative growth rate of the plant (RGR_p), and the net assimilation rate (NAR) for each time period between successive harvests were calculated using the standard formulae (see Blackman 1968):

$$(1)\quad Rdmp = \frac{W_2 - W_1}{t_2 - t_1} \qquad (\text{weight} \cdot \text{time}^{-1})$$

$$(2)\quad RGR_p = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \qquad (\text{weight} \cdot \text{weight}^{-1} \cdot \text{time}^{-1})$$

$$(3)\quad NAR = \frac{W_2 - W_1}{t_2 - t_1}\ \frac{\log_e A_2 - \log_e A_1}{A_2 - A_1} \quad (\text{weight} \cdot dm^{-2} \cdot \text{time}^{-1})$$

where W_1 and W_2 are the mean total plant dry weights, and A_1 and A_2 the mean total leaf areas per plant, respectively, between two harvest times, t_1 and t_2. Relative growth rates of leaves (RGR_L) and roots (RGR_R) were also calculated between successive harvest dates in a similar manner as that shown for the relative growth rate of the plant.

The distribution of dry matter between the plant components (leaf, stem, root and nodule) was calculated at each harvest by determining ratios of weight of individual components to total plant weight, thus obtaining leaf weight ratio (LWR), stem weight ratio (SWR), root weight ratio (RWR), and nodule weight ratio (NWR). The ratio of total leaf area to plant dry weight (leaf area ratio, LAR) and the ratio of leaf area to leaf dry weight (specific leaf area, SLA) were also calculated at each harvest.

Nitrogen fixation rates, nitrogen transfer and nodule efficiency were calculated following Stewart (1962). The rate of nitrogen fixation (mg N fixed $plant^{-1}$ day^{-1}) was calculated by subtracting the mean nitrogen content per plant including nodules at each harvest date from the corresponding figure at the following harvest date. Similarly, the mean nitrogen transferred from the nodules to the rest of the plant was calculated by subtracting the mean nitrogen content per plant less nodules at each sampling date from the corresponding figure at the following sample date. Nodule efficiency (mg N fixed day^{-1} g^{-1} dry weight of

nodule) was calculated by dividing the nitrogen fixation rate for each period between successive harvests by the mean nodule dry weight for each period between successive harvests.

Data were analyzed statistically to determine whether there were any significant seasonal differences. Analysis of variance models (ANOVA) were established for the data following Sokal and Rohlf (1969).

RESULTS

Plant Growth

In the first six weeks of growth, non-nodulated seedlings showed relatively poor growth compared to nodulated seedlings. They had small yellowish leaves and long root systems with little branching (Fig.5). The nodulated seedlings, however, had dark green leaves and proportionally shorter but much branched root systems. Nodules occurred in a 'clumped' pattern at the top of the roots in nodulated seedlings, and they were seldom found distributed uniformly over the entire root system.

Figure 5. Growth differences between nodulated (left) and non-nodulated (right) alder seedlings at Harvest 4 (14 July). Seedlings were grown on a N-free nutrient solution.

Comparison of biomass for nodulated and non-nodulated plants

At Harvest 3 (June 30), nodulated plant biomass (0.27 g) was approximately two to three times greater than the biomass of the non-nodulated plants (Table 2). The non-nodulated plants attained a mean total plant dry weight of 0.01 g in late June before dying from apparent nitrogen deficiency. Nodulated plants increased about 700 times in biomass over the growing season and attained a mean total plant dry weight of 3.24 g in early October. From the initial harvest (2 June) to September 8, differences between mean total plant dry weight were significant ($P<0.05$) between successive harvests for nodulated plants but not significantly different between September 8 and October 6 (Table 2).

Noticeable differences also occurred in dry matter distribution between nodulated and non-nodulated seedlings during the first six-weeks growth (Fig. 6). At June 30, root weight ratios (RWR) of non-nodulated seedlings were almost three times greater than those of nodulated seedlings. Almost 50 percent of the total plant dry weight in non-nodulated seedlings was present in the roots compared to approximately 18 percent for nodulated seedlings. Leaf weight ratios (LWR), however, were almost two times greater for nodulated seedlings than for non-nodulated seedlings; about 60 percent of the total plant dry weight in nodulated seedlings was represented by the leaves as compared to 30 percent for the non-nodulated seedlings.

Differences in root-shoot ratios emphasize the marked difference in growth pattern and dry matter distribution between nodulated and non-

Table 2. Mean dry weight and growth measurements for the nodulated (+) and non-nodulated (-) alder seedlings for successive harvests throughout the growing season. Values for dry weight include standard errors; n = 8 for nodulated plants, and n = 4 for non-nodulated plants.

Harvest date	Plants	Leaf no.	Leaf area (dm^2)	Area $leaf^{-1}$ (dm^2)	Stem ht. (cm)	Dry weight (mg)					Root/shoot ratio
						Leaf	Stem	Root	Nodule	Plant	
2 June	+	3	0.006	0.002	1.3	2.56 ± .26	0.85 ± .15	1.11 ± .14	0.17 ± .03	4.67 ± .40	0.38
	-	3	-	-	1.2	2.22 ± .39	0.98 ± .27	1.52 ± .20		4.72 ± .79	0.48
16 June	+	6	0.014	0.002	2.6	6.48 ± .50	2.03 ± .11	2.35 ± .25	0.21 ± .04	11.08 ± .79	0.30
	-	5	-	-	-	4.02 ± .49	1.62 ± .15	3.27 ± .24		8.90 ± .83	0.58
* 30 June	+	7	0.045	0.006	3.6	16.73 ±3.38	4.18 ± .66	4.89 ±1.03	1.02 ± .28	26.82 ±5.25	0.28
	-	5	-	-	-	4.31 ± .06	1.90 ± .19	5.30 ± .66		11.51 ± .63	0.85
14 July	+	8	0.130	0.016	4.6	50.96 ±7.65	13.65 ±2.29	12.21 ±1.37	5.00 ± .88	81.82 ±11.93	0.27
28 July	+	9	0.330	0.037	6.4	127.9 ±23.0	35.31 ±8.27	30.72 ±5.39	13.35 ±3.93	207.2 ± 40.1	0.27
11 Aug.	+	13	0.878	0.068	10.7	361.1 ±54.1	124.7 ±23.1	68.90 ±10.56	32.73 ±4.73	587.5 ± 88.7	0.21
25 Aug.	+	16	1.667	0.104	14.8	792.7 ±82.8	311.0 ±41.1	207.2 ±30.2	78.78 ±11.74	1390 ± 160	0.26
8 Sept.	+	17	2.393	0.141	17.1	1102 ± 58	583.1 ±42.8	426.6 ±55.8	96.77 ±9.57	2208 ± 147	0.31
22 Sept.	+	17	3.103	0.182	18.5	1449 ± 149	848.3 ± 102	641.1 ± 106	138.8 ±18.6	3077 ± 299	0.34
6 Oct.	+	16	2.260	0.141	18.3	**1347 ± 213	1009 ± 174	732.2 ± 130	163.8 ±21.5	3243 ± 512	0.38

* Non-nodulated seedlings died following this harvest date

** Decrease in mean leaf dry weight at this harvest may represent some leaf fall

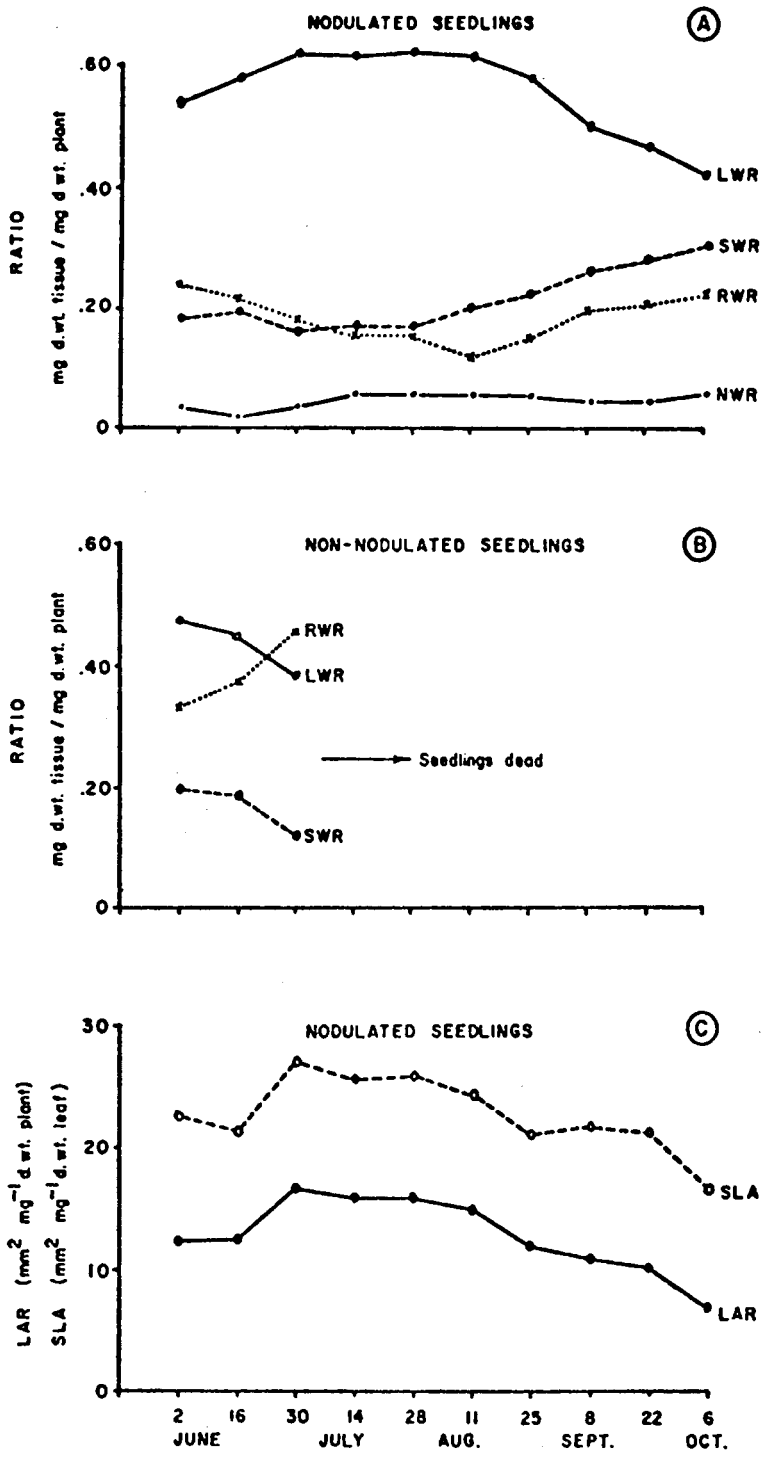


Figure 6. Dry weight distribution in (a) nodulated and (b) non-nodulated plants, and (c) leaf area ratios and specific leaf areas of nodulated plants during the growing season. Values calculated from Table 2.

nodulated seedlings (Table 2). The root-shoot ratios of non-nodulated plants increased two-fold between the initial harvest on 2 June (0.48) and late June 0.85), whereas root-shoot ratios of the nodulated seedlings decreased from 0.38 to 0.28 during the same period. As a result, root-shoot ratios of the non-nodulated seedlings were about three times greater than those of the nodulated seedlings on 30 June.

Seasonal pattern of dry matter distribution in nodulated seedlings

During the growing season, the greatest proportion of dry matter within nodulated seedlings was found in the leaves (approx. 40 - 65 percent). Stems represented about 16 - 30 percent of the dry matter, and roots about 11 - 24 percent. The proportion of dry matter represented by nodules ranged from about 2 - 6 percent throughout the season (Fig.6; Appendix 1, Table 2).

The seasonal pattern of dry matter production in leaves, however, differed from the seasonal pattern for the roots and stem (Fig.6). The leaf weight ratio increased significantly ($P<0.001$) from the initial harvest in early June to a maximum (0.62) in late June and then remained largely constant until mid-August. The leaf weight ratio then progressively decreased to 0.42 at the end of the season resulting in a significant difference ($P<0.001$) between mid-season and late season ratios. Stem and root weight ratios followed an opposite pattern with lowest ratios from late June to early August.

Stem weight ratios of the nodulated plants decreased from 0.18 and 0.19 in early June to 0.16 in July and then progressively increased to

0.30 at the final harvest in early October (Fig.6). A more pronounced mid-season depression occurred in root weight ratios. Mean root weight ratios progressively decreased from 0.24 in early June to 0.12 in mid-August and then progressively increased to 0.22 in early October at the end of the season. Differences between the mid-season root weight ratios and the peaks at the beginning and end of the season were significant ($P<0.001$).

Except for a significant decrease in mid-June ($P<0.001$), nodule weight ratios remained largely constant (Fig.6) indicating that nodule growth was directly proportional to plant growth throughout most of the growing season.

Changes in leaf structure during the growing season were evident in the specific leaf area pattern (Fig.6). The highest value occurred in late June (27.08 mm^2 leaf mg^{-1} leaf), and following this peak, there was a gradual decrease as the season progressed. Consequently, leaves became proportionately thicker near the end of the season. The leaf area ratio (LAR), which represents the ratio of leaf area to plant dry weight, followed a similar seasonal pattern as that shown for the specific leaf area (Fig. 6), with the highest value occurring in late June (16.89 mm^2 leaf mg^{-1} plant) and the lowest at the end of the growing season (6.97).

Seasonal pattern of dry matter production, relative growth rates and net assimilation rates in nodulated plants

The rate of dry matter production (Rdmp) in nodulated plants increased throughout the season to a peak in late September (Fig.7). Following this peak, a sharp reduction occurred in early October, and this was

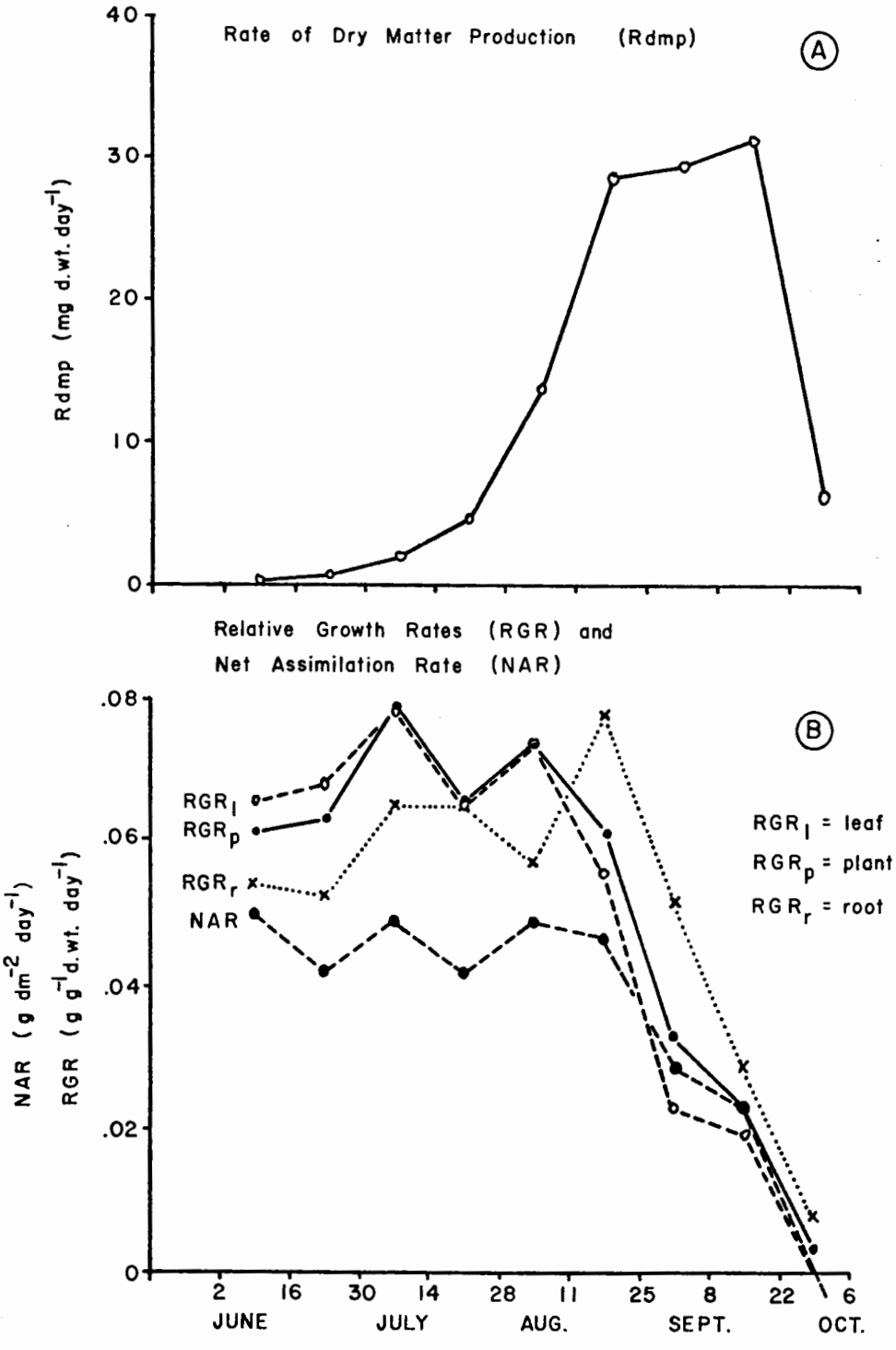


Figure 7. (a) Rate of dry matter production (Rdmp) and (b) relative growth rate of the plant (RGR_P), leaves (RGR_L) and roots (RGR_R) and the net assimilation rate (NAR) of nodulated plants between successive harvests. Values calculated from Table 2.

associated with a non-significant difference in mean total plant biomass (Table 2).

As plant growth is essentially an exponential and cumulative process depending upon the amount of tissue initially present (Blackman 1919), the relative growth rate of the plant (RGR_p) was calculated to eliminate the effect of biomass differences on the growth rates (Fig.7). Highest plant relative growth rate occurred in late June - early July and this coincided with peaks in the net assimilation rate and the relative growth rate of the leaves (Fig.7). Following this peak in late June, the RGR_p showed no consistent trend until early August, and then decreased as the season progressed. This decrease in RGR_p was associated with similar reductions in RGR_L, LAR, SLA and the NAR (Figs. 6 and 7). The relative growth rate of the roots (RGR_R) followed a similar seasonal pattern as that found for leaf and plant relative growth rates from early June to mid-August, but reached a maximum in late-August, about five weeks later than the peaks for leaves and the plant (Fig.7).

Comparison of relative growth rates of leaves and roots during the season gave higher rates for leaves vs. roots from early June to mid-August, but this pattern was reversed near the end of the growing season (Fig.7). A decrease in RGR_R between 28 July - 11 August probably gave rise to the reduction in root-weight ratio (Fig.6) and the root-shoot ratio (Table 2) in early August.

Carbon Dioxide Exchange

Apparent photosynthetic rates for nodulated and non-nodulated seedlings follow the standard rate vs. light intensity curves (Fig.8;

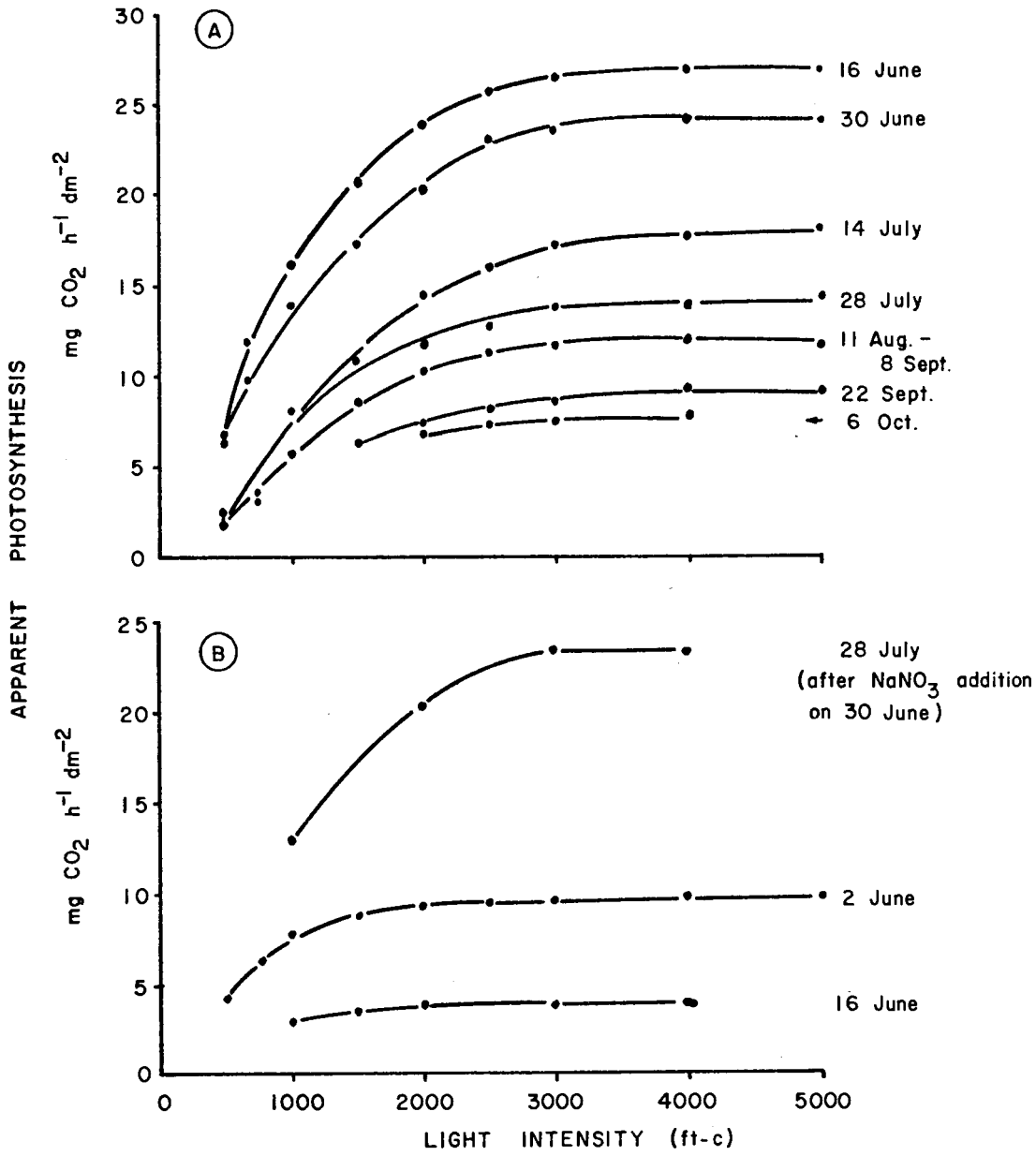


Figure 8. Apparent photosynthetic rates for (a) nodulated and (b) non-nodulated alder seedlings at the measurement light intensities used throughout the growing season. Mean values are plotted for each measurement light intensity; values for individual plants at each harvest date are given in Appendix 1, Table 3. The value plotted for August 11 - September 8 is a pooled mean of those harvest dates since the individual curves were essentially identical.

Appendix 1, Table 3). Important areas of the rate - intensity curves are the upper asymptote which estimates the photosynthetic rate at light saturation intensities, and the initial, essentially linear, portion of the curve at low light intensities which estimates the photochemical capacity of the photosynthetic system (Peat 1970; Bjorkman and Holmgren 1963; Rabinowitch 1951).

At Harvest 2 (16 June), nodulated seedlings had a higher light saturation level and greater photochemical capacity (initial slope of the rate-intensity curve between 500 - 1000 ft-c) than non-nodulated seedlings (Fig.8). The light saturation level occurred between 2000 - 2500 ft-c for non-nodulated seedlings and between 3000 - 5000 ft-c for nodulated seedlings. Differences in light saturation level during the growing season were not significant ($P>0.05$) in nodulated and non-nodulated plants. Nodulated plants, however, showed a progressive decrease in the initial slope of the rate-intensity curves as the season progressed (Fig.8).

At every measurement light intensity, non-nodulated plants had significantly lower mean APS rates than nodulated plants (Table 3). These lower APS rates found for non-nodulated plants appeared to be a result of nitrogen deficiency. Following addition of $NaNO_3$ to non-nodulated plants on June 30, the APS rate at 3000 ft-c increased 8 times from 3.73 in late June to 24.22 mg CO_2 hr^{-1} dm^{-2} in late July. Furthermore, the APS rate at 3000 ft-c for non-nodulated plants provided with nitrogen (24.22) was almost twice as great as the APS rate for nodulated plants (13.77) at the same harvest date. Nitrogen addition to non-nodulated plants also increased the light saturation level from 2000 to 3000 ft-c (Fig.8).

Table 3. Comparison of mean apparent photosynthetic and dark respiration rates for nodulated (+) and non-nodulated (-) plants on 16 June and 30 June, and for non-nodulated (+N) plants with nodulated plants on 28 July.

Harvest date	Plants	Light Intensity (ft-c) 5000	3000	2000	1000	500	0
		APS (mg CO_2 hr^{-1} dm^{-2})					RS (mg CO_2 hr^{-1} dm^{-2})
16 June	+	26.93	26.38	23.89	15.85	7.16	4.64
	-	9.61	9.34	9.21	7.76	4.28	4.07
*30 June	+	24.02	23.53	20.22	13.83	6.40	4.00
	-	-	3.73	3.73	2.90	-	2.49
28 July	+	14.47	13.77	11.72	7.38	2.57	2.17
	**-(+N)	24.22	24.22	20.10	13.00	-	6.33

* $NaNO_3$ added to non-nodulated seedlings
** only one seedling measured

There were no significant differences in dark respiration rates between nodulated and non-nodulated plants (Table 3). However, when nitrogen was added to non-nodulated plants at Harvest 3 (June 30), the dark respiration rate increased almost two-fold within 4 weeks (Harvest 5). In addition, the dark respiration rate was almost 3 times higher in non-nodulated seedlings following addition of combined nitrogen than in nodulated plants on the same harvest date (Table 3).

Differences in APS rates at 3000 ft-c, which approximates the light saturation level in nodulated plants (Fig.8), and changes in dark RS rates were significant during the season (Table 4; Fig.9). Both photosynthetic and dark RS rates per plant increased about 100 - 200 times

Table 4. Mean apparent photosynthetic rates at 3000 ft-c and dark respiration rates per plant and per unit leaf area, and mean RS:APS 3000 ft-c ratios (expressed on a leaf area basis) for nodulated plants at each harvest date throughout the growing season. APS and dark RS rates per unit leaf area for individual plants at each harvest date are given in Appendix 1, Table 3.

Harvest date	APS (mg CO_2 hr^{-1} $plant^{-1}$)	RS (mg CO_2 hr^{-1} $plant^{-1}$)	Mean leaf area (dm^{-2})	Specific leaf area (mm^2 mg^{-1} leaf)	*APS (mg CO_2 hr^{-1} dm^{-2})		*RS (mg CO_2 hr^{-1} dm^{-2}		Mean RS:APS 3000 ft-c ratio
2 June	0.12	0.04	0.0074	20.67	16.32	a	6.53		0.40
16 June	0.38	0.07	0.0143	20.63	26.38	b	4.64	a	0.18
30 June	0.80	0.14	0.0340	28.05	23.53		4.00		0.17
14 July	1.35	0.32	0.0787	26.05	17.14	a	4.07		0.24
28 July	5.10	0.80	0.3705	26.73	13.77		2.17		0.16
11 Aug.	10.38	1.46	0.8783	25.55	11.82	c	1.66		0.14
25 Aug.	21.05	3.43	1.8333	25.77	11.48		1.87		0.16
8 Sept.	28.17	4.31	2.3933	20.13	11.77		1.80	b	0.15
22 Sept.	26.41	5.28	3.1033	17.26	8.51	d	1.70		0.20
6 Oct.	16.86	2.96	2.2600	20.08	7.46		1.31		0.18

* Means connected by the same vertical bar and the same letter are not significantly different ($P>0.05$).

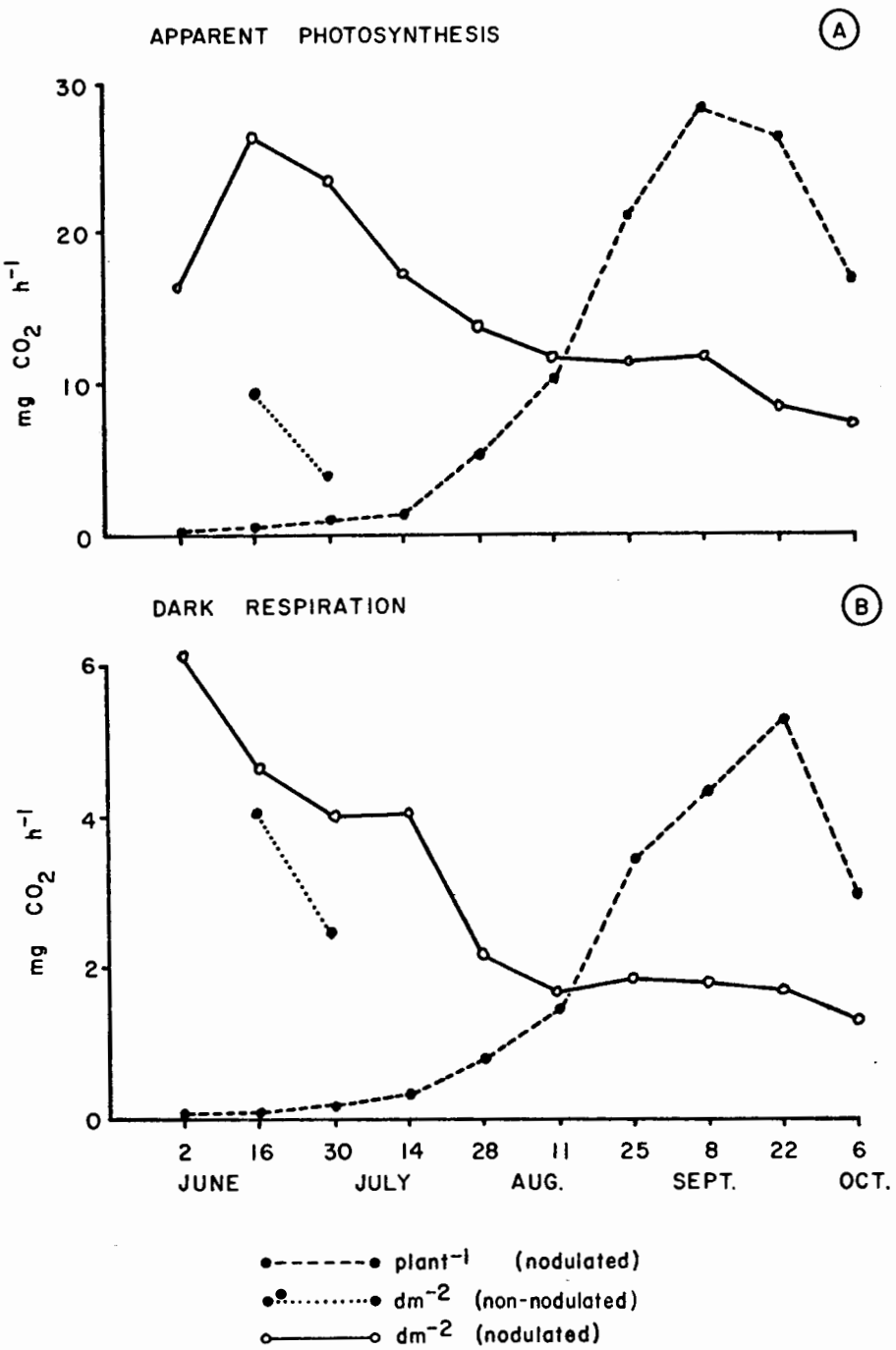


Figure 9. (a) Apparent photosynthetic rates at 3000 ft-c and (b) dark respiration rates per plant and per unit leaf area (dm^{-2}) for nodulated plants at each harvest date throughout the growing season. APS and dark RS rates dm^{-2} are also given for non-nodulated plants. (Data given in Appendix I, Table 3).

over the season to a maximum in September, and then decreased (Fig.9). Although both followed similar seasonal patterns, dark RS rates continued to increase in late September when APS rates per plant were already decreasing. This pattern probably gave rise, in part, to the sharp decrease in NAR which occurred between the final harvests (Fig.7). The progressive increase in dark RS and APS rates per plant during most of the season was also closely associated with a similar increase in seedling biomass (Table 2).

When expressed on a leaf area basis, APS and dark RS rates per plant followed opposite patterns to those shown for rates expressed on a plant basis (Fig.9). Highest APS and dark RS rates occurred in June, and were closely associated with peaks in the RGR_p and the NAR (Fig.7). From June to the end of the season, there was a progressive four-fold decrease in APS rates and a corresponding five-fold decrease in dark RS rates in nodulated plants. Non-nodulated plants also showed a reduction in APS and dark RS rates up until the time of their death in early July (Fig.9).

Nitrogen

Although nodulated plants had higher mean N content (about 30 percent) than non-nodulated seedlings on June 2 at the beginning of the experiment, this difference in nitrogen content became more pronounced as the season progressed (Table 5). Non-nodulated seedlings showed no net gain in mean total plant nitrogen, averaging 0.07 mg from the initial harvest in early June until their death following Harvest 3 (June 30). Nodulated

Table 5. Mean total nitrogen content for successive harvests of nodulated (+) and non-nodulated (-) plants throughout the growing season. Values for nitrogen content include standard errors; n=8 for nodulated plants, and n=4 for non-nodulated plants.

Harvest date	*Nitrogen (mg)				
	Leaf	Stem	Root	Nodule	Plant
2 June					
+	0.06 ± .01	0.02 ± .00	0.02 ± .00	TRACE	0.10 ± .01
-	0.03 ± .00	0.01 ± .00	0.02 ± .00	---	0.07 ± .01
16 June					
+	0.13 ± .02	0.02 ± .00	0.04 ± .00	0.01 ± .00	0.20 ± .02
-	0.03 ± .00	0.01 ± .00	0.04 ± .00	---	0.08 ± .01
30 June					
+	0.35 ± .09	0.06 ± .01	0.08 ± .02	0.04 ± .01	0.53 ± .12
-	0.03 ± .00	0.01 ± .00	0.04 ± .00	---	0.07 ± .00
14 July	1.18 ± .18	0.19 ± .03	0.19 ± .02	0.16 ± .03	1.72 ± .26
28 July	2.88 ± .44	0.47 ± .13	0.40 ± .06	0.42 ± .13	4.17 ± .73
11 Aug.	8.59 ± 1.26	1.49 ± .24	1.23 ± .20	1.01 ± .16	12.32 ± 1.83
25 Aug.	21.53 ± 1.94	4.10 ± .43	3.57 ± .52	2.17 ± .28	31.37 ± 3.00
8 Sept.	32.68 ± 1.64	5.65 ± .49	5.94 ± .59	2.86 ± .27	47.13 ± 2.59
22 Sept.	38.90 ± 4.30	9.30 ± 1.24	10.65 ± 1.63	3.60 ± .48	62.45 ± 5.75
6 Oct.	35.18 ± 6.25	11.94 ± 2.29	12.76 ± 2.30	3.65 ± .52	63.53 ± 10.76

*Mean total nitrogen values shown here were calculated, by extrapolation, from the total nitrogen content of a weighed subsample of each plant component. Variation within each subsample (expressed as standard error) was determined by measuring the nitrogen content of 2 replicates of approximately 5-7 subsamples of each plant component during the season. Variation between replicates on each subsample was 2.28 ± 0.17, 0.95 ± 0.05, 1.20 ± 0.07 and 3.12 ± 0.22 mg N/100 mg tissue for leaf, stem, root and nodule components, respectively.

plants, however, reached a mean total plant N content of 63 mg at the final harvest in early October (Table 5), indicating that red alder root nodules were active in nitrogen fixation.

From the initial harvest (2 June) to September 22, differences in total plant nitrogen were significant ($P<0.05$) between successive harvests for nodulated plants but not significantly different between September 22 and October 6 (Table 5).

Nitrogen concentration in plant components

During the growing season, the highest mean nitrogen concentration (Fig.10) usually occurred in the nodules (2.85), followed by the leaves (2.40), roots (1.60) and stem (1.30). Nitrogen concentration in the plant as a whole, averaged about 2.00 mg N mg^{-1} d.wt. tissue over the growing season.

The mean nitrogen concentration also differed significantly within each plant component during the season (Fig.10). In the leaves, the nitrogen concentration increased from a depression in late June (1.82) to a maximum in early September (2.96), and then showed a decrease towards the end of the season. This decrease in leaf nitrogen concentration at the end of the season was associated with increases in stem and root nitrogen concentration, and with a decrease in nodule nitrogen concentration (Fig.10).

At the beginning of the season (2-16 June), leaf and stem nitrogen concentration decreased and this coincided with an increase in nodule nitrogen concentration (Fig.10). Stem nitrogen concentration exhibited

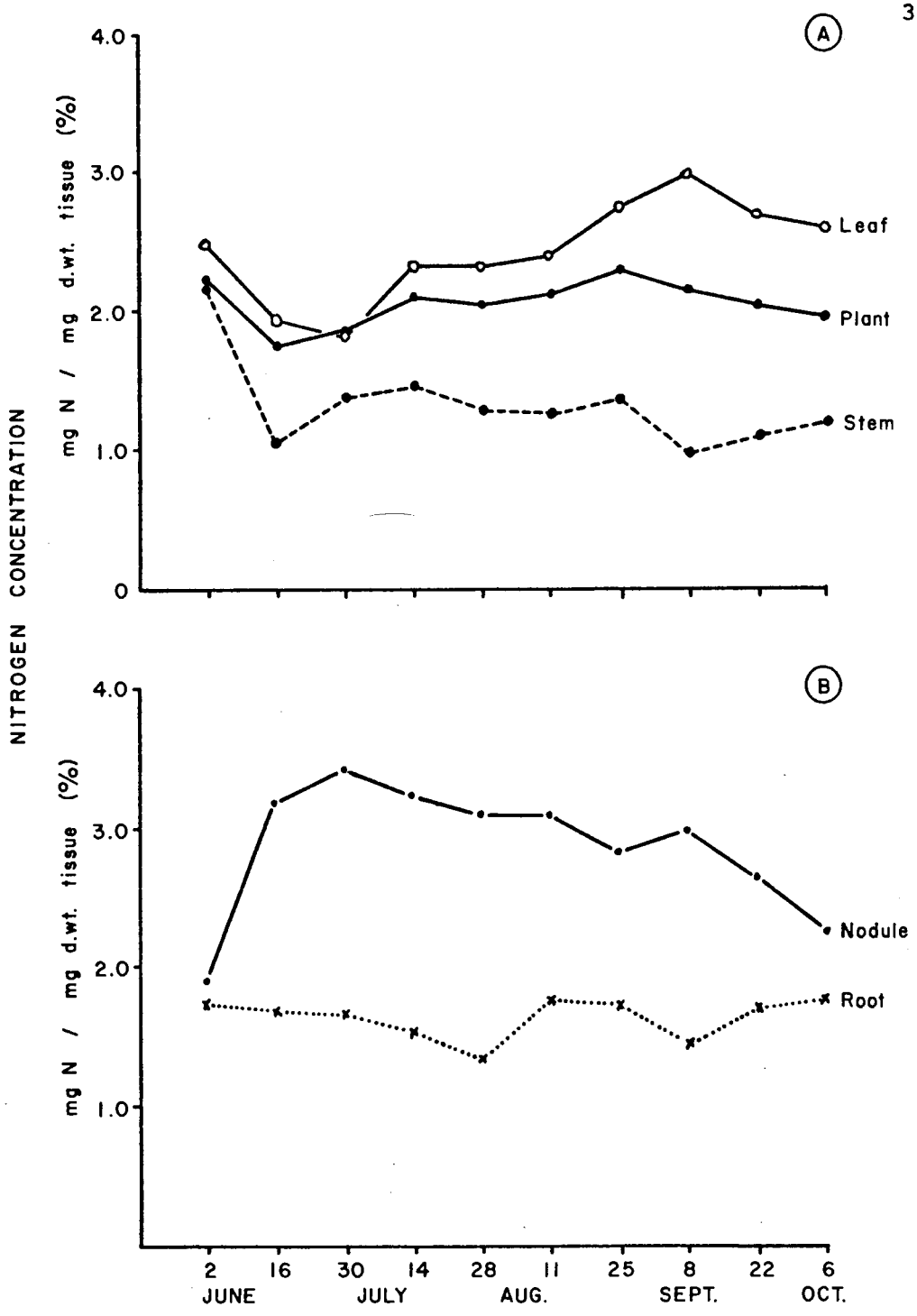


Figure 10. Nitrogen concentration in (a) leaf, stem and plant and (b) nodule and root tissues at each harvest date throughout the growing season. Each value is a mean of 8 plants. Mean values ± standard errors for individual plant components at each harvest date are given in Appendix I, Table 4.

two statistically significant depressions during the growing season; one in mid-June and the other in early September. The depression in stem nitrogen concentration in early September coincided with peaks in leaf and nodule nitrogen concentration, and with a slight depression in root nitrogen concentration. Roots generally showed a less variable nitrogen concentration pattern during the growing season than the other plant components (Fig.10).

Nitrogen fixation, nodule efficiency and nitrogen transfer

The rate of nitrogen fixation (mg N fixed plant^{-1} day^{-1}) increased approximately 130 times over the season, from an initial value of 0.10 in early June to a maximum of 1.36 in mid-August (Table 6). From mid-August to the end of the season there was a 94 percent reduction in nitrogen fixation rate from 1.36 to 0.08 mg N fixed plant^{-1} day^{-1}).

Nodule efficiency (mg N fixed day^{-1} g^{-1} d. wt nodule) was maximum in June (52.63) and then decreased by almost 40 percent from mid-June to June 30 (32.26) (Table 6). No significant difference in nodule efficiency occurred between June 30 and early September (12.76). However, from mid-September (9.27) to early October (0.53) there was a 94 percent reduction in nodule efficiency and this was associated with a similar decrease in nitrogen fixation rate (Table 6).

Nitrogen transfer from the nodules to the rest of the plant, when expressed as a percent of the nitrogen fixed, ranged from 90 to 95 percent throughout the growing season and reached a maximum of 95 percent between late August and the end of the season (Table 6).

Table 6. Nitrogen fixation, nodule efficiency and nitrogen transfer data for periods between successive harvests of nodulated plants throughout growing season. Each value is a mean of 8 plants. Means for nodule efficiencies connected by the same letter are not significantly different (P>0.05).

Harvest period	Mean N fixed plant^{-1} (mg)	Mean N fixed plant^{-1} day^{-1} (mg)	Mean N trans. from nod. to rest of plant (mg)	N trans. as % N fixed	Mean nod. dry weight (mg)	Efficiency of nodules (mg N fixed day^{-1} g^{-1} d. wt nodule)	
2-16 June	0.10	0.01	0.09	90.00	0.19	52.63	
16-30 June	0.33	0.02	0.30	90.91	0.62	32.26	a
30 June - 14 July	1.19	0.08	1.07	89.92	3.01	26.58	a
14-28 July	2.45	0.18	2.19	89.39	9.18	19.61	a
28 July - 11 Aug.	8.15	0.58	7.56	92.76	23.04	25.17	a
11-25 Aug.	19.05	1.36	17.89	93.91	55.76	24.39	a
25 Aug. - 8 Sept.	15.76	1.12	15.07	95.62	87.78	12.76	b
8-22 Sept.	15.32	1.09	14.58	95.17	117.54	9.27	b
22 Sept. - 6 Oct.	1.08	0.08	1.03	95.37	151.05	0.53	

DISCUSSION

Comparison of Nodulated and Non-nodulated Plants

Non-nodulated control plants up to the time of their death exhibited marked differences from nodulated plants in growth pattern and in dark respiration and apparent photosynthetic rates. The most noticeable difference in growth occurred in the relative proportion of dry matter devoted to root production (Table 2). Non-nodulated seedlings had much higher root weight ratios and lower leaf weight ratios than nodulated seedlings, and these differences became more noticeable as the season progressed. The striking differences in nitrogen content between nodulated and non-nodulated and the marked response of non-nodulated seedlings to nitrogen addition suggest that the growth pattern differences were a direct result of increasing nitrogen stress in the non-nodulated seedlings.

Many workers have shown that plants grown under conditions of nitrogen stress exhibit higher than normal root-shoot ratios (Bouma 1970 b; Davidson 1969; Wilkinson and Ohlrogge 1964). The mechanism for increased root production under nitrogen stress is not entirely clear, but Wilkinson and Ohlrogge (1964) have suggested that decreased nitrogen levels result in decreased 'growth hormone' concentration which, in turn, stimulates root growth and decreases shoot growth in intact plants. Davidson (1969) has suggested that a partitioning mechanism may occur in the plant which serves to maintain a quantitative

balance between leaf and root growth. He found that under unfavourable edaphic conditions, the weight of the root system relative to the foliage weight in Lolium and Trifolium spp. was greater than it was under more favourable edaphic conditions. This growth response may be similar to that of non-nodulated plants rooted in a medium of low nitrogen supply. Nodulated plants, on the other hand, could compensate for these reduced nitrogen levels in the root medium by providing their own nitrogen via nitrogen fixation. Bouma (1970 a) has also shown that a decline in nitrogen levels resulted in a marked reduction in leaf expansion in clover plants, and the reduced leaf growth would tend to increase the root:shoot ratio in plants growing under low nitrogen levels. A similar pattern of root:shoot ratios (Table 2) and growth of nodulated and non-nodulated alder seedlings (Fig.5) was found in this study.

The marked reduction in APS and dark respiration rates in non-nodulated plants as the season progressed also appears to be the result of nitrogen stress. Recent studies have shown that reduced nitrogen levels result in depressed rates of photosynthesis. The depressed rate has been correlated with reductions in leaf chlorophyll concentration and protein content, and with increased CO_2 diffusion resistances (Bouma 1970 a; Nevins and Loomis 1970; Ryle and Hesketh 1969). The effect of nitrogen supply on the APS rate in non-nodulated alder seedlings has been shown in Table 3, where the addition of nitrate nitrogen resulted in a five-fold increase in APS rate and a three-fold increase in dark respiration rate within three weeks. Similar responses

to nitrogen addition have been shown by other workers. In Beta vulgaris L., Nevins and Loomis (1970) reported a 40 percent reduction in APS rates when plants were grown for 14 days without nitrogen. Furthermore, they have shown that APS rates could be restored to normal levels within 4 days after the addition of nitrate nitrogen. Brix (1971) and Keay et al. (1968) have reported increased APS rates in Douglas-fir and Pinus pinaster respectively when the trees were fertilized with nitrogen. In Pinus pinaster, the increase in photosynthetic ability was associated with higher concentrations of nitrogen, phosphorus, chlorophylls "a" and "b" and moisture in the needles. Bouma (1970 a) similarly found that increased APS rates following nitrogen addition in clover plants were correlated with increased chlorophyll content of the leaves, although he found that during the early stages of recovery from a severe nitrogen stress, photosynthesis began to increase before the chlorophyll content of the leaves.

Although only a single plant was measured for the effect of nitrogen addition on APS rates in non-nodulated plants, it was apparent that the addition of nitrate nitrogen resulted in higher APS rates than for nodulated plants supplied with no combined nitrogen when measured at the same harvest date (Table 3). This may suggest, in part, that the full nitrogen requirements for plant growth in nodulated plants is not completely provided by the fixation of atmospheric nitrogen in root nodules (Bouma 1970 b; Stewart and Bond 1961).

Growth, CO_2 Exchange and Nitrogen-fixation Rates of Alder

The maximum relative growth rate (RGR_p) and net assimilation rate (NAR) found for alder occurred in late June (Fig.7) and fell within the ranges reported for broad-leafed woody plants (Jarvis and Jarvis 1964):

	Alder	Broad-leafed Woody Plants
RGR_p (mg g^{-1} $week^{-1}$)	556	53-822
NAR (g m^{-2} $week^{-1}$)	34	20-50

Light saturation level was high in alder, occurring between 3000-5000 ft-c throughout the growing season (Fig.8). A high light saturation level (5000 ft-c) was also reported by Littell (1972) and Krueger and Ruth (1969) for alder seedlings grown under full light conditions.

Maximum APS rates found for alder (Fig.8) compared favourably with maximum reported rates for temperate zone deciduous broad-leafed trees (10-20 mg CO_2 hr^{-1} dm^{-2}, Jarvis and Jarvis 1964), and were similar to rates reported for alder by other workers (Littell 1972; Krueger and Ruth 1969). At 3000 ft-c, alder seedlings grown in 40 percent shade had APS rates (mg CO_2 hr^{-1} dm^{-2}) of 17.14 on July 14 and 13.77 on 29 July (Table 4). Krueger and Ruth (1969) found APS rates of 12.46 at 2300 ft-c and 17.62 at 5100 ft-c between June 20 and August 9 for plants grown in 31 percent shade. Dark respiration rates (Table 4) were also similar to rates reported by other workers (Littell 1972; Krueger and

Ruth 1969; Grime 1965).

Nitrogen fixation rates of red alder compared favourably with those found by Stewart (1962) and Daly (1966) for A. glutinosa and A. rugosa, and followed a similar seasonal pattern. The maximum nitrogen fixation rates were 2.50 mg N per day in late August for A. glutinosa and 1.26 mg N per day in early August for A. rugosa. Nitrogen fixation rate for red alder reached a maximum of 1.36 mg N per day in mid-August.

Nodule efficiency (mg N fixed day^{-1} g^{-1} d. wt nodule) followed a similar seasonal pattern as that shown for A. glutinosa and A. rugosa, but was higher in red alder than for the other two species. In August when the nitrogen fixation rate was maximum, the nodule efficiences were 24.39 for A. rubra, 10.30 for A. glutinosa and 7.50 for A. rugosa.

Seasonal Growth and CO_2 Exchange Patterns in Alder

Many variations in growth and CO_2 exchange patterns may occur between different plant species (Kozlowski and Keller 1966; Kramer and Kozlowski 1960), and these are essentially determined by the interaction between 'intrinsic' (plant) and extrinsic (environment) factors influencing growth (Williams 1946). The increase in the proportion of total plant biomass devoted to leaves (LWR) and the increase in LAR early in the season for alder (Fig.6) appear to be characteristic of many temperate zone deciduous tree species. Many coniferous species, however, respond more slowly during the season (Newhouse and Madgwick

1968; Pollard and Wareing 1968; Sweet and Wareing 1968 a). The increase in root and stem weight ratios combined with a decrease in LWR found for alder near the end of the season (Fig.6) is common for many species (Littell 1972; Kramer and Kozlowski 1960). This pattern probably arises from proportionately higher root vs. leaf relative growth rates at the end of the season (Fig.7). Although a bimodal root growth pattern has been reported in conifers (Lister et al. 1967; Shiroya et al. 1966), there was no definite bimodal root growth pattern found for alder in this study (Fig.7).

During the growing season, the RGR_p pattern was closely paralleled by changes in the NAR and the LAR (Figs. 6 and 7). In each case, there was a marked reduction near the end of the season. Apart from seasonal environmental changes such as reduction in light intensity, day length and temperature, the reduction in RGR_p and NAR during the latter half of the season in alder probably resulted from a combination of factors including (a) a decline in leaf weight ratio, and hence, a reduction in the proportion of photosynthesizing to respiring tissue with increasing plant size (Fig.6), (b) a reduction in apparent photosynthetic rate with increasing plant age (Fig.9), and (c) increased mutual shading of foliage, and hence, a reduction in the photosynthetic component of the NAR (Blackman 1968) with increasing plant size (Eagles 1971; 1969; Rutter 1957; Williams 1946). At the end of the growing season, the sharp reduction in APS combined with an increase in dark RS per plant (Fig.9) probably accounted for the reduction in NAR (Fig.7). As the RGR_p is the product of the NAR and LAR (Blackman 1968), the reduction

in RGR_p from mid-August to the end of the season resulted from a corresponding reduction in both the NAR and the LAR. Changes in RGR_p during the season, however, were more closely paralleled by changes in NAR than LAR (Figs 6 and 7).

The NAR pattern for alder during the growing season was closely associated with changes in the photosynthetic rate (dm^{-2}) (Fig.9). A similar APS and dark RS pattern for red alder has been reported by Littell (1972). The general decline in APS (dm^{-2}) as the season progressed may have resulted from (1) increased mutual shading of foliage during the CO_2 exchange measurements, arising from increased plant size and/or (2) aging processes within the leaves (Larson and Gordon 1969; Wilson and Cooper 1969a; Jewiss and Woledge 1967). Throughout most of the season, it was not possible to distinguish between the two above factors. It seems likely, however, that when leaves were approaching senescence in late-season, the reduction in APS rate was a result of aging processes within the leaves because the leaf area decreased (Table 4). A decrease in leaf area would, in turn, reduce the level of mutual shading of foliage during the APS measurements. Hardwick et al. (1968) reported a similar late season decline in APS rate at the time of leaf senescence, and this was associated with decreasing RNA and protein content of the leaves, and with no difference in chlorophyll content. For alder, nitrogen data show that when leaf growth was minimal (Fig.7) and when the APS and dark RS rates were decreasing near the end of the season (Fig.9),

there was a significant decrease in leaf nitrogen concentration (Fig.10) The reduction in APS rate in late season was also associated with a sharp reduction in specific leaf area, and hence, increased thickening of the leaves (Fig.6).

The high photochemical capacity of alder combined with its higher APS rates (dm^{-2}) early in the season (Fig.8) suggests that alder may be more shade tolerant in early season than in late season. The most important determinant of success or failure in woodland shade, however, may be the respiration rate (Loach 1967). In June, the dark respiration rate of alder was almost 5 times higher than at the end of the season, and this was associated with a high RS:APS 3000 ft-c ratio (Table 4). As a result, the apparent inability of alder to establish itself under shaded conditions may arise at the critical seedling stage at the beginning of the growing season.

Relationship between Photosynthesis and Nitrogen Fixation in Alder

Early studies using leguminous nodule-bearing plants have demonstrated a close dependence of nitrogen fixation in root nodules on a source of substrates provided by the photosynthesizing plant (Virtanen et al. 1955; Lindstrom et al. 1952). More recent studies using radioisotopes and the acetylene reduction technique have shown that nitrogen fixation in root nodules may be more closely related to the influx of immediate products of photosynthesis rather than reserve substrates found in the nodules and the plant. Wheeler (1971; 1969) reported that products of photosynthesis in A. glutinosa reach the nodules only

10 minutes after their original production in the leaves and that maximal rates of fixation are only attained when new photosynthates enter the nodules in quantity. Others have also found a rapid accumulation of ^{14}C-labelled products of photosynthesis in the nodules (Small and Leonard 1969; Pate 1966). These results suggest that there is a close balance between the nodules and the leaves in the form of a daily exchange of metabolites (Pate et al. 1965; Pate and Grieg 1964; Pate 1958; Bond 1956).

For red alder, the seasonal patterns of nitrogen fixation and apparent photosynthetic rates per plant were coincident (Fig.11), which suggests a similar relationship as that described above, between APS and nitrogen fixation. It is important to note, however, that APS rates are spot measurements from a single harvest date while nitrogen fixation rates are calculated from data of successive harvests. When the net change in APS rate per plant is calculated between successive harvests, the greatest net increase in APS rate per plant is associated with the maximum nitrogen fixation rate in mid-August (Table 7).

A close relationship between the nodules and the leaves of red alder is also suggested when comparing nodule efficiency and APS rate per unit leaf area patterns throughout the season (Fig.11). Both followed similar seasonal patterns with maximum values for each occurring early in the season when nodules were young and active and when new leaves were rapidly expanding. The reduction in nodule efficiency as the season progressed was likely the result of an increasing proportion of xylem and cork tissue within the nodule

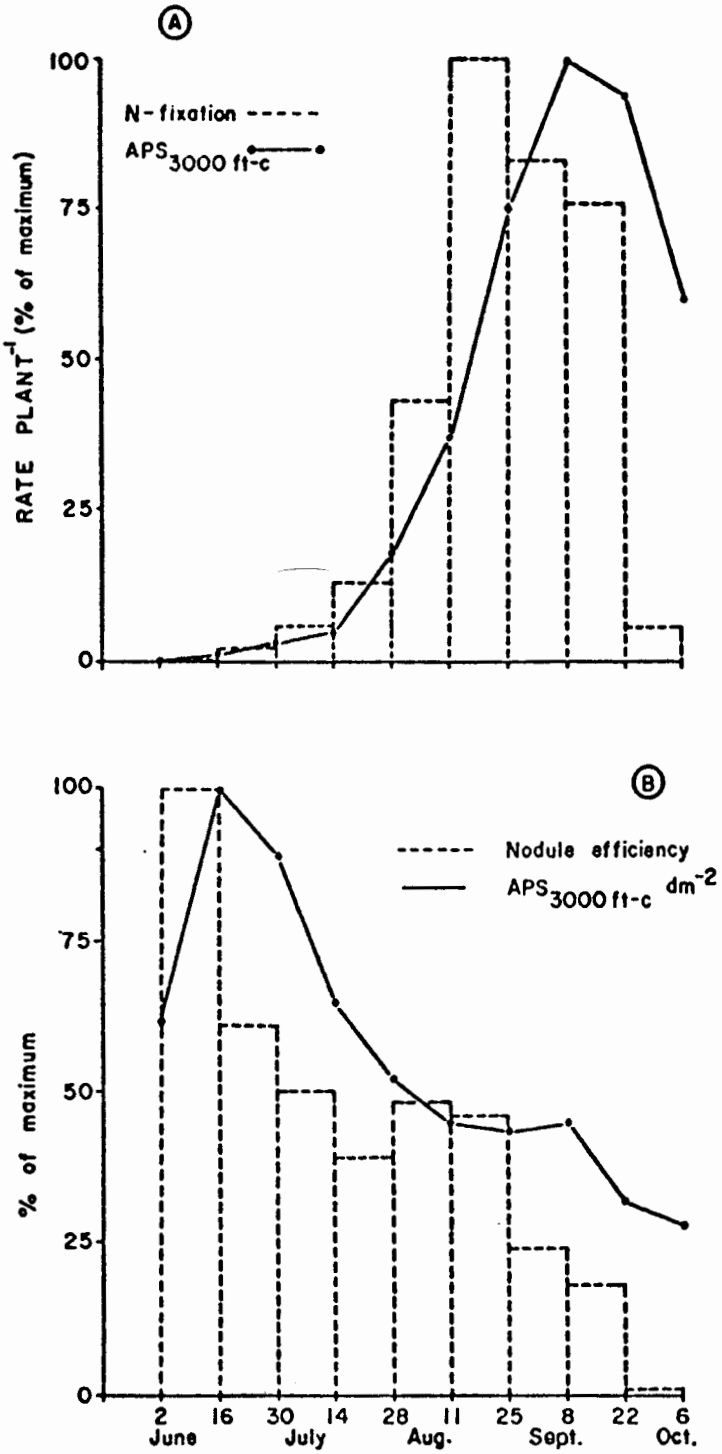


Figure 11. Seasonal patterns of (a) nitrogen fixation and APS rates per plant and (b) nodule efficiency and APS rates per unit leaf area of nodulated plants expressed as a percent of maximum. Data are recalculated from Tables 4 and 6.

Table 7. Comparison of nitrogen fixation rate and mean net change in APS rate per plant between successive harvests. Data for APS rates are calculated from Table 4.

	HARVEST PERIOD								
	2-16 June	16-30 June	30 June 14 July	14-28 July	28 July 11 Aug.	11-25 Aug.	25 Aug. 8 Sept.	8-22 Sept.	22 Sept. 6 Oct.
Mean N fixed plant^{-1} day^{-1} [mg]	0.01	0.02	0.08	.17	.58	1.36	1.12	1.10	0.08
Mean net increase in APS rate plant^{-1} [mg CO_2] hr^{-1}	0.26	0.42	0.54	3.74	5.26	10.22	7.37	-2.00	-9.07

which did not contribute to the fixation process (Stewart 1962). Factors such as leaf aging and subsequent changes in leaf composition may give rise to the decrease in APS rate per unit leaf area throughout the season. Different but related processes therefore may give rise to the close association between nodule efficiency and 'leaf efficiency'.

Pate and coworkers (1966; 1965; 1964) and Bond (1956) have shown that nitrogen fixed in the nodule is transferred rapidly via the transpiration stream and that nitrogen products are re-translocated from the leaves to the rest of the plant. The pattern of increasing nitrogen concentrations in the root and stem and the decreasing nitrogen concentrations in the nodules and the leaves near the end of the season (Fig.10) probably reflects the pattern of nitrogen and photosynthate re-distribution in the plant and also lends support to the close balance existing between nodules and leaves. Furthermore, if the rate of nitrogen fixation is directly related to influx of immediate products of photosynthesis to the nodule (Wheeler 1971), then the marked reduction in nitrogen fixation at the end of the season may have been a result of translocation of photosynthates to other regions of the plant. These regions may have been the stem and roots which were actively growing rather than to the nodules.

The pattern of decreasing leaf nitrogen concentrations combined with increases in stem and root nitrogen concentration near the end of the season (Fig.10) may be an adaptive response of the plant to

conserve nitrogen which would otherwise be lost at the time of leaf fall. An autumn movement of nitrogen from the leaves to the stem and eventually to the roots (Hardwick et al.1969; Tamm 1951) may be a result of senescent leaves being no longer able to retain substances against competition from other regions of the plant which are more active physiologically (Kramer and Kozlowski 1960).

SUMMARY

1) Seasonal patterns of growth, apparent photosynthesis (APS) dark respiration (RS), nitrogen fixation and nodule efficiency were followed concurrently in first-year seedlings of nodulated red alder (Alnus rubra Bong.) grown in vermiculite supplied with Crone's nitrogen-free nutrient solution. Nitrogen fixation was determined in nodulated plants by measuring the net gain in total plant nitrogen between successive harvests.

2) Significant growth differences occurred in alder throughout the growing season. The leaf weight ratio (LWR), leaf area ratio (LAR) and specific leaf area (SLA) had highest values in late June and then decreased slowly as the season progressed. Root weight ratio (RWR) had a bimodal pattern during the season, with a depression in early August resulting from a reduction in root relative growth rate (RGR_R) combined with an increase in leaf relative growth rate (RGR_L). Stem and root weight ratios increased near the end of the season and coincided with increasing nitrogen concentrations in the root and stem and with decreasing nitrogen concentrations in the nodules and leaves.

3) The plant relative growth rate (RGR_P) increased early in the season to a maximum in late June - early July and showed a marked decrease near the end of the season. This decrease in RGR_P was closely paralleled with changes in LAR and net assimilation rate (NAR). During the season, differences in RGR_P were more closely associated

with changes in NAR than LAR.

4) The highest rate of nitrogen fixation occurred in late August (1.36 mg N fixed $plant^{-1}$ day^{-1}) when the APS rate per plant was maximum. Following this peak, the nitrogen fixation rate decreased sharply near the end of the season. Nodule efficiency and APS rates per unit leaf area also followed similar seasonal patterns, with the highest values occurring in June and the lowest in October. Similar seasonal nitrogen fixation and APS patterns suggested a close relationship between nodules and leaves throughout the growing season.

5) Light saturation level for photosynthesis in nodulated plants did not change significantly throughout the season and averaged between 3000 - 5000 ft-c. The photochemical capacity of these seedlings was highest in June and then decreased as the season progressed.

6) Non-nodulated plants had higher root/shoot ratios and lower light saturation levels, dark respiration rates and APS rates than nodulated plants and this was attributed to nitrogen deficiency. When nitrate nitrogen was added to the non-nodulated seedlings, there was a five-fold increase in APS rate at 3000 ft-c, and a three-fold increase in dark respiration rates within three weeks of the addition.

PART II

INTERACTIONS OF RED ALDER AND DOUGLAS FIR SEEDLINGS GROWN AT DIFFERENT DENSITIES

INTRODUCTION

The ability of a plant to grow and survive in shade depends on its capacity to maintain a net increase in carbon ie. where the gain from photosynthetic products is greater than the respiration losses. Plants that can establish and maintain themselves under shaded conditions are termed "shade tolerant" (Baker 1945).

Recent studies of shade tolerance in herbaceous and forest tree species have suggested 1) that shade plants may depend on conservation of assimilated energy rather than the efficiency of its capture, and 2) that there is no clear-cut distinction between shade tolerant and intolerant species on the basis of the relative size or efficiency of their photosythetic systems in low light (Loach 1970, 1967; Logan 1970; Krueger and Ruth 1969; Grime 1965; Bourdeau and Laverick 1958; Bohning and Burnside 1956; Baker 1945).

Under shaded conditions, many plants exhibit 'plastic' modifications usually in the form of changes in the proportion of dry matter devoted

to root, stem and leaf production (Blackman 1968; Jarvis 1964). Most studies of shade tolerance and plant productivity in response to shading effects have been concerned largely with morphological and anatomical differences associated with the photosynthetic tissue. Under shaded conditions these include increased leaf area, reduced leaf thickness, increased chlorophyll content and laminae inclined at right angles to the light source (Littell 1972; Loach 1970; Logan 1970; Holmgren 1968; Grime 1965; Bjorkman and Holmgren 1963; Blackman and Black 1959; Wassink et al. 1956; Blackman and Wilson 1951; Shirley 1945; 1929).

Growth analysis has been a common technique used for assessing the overall influence of environment (mainly light intensity) on plant growth. Here the effect of environment on the relative growth rate (RGR) of a plant is partitioned into effects on the production of leaf area (leaf area ratio=LAR) and on dry matter production per unit leaf area (net assimilation rate=NAR). Early studies using this technique have shown that differences in productivity of annual plant species of agricultural importance are related more to differences in rates of leaf production than to differences in net assimilation rates (Watson 1958; 1952; Heath and Gregory 1938). However, there is increasing evidence that the net assimilation rate may be an equally important factor determining differences in productivity in many herbaceous species (Eagles 1971; 1967; Wilson and Cooper 1969 b) and in forest tree species (Loach 1970; Sweet and Wareing 1968 a; 1968 b; Rutter 1957).

One would expect plastic responses at both morphological and physiological levels to be more pronounced under conditions of increasing

density stress, where both root and shoot competition are active in controlling the growth (productivity) and survival of the plant. Most competition studies, however, have been done using herbaceous species (Blackman 1968; Gasser 1968; Harper 1967; 1961; Stern 1965) while forest tree species have been almost ignored (Van den Driessche 1971). For herbaceous species, density effects on plant growth have included reduced plant growth and changes in the distribution of dry matter devoted to leaf, stem, roots and reproductive organs (Harper 1967; 1964).

The objectives of this study were to examine morphological and physiological modifications of two local forest tree species, Douglas-fir and red alder, in response to increasing density stress. Douglas-fir was utilized in the study as it is a commercially important coniferous species and is a main competitor of red alder in the Pacific Northwest. Douglas-fir is also recognised as a species intermediate in shade tolerance (Baker 1950). Alder, on the other hand, is a representative example of a deciduous forest tree species and is known to exhibit photosynthetic and respiration rates characteristic of shade intolerant species (Krueger and Ruth 1969).

Second-year seedlings of each species were grown in pure and mixed cultures at four densities (2, 4, 8 and 16 plants dm^{-2}) in a perlite-vermiculite medium supplied with Crone's nutrient solution (Bond 1951) and an added nitrogen supplement. Seedlings were harvested at 38 day intervals throughout the growing season. The approach used was to combine growth analysis techniques with measurements of carbon-dioxide exchange (apparent photosynthesis and dark respiration).

METHODS

Plant Material and Establishment

Second-year red alder seedlings fully nodulated and at the two-leaf stage were collected locally in early June from an exposed habitat on Burnaby Mountain, British Columbia (elevation, 350 m). One-year old Douglas-fir seedlings were obtained from the British Columbia Forest Service "Green Timbers" nursery (seed source:Chilliwack river valley, 350 m elevation). For each species, approximately 560 seedlings of similar size were selected. Roots were washed to remove excess soil, and the seedlings transplanted into half-gallon milk cartons (wlh = 10 x 10 x 30 cm) containing a 75:25 vermiculite:perlite mixture to ensure a standard homogeneous root medium for growth.

The experimental design for the study is shown in Table 8. Seedlings were spaced in each container at four densities (2, 4, 8 and 16 plants dm^{-2}) in pure and mixed cultures (Figs. 12 and 13). Three harvests were made at 38-day intervals during the growing season, commencing on July 23 and ending on October 8. At each harvest date, 4 replicates of each density:treatment interaction were chosen for analysis. To provide an initial base level (t_o) for the growth analysis, 15 seedlings of each species were harvested on June 15, ten days after transplanting.

Table 8. Experimental design for the competition study.

Treatment	Density (No. plants dm^{-2})	No. of harvests	No. of replicates per density at each harvest	Total No. of replicates during season for each density
Alder-pure	2 4 8 16	3	4	12
*Alder-fir mixed	2 4 8 16	3	4	12
Fir-pure	2 4 8 16	3	4	12

*In mixed treatments the crop density of each species is 1, 2, 4 and 8 plants dm^{-2}.

Seedlings were arranged in the field under a shelter of fibreglass screening (mesh size 2 mm) and clear plastic (0.6 mm) which prevented rain from reaching the seedlings. Seedlings at the same density were grouped together beneath the shelter so that uniform light relations within each density could be approximated. To avoid possible 'edge effects', containers were rotated 90-180° at two-week intervals throughout the growing season. Light intensity below the shelter was reduced approximately 40 percent on both clear and cloudy days as measured with a Brockway Sekonic Studio exposure meter. Daily temperature patterns during the growing season were obtained from the nearby Burnaby Mountain weather station (Fig.14).

Every two to three days throughout the growing season, plants were watered with 500 mls. of tap water per pot. Following each harvest date,

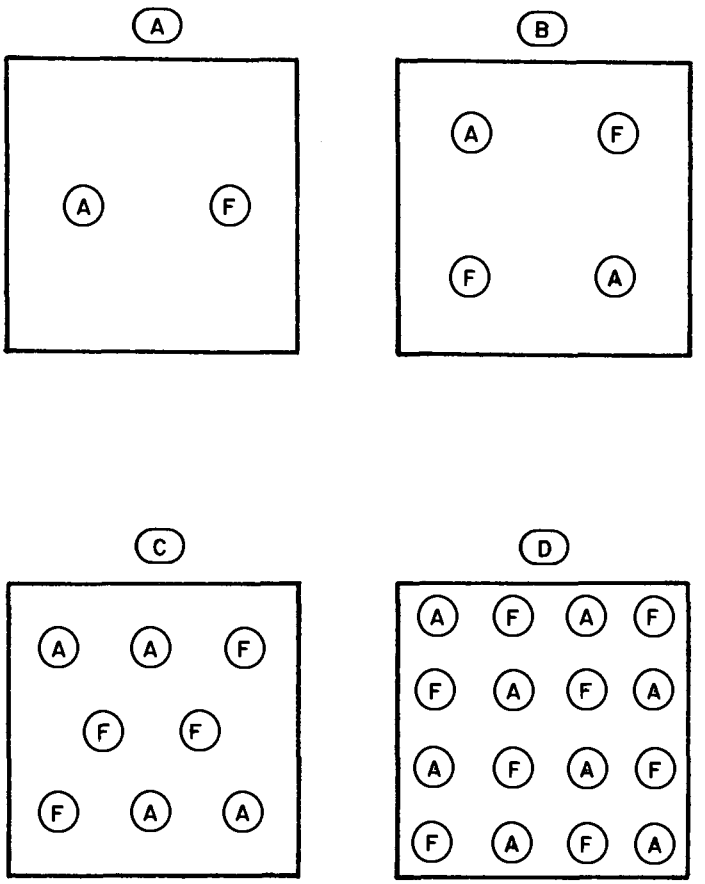


Figure 12. Spacing of seedlings in containers: (A) density 2 (B) density 4 (C) density 8 and (D) density 16. (A) represents a single alder seedling and (F), a single Douglas-fir seedling. Above diagrams are for mixed treatments. Pure treatments have the same spacing.

Figure 13. Spacing of alder and Douglas-fir seedlings at four densities (2, 4, 8 and 16 plants dm^{-2}) in A-pure (above), AF mixed (middle) and F-pure (lower) treatments on September 1.

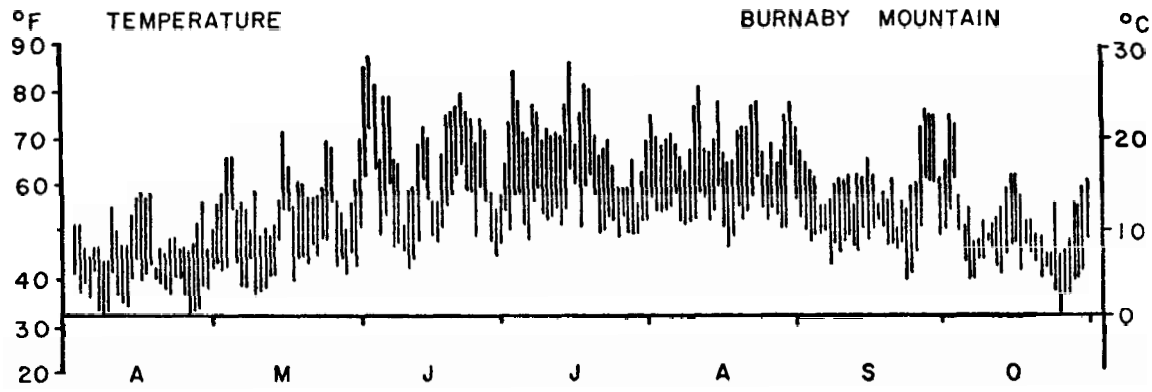


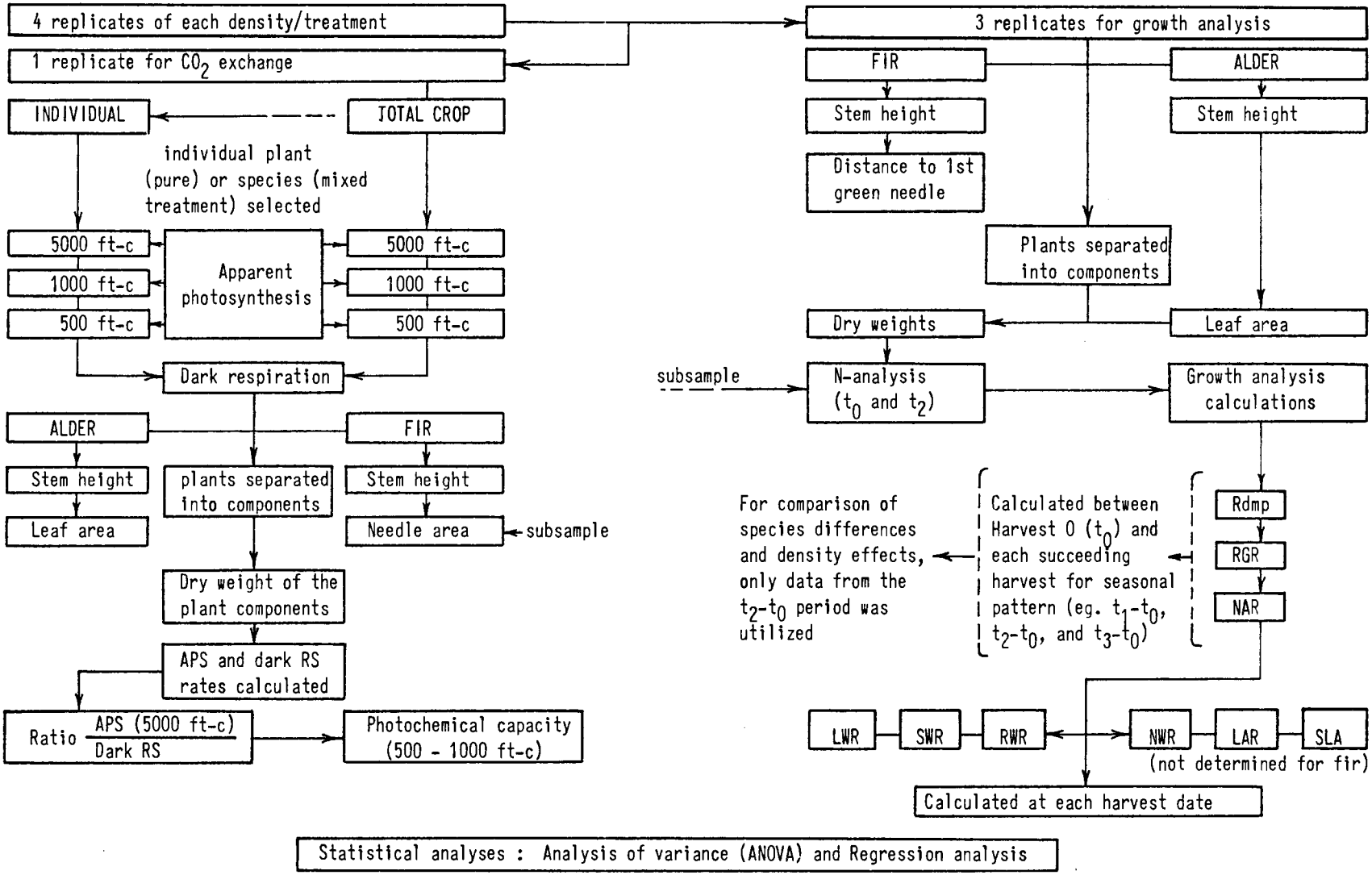
Figure 14. Daily temperature pattern on Burnaby Mountain (elev. 350 m) during the 1970 growing season (Canada Dept. Transport, Meteorological Branch. 1970).

the remaining experimental seedlings were supplied with 500 mls. of Crone's nitrogen-free nutrient solution per pot. To provide the plants with a full complement of nutrients, KCl was replaced with an equal weight of KNO_3 per litre of distilled water in the original nutrient solution, and a micro-nutrient supplement was also added (see Part I, Table 1, p. 6). Excess nutrient solution drained freely through holes provided in the bottom of the pots.

Measurements

At each harvest, the growth and CO_2 exchange measurement sequence for each species is shown in the following flow chart:

MEASUREMENT SEQUENCE FOR HARVESTS T_1, T_2 AND T_3



Statistical analyses : Analysis of variance (ANOVA) and Regression analysis

Growth characteristics, biomass and total nitrogen content

Stem height for each species was measured from the stem-root junction to the top of the dominant leading shoot. Distance between the stem-root junction and the first 'green' needle in fir was also measured, and used as an approximate measure of self-thinning of needles over the density range. Nodules of red alder were removed under a dissecting microscope.

Leaf areas for alder were determined by tracing leaf outlines onto mm. graph paper and counting squares. As determination of conifer needle area is difficult (Barker 1968), needle area was only estimated for those seedlings used in CO_2 exchange measurements. A random sample of 30 needles was taken from approximately one-half the number of seedlings at each density. Needle area of the sample was determined by placing needles on clear mm. graph paper and counting squares. From the area and dry weight of the needle sample, the total needle area of the plant was estimated as follows:

$$\text{Total needle area of plant} = \frac{\text{Needle Area (sample)} \times \text{Needle D. wt. (plant)}}{\text{Needle D. wt. (sample)}}$$

All plant components were dried at 85°C for at least 24 hours and weighed. For harvests t_o (June 15) and t_2 (September 1), total nitrogen content was determined for each species on pooled samples of each plant component (leaves, stem, root and nodules) at each density using a Perkin Elmer Model 240 elemental analyzer. Each component was ground to a powder and nitrogen content determined from a sub-sample. The total

plant nitrogen content was estimated in a manner similar to that shown above for needle area.

Growth analysis

At each harvest date, three replicates from each density:treatment interaction were selected for growth analysis (Table 8). The final replicate was used for CO_2 gas exchange measurements, and was not included in the growth analysis owing to the length of time taken to complete the CO_2 exchange measurements. The CO_2 measurements (24 separate measurements at each harvest date) took approximately 15-20 days to complete and hence, the final CO_2 exchange measurements approached the next harvest date. To reduce the source of error in the growth analysis arising from possible differences in plant growth during the time taken for the CO_2 exchange measurements, only the 3 replicates harvested immediately on the harvest date were used in the growth analysis.

Harvest 2 (September 1) was chosen for comparison of density effects and species differences on growth analysis parameters. Calculations of rate of dry matter production (Rdmp), plant relative growth rate (RGR_P), leaf relative growth rate (RGR_L) and net assimilation rate (NAR) were made between t_o (June 15) and t_2 (September 1) for the major analysis of density effects and species differences. Seasonal patterns, however, were determined using selected growth analysis parameters calculated between t_o (June 15) and the three successive harvests (t_1, t_2 and t_3) where important trends existed.

The rate of dry matter production (Rdmp) and the plant relative growth rate (RGR_p) were calculated using the following standard formulae (Blackman 1968).

$$(1) \quad Rdmp = \frac{W_1 - W_o}{t_1 - t_o}$$

$$(2) \quad RGR_p = \frac{\log_e W_1 - \log_e W_o}{t_1 - t_o}$$

where W_o and W_1 are mean total plant dry weights between two harvest times, t_o and t_1. The leaf relative growth rate was calculated in a similar manner as:

$$(3) \quad RGR_L = \frac{\log_e L_1 - \log_e L_o}{t_1 - t_o}$$

where L_o and L_1 are mean leaf dry weights per plant between two harvest times, t_o and t_1.

For determination of net assimilation rate (NAR), leaf dry weight was used as a measure of "assimilation material" rather than leaf area, using the following formula (Kvet et al. 1972; Sweet and Wareing 1968 a; Rutter 1957):

$$(4) \quad NAR = \frac{(W_1 - W_o)}{L_1 - L_o} \cdot \frac{(\log_e L_1 - \log_e L_o)}{t_1 - t_o}$$

where W_o and W_1 are mean total plant dry weights, and L_o and L_1 are mean total leaf dry weights per plant between two harvest times, t_o and t_1.

The distribution of dry matter between plant components (leaf, stem, root and nodule) was determined at each harvest date by calculating the ratio of the weight of each component to the total plant weight, thus giving the leaf weight ratio (LWR), stem weight ratio (SWR), root weight ratio (RWR) and nodule weight ratio (NWR).

The ratio of leaf area:plant dry weight (leaf area ratio, LAR) and the ratio of leaf area:leaf weight (specific leaf area, SLA) were calculated at each harvest date for individuals of alder from the alder treatments.

Carbon-dioxide exchange

Carbon-dioxide exchange was measured with a Uras II infra-red gas analyzer (0-600 ppm v/v range) in a closed system as described in Part I (p.8). Volume of the measuring system excluding the plant chamber was approximately 530 ml. Two chamber sizes were used: 868 and 5620 mls. Each chamber consisted of a brass cylinder fitted with a clear 3 mm thick plexiglass plate at one end (Part I; p.10). For the large chamber (5620 ml), a fan was built into the side of the chamber, and used for mixing the air inside the chamber for crop CO_2 exchange measurements. The speed of the fan was controlled outside the chamber with a magnetic stirrer.

To measure the CO_2 exchange rate of the total above ground crop per container, in a closed system, plant stems in the container were placed in slotted holes of a plexiglass base plate and sealed with Apiezon Q. The brass cylinder (plant chamber) was then sealed onto the base plate.

To obtain a measure of the effect of density on individual plant performance in pure treatments, a representative individual from each crop was selected for further analysis of CO_2 exchange immediately following the crop measurement. All plants but the selected individual were cut away at the stem near the base, the shoots were removed and the cut ends sealed in Apiezon Q to eliminate possible effects on the carbon-dioxide exchange measurements of the remaining individual. For mixed treatments (alder-fir), the fir component of the mixture was removed after measurement of the total crop and CO_2 exchange measured for the remaining alder seedlings. No CO_2 exchange measurements were made on single seedlings from mixed treatments except at density 2. It was possible, therefore, to compare CO_2 exchange rates for 'alder grown with fir' and for 'alder grown with itself'. For example, CO_2 exchange measurements for alder grown in pure treatment at density 4 (4 seedlings) could be compared with the CO_2 measurements of alder grown in mixed treatments at density 4 (2 seedlings), or with the CO_2 measurements of alder grown in mixed treatments at density 8 (4 alder seedlings).

By subtracting the rate of CO_2 exchange for the remaining alder from the rate for the total above ground crop in mixed treatments, it was possible to estimate a theoretical CO_2 exchange rate for the fir as follows:

$$\text{mg } CO_2 \text{ exchange } hr^{-1} \text{ (fir)} = \text{mg } CO_2 \text{ exchange } hr^{-1} \text{ (alder-fir)} - \text{mg } CO_2 \text{ exchange } hr^{-1} \text{ (alder)}.$$

The APS rate of fir seedlings calculated in this manner is only a crude

estimate because differences in mutual shading of foliage (and hence reduction in available light levels) during the APS measurements are not accounted for.

For the APS measurements, plants received light from two 500 watt Dicrolite quartz-iodine lamps (color temp. 3300° K) positioned above the plant chamber. Light intensity was varied by changing the distance between the light source and the plant chamber, and measured at the chamber top with a Brockway Sekonic Studio exposure meter. For the low light intensity (500 ft-c) pieces of neutral grey fibreglass screening were placed over the chamber. Spectral intensity (μ watts cm^{-2} 400-750 mm) for each light intensity was recorded with an Isco Model SRR spectroradiometer (Part I; Fig. 4, p.11). The fibreglass screening did not appear to alter the spectral distribution of energy (400-750 mm).

Air temperature in the plant chamber was measured with a shielded 24-gauge copper-constantan thermocouple held just underneath a leaf. Temperature within the plant chamber was maintained at $20^{\circ} \pm 1^{\circ}C$ with a Lauda K-2/R temperature controlled water bath which forced cool water through copper tubing coiled around the chamber. To reduce the infra-red component for additional temperature control, a water bath 5 cm deep was positioned between the plant chamber and the light source.

Measurement of apparent photosynthesis (APS) was made at three light intensities: 5000, 1000 and 500 ft-c in descending order. Approximately twenty minutes was allowed at each light intensity change for plant stabilization before a new sequence of measurements was commenced. Three separate APS 'runs' were made at each light intensity within an ambient

$[CO_2]$ of 375 to 225 ppm v/v. Dark respiration was measured at the end of the day when photosynthetic measurements were completed. Following the CO_2 exchange measurements, the leaf area was determined and the plant(s) harvested.

The infra-red gas analyzer was calibrated at the start and end of each day's measurements. The computer program of Bulley (1969) was used for determination of APS and dark RS rates from the curves of $[CO_2]$ versus time recorded as described in Part I (p.13).

RESULTS

Growth, Biomass and Nitrogen Content

Physical characteristics

The most pronounced density effect on growth occurred in alder seedlings from the mixed treatment, where leaves were generally thinner, smoother and more irregular-shaped and stems thinner at densities 8 and 16 than at the lower densities. In alder seedlings from the pure treatment, no major visual differences in leaves or stems occurred with increasing density stress (Figs. 13 and 15).

Fir seedlings at the lower densities in both pure and mixed treatments had thick stems and larger, more branched root systems whereas seedlings grown at the higher densities had less dense foliage and showed greater self thinning of needles (Figs. 15 and 16). Distance from the stem-root junction to the first green needle (self thinning), however, was not significantly different between densities in each treatment, but fir seedlings had greater self-thinning of needles in F-pure than in AF-mixed treatment (Table 9).

Stem height did not differ significantly ($P>0.05$) with density and between treatments in both alder and fir seedlings (Table 9).

Poorest growth and greatest mortality occurred in alder seedlings grown with fir at the higher densities (Table 9). This high alder mortality may have resulted from extreme shading effects of the fir

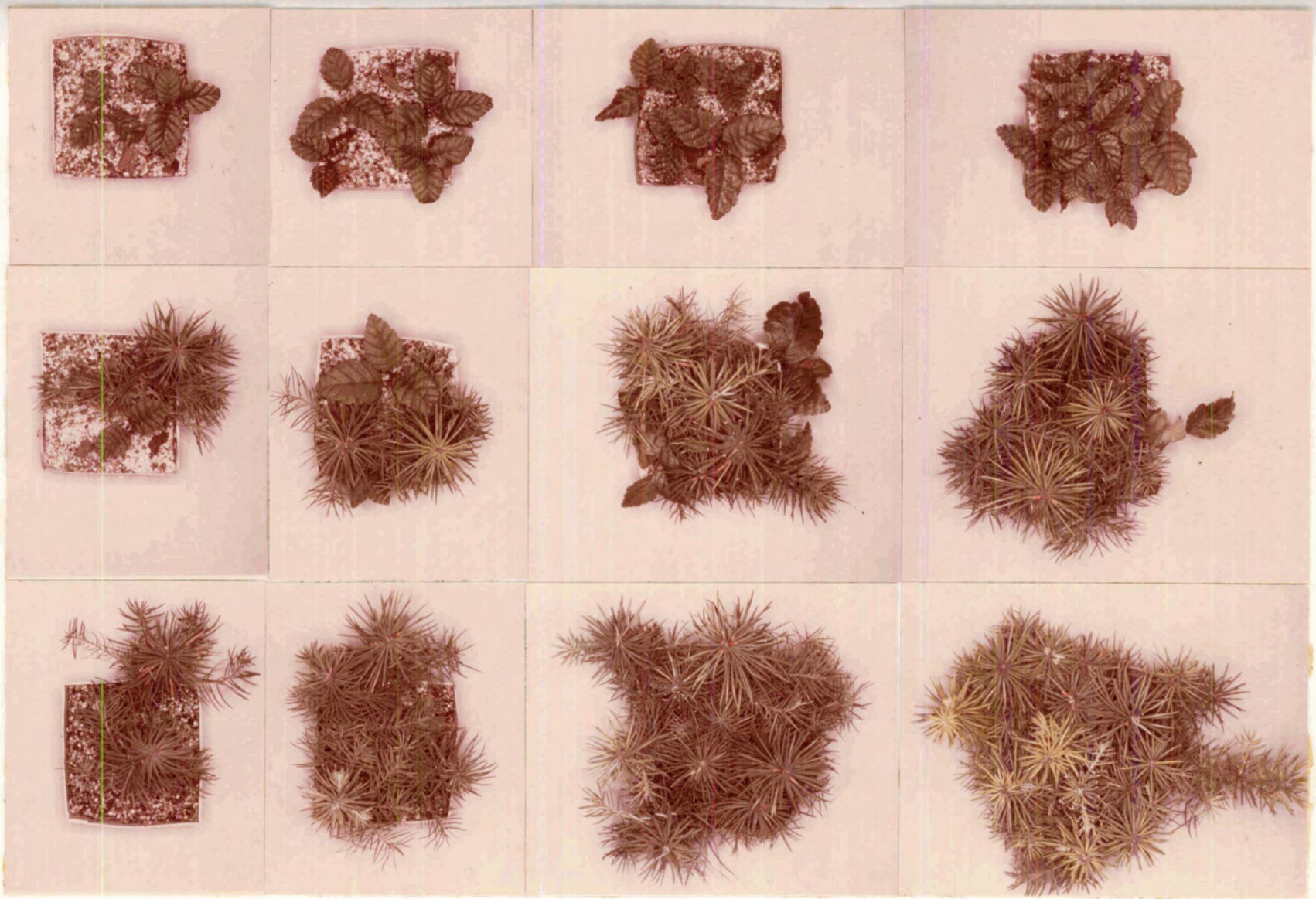


Figure 15. Above total crop biomass of seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure (top), AF-mixed (middle) and F-pure (lower) treatments, September 1, 1970.

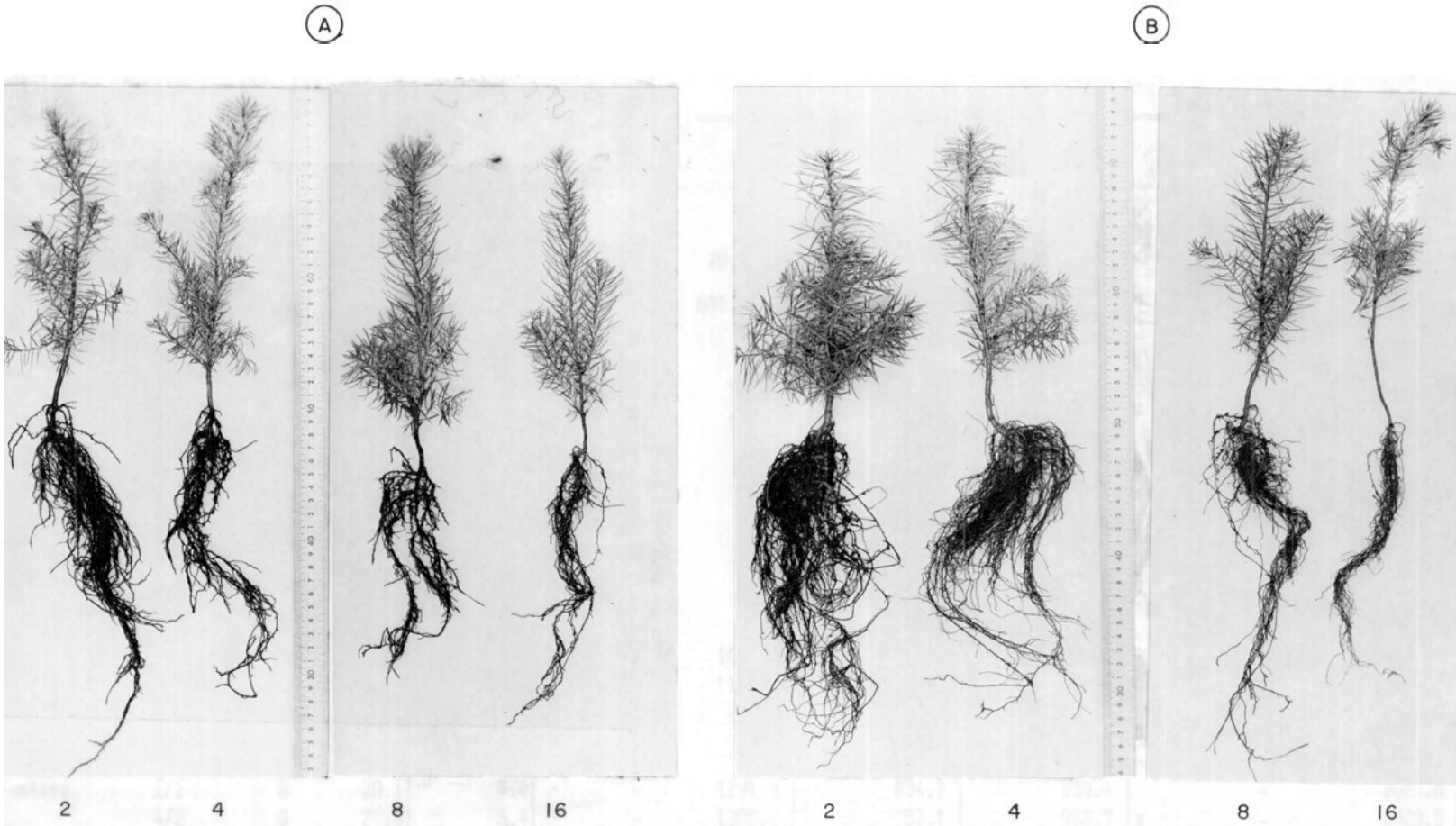


Figure 16. Comparison of fir seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2} in (a) F-pure and (b) AF-mixed treatments on September 1.

Table 9. Dry weight and growth measurements for the mean seedling grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure, AF-mixed and F-pure treatments. Each value is a mean of 3 replicates at Harvest 2 (t_2 = 1 September); individual values are given in Appendix II, Table 1. Means connected by the same vertical bar and letter within each treatment are not significantly different ($P > 0.05$). Values and standard errors given for alder and fir seedlings at the base harvest (t_0 = 15 June) are means of 15 seedlings.

*Treatment	Density (plants dm^{-2})	**Mortality	Stem height (cm)	Distance to first green needle (cm)	Leaf area (mm^2)	Dry weight (mg)				
						Leaf	Stem	Root	Nodule	Plant
Base harvest										
Alder	-	-	5.6	-	-	20.5 ± 1.7	13.7 ± 0.9	8.7 ± 0.8	1.25 ± 0.20	44.2 ± 3.0
Fir	-	-	17.4	3.4	-	601.8 ±49.0	267.4 ±20.5	195.5 ±14.7	-	1065 ± 76
Harvest 2										
A-pure	2	0	8.7 a	-	3796 a	169.99 a	68.83 a	56.53 a	6.30 a	301.65 a
	4	0	8.0 a	-	2817 a	138.96 a	57.06 a	60.37 a	5.31 a	261.71 a
	8	0	7.6 a	-	1609 b	74.78 b	40.29 b	30.18 b	3.45 b	148.71
	16	0	7.7 a	-	1443 b	61.06 b	36.10 b	26.46 b	4.08 b	127.70
" A-mixed	2/1	0	5.2	-	535 a	36.89	27.23	43.89	2.46 b	110.47
	4/2	0	7.5 a	-	1271	52.01 a	37.10 a	32.72 a	3.24 a	125.07 a
	8/4	3	8.1 a	-	1621	47.57 a	40.92 a	28.82 a	3.64	120.97
	16/8	6	7.6	-	515 a	15.38	18.51	10.22	2.28 b	46.39
F-pure	2	0	18.8 a	3.8 a	-	1072.0 a	733.7	1173.9	-	2979.6 a
	4	0	21.1 a	3.8 a	-	1125.4 a	826.0	966.2	-	2917.7 a
	8	1	21.0 a	3.9 a	-	860.0 b	587.7 a	588.3 a	-	2034.0 b
	16	1	21.9 a	4.8 a	-	707.0 b	523.1 a	488.5 a	-	1718.6 b
F-mixed	2/1	0	20.1 a	3.3 a	-	1291.9 a	834.3 a	959.4 a	-	3085.6 a
	4/2	0	21.6 a	3.4 a	-	1308.1 a	757.1 a	963.7 a	-	3028.9 a
	8/4	0	20.8 a	3.2 a	-	1159.4 b	676.7 a	779.2 a	-	2615.2 a
	16/8	0	21.8 a	4.4 a	-	770.4 b	589.3 a	509.6 a	-	1869.3 a

* A-pure and F-pure refer to alder and fir seedlings grown in pure treatments; A-mixed and F-mixed refer to alder and fir seedlings from the mixed treatment (AF-mixed).

** Mortality refers to the total number of seedlings dead in all replicates and is not a mean.

" For the mixed treatments, 2/ indicates total crop density, and /1 indicates species density in the crop from the AF-mixed treatment.

Note: Statistical comparisons of differences in growth of each species between treatments are summarized in Table 20, p. 113.

seedlings at the beginning of the experiment as the alder seedlings were much smaller in size than the fir at transplanting. Mortality was also greater in fir seedlings grown in pure vs mixed treatments at the higher densities (Table 9).

Density effects on seedling biomass

Differences in growth of the seedlings with density and treatment were further reflected in the dry weights of seedlings and their components (Table 9). The most noticeable effect of density was to reduce the mean seedling biomass at the higher densities, although fir seedlings from the mixed treatment showed no significant difference in biomass with density. Alder seedlings usually showed the greatest reduction in biomass at the higher densities, especially in the mixed treatment, where there was almost a three-fold reduction from density 8 to 16 (Table 9).

Density effects on biomass of the plant components (leaf, stem, root and nodule) were similar, in most cases, to trends shown for total seedling biomass in each treatment (Table 9). Seedlings from each treatment usually had lower leaf, stem and root biomass at densities 8 and 16 than at the lower densities. At the higher densities, nodule biomass was also reduced in alder seedlings from each treatment.

Significantly higher ($P<0.001$) plant, leaf, stem, root and nodule biomass occurred in alder seedlings from the pure versus mixed treatment. Although there were no significant differences in mean seedling biomass and in stem and root biomass of fir seedlings between

treatments, leaf dry weights were higher (P 0.001) in fir seedlings from the mixed vs. pure treatment (Table 9).

Total crop biomass

To obtain a relative measure of 'competition' or 'interference' for each species in each density:treatment interaction, a theoretical: actual crop biomass ratio was calculated (Table 10). The crop biomass for a species at density 2 in each treatment was considered a measure of the lowest level of interference. The theoretical biomass that should have been obtained at each higher density if competition was absent was calculated by multiplying the biomass of each species at density 2 by the number of seedlings of each species at each higher density within each treatment. The theoretical to actual crop biomass ratio for each species at density 2 within each treatment was assumed to be equal to 1.00, and the ratios at each higher density in each treatment were compared to this value.

In A-pure and F-pure treatments, the theoretical:actual crop biomass ratio increased with increasing density and was highest at density 16 (Table 10), indicating that interference was greatest at the higher densities. A similar pattern was evident in alder and fir seedlings from AF-mixed treatment, although the ratio was higher at density 2 than at density 4 in alder seedlings grown in the AF-mixed treatment. At density 16, where the theoretical:actual crop biomass ratio was greatest for each species, interference was higher for alder grown in mixed vs. pure treatment (3.14 vs. 2.35), but higher for fir grown in pure vs. mixed treatment (1.78 vs. 1.65) (Table 10).

Table 10. Comparison of total plant biomass with calculated theoretical mean total plant biomass for each species grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure, AF-mixed and F-pure treatments. Each value is a mean of 3 replicates at t_2 (1 September).

Treatment	Total Plant Density (No. plants dm^{-2})	Total Species Density (No. plants dm^{-2})	*Actual Crop Biomass (g)	Mean Theoretical Crop Biomass (g)	Theoretical:Actual Biomass Ratio
A-pure	2	2	0.60	0.60	1.00
	4	4	1.05	1.20	1.14
	8	8	1.19	2.40	2.02
	16	16	2.04	4.80	2.35
A-mixed	2	1	0.11	0.11	1.00
	4	2	0.25	0.22	0.88
	8	4	0.36	0.44	1.22
	16	8	0.28	0.88	3.14
F-pure	2	2	5.96	5.96	1.00
	4	4	11.67	11.92	1.02
	8	8	15.55	23.84	1.53
	16	16	26.84	47.68	1.78
F-mixed	2	1	3.08	3.08	1.00
	4	2	6.06	6.16	1.02
	8	4	10.46	12.32	1.18
	16	8	14.95	24.64	1.65

*Values shown here for A-mixed and F-pure seedlings do not include biomass of dead seedlings (see Table 9).

Distribution of dry matter within seedlings

An important response of plants to density stress, and hence shading effects, is found in the distributional changes of biomass devoted to leaves, stem, roots and nodules (Table 11). In alder seedlings, the proportion of total plant biomass devoted to leaves, representing the amount of photosynthetic tissue in the plant, was reduced at the higher densities (Fig.17). This reduction in leaf weight ratio probably occurred at the expense of a corresponding increase in stem weight ratio (Table 11), as the root weight ratio either remained largely constant (A-pure) or decreased (A-mixed) with increasing density (Table 11). Differences in nodule weight ratio with density were also significant ($P<0.05$), with the highest values occurring at the higher densities in alder seedlings from both pure and mixed treatments (Table 11).

In fir seedlings, the leaf weight ratio remained either constant (F-mixed) or increased (F-pure) with increasing density (Table 11), and hence, showed in most cases an opposite pattern to that found for alder seedlings. The increase in LWR which occurred in fir seedlings from the pure treatment (Fig. 17) was probably at the expense of a decrease in the root weight ratio or the proportion of dry matter devoted to the roots. Here, in the F-pure treatment there was a marked decrease in RWR between densities 2 and 8, with no corresponding change in the stem weight ratio (Table 11). As a result, fir seedlings from the F-pure treatment, (representing the highest level of interference for fir in the study (Table 10)), responded to increasing density

Table 11. Proportion of mean total plant biomass devoted to leaf, stem, root and nodules in seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure, AF-mixed and F-pure treatments. Each value is a mean of 3 replicates at t_2 (1 September); each replicate consists of total crop biomass (plants, roots, stems, leaves) of each species at the density indicated. Values for each replicate are given in Appendix II, Table 2. Means connected by the same vertical bar and the same letter within each treatment are not significantly different (P>0.05).

Treatment	Density (No. plants dm^{-2})	LWR (mg leaf mg^{-1} plant)		*SLA (mm^2 leaf mg^{-1} leaf)		LAR (mm^2 leaf mg^{-1} plant)		SWR (mg stem mg^{-1} plant)		RWR (mg root mg^{-1} plant)		NWR (mg nodules mg^{-1} plant)	
A-pure	2	.564	a	22.29	a	12.58	a	.228	a	.187	a	.021	a
	4	.531		20.37		10.86		.218		.231		.020	
	8	.503	b	21.43		10.68		.271	b	.203		.023	
	16	.478		23.85		11.14		.283		.207		.032	
A-mixed	2/1	.334	a	14.64		4.85		.246		.397		.022	a
	4/2	.416		24.18		10.10	a	.297		.262		.026	
	8/4	.393	b	35.78	a	13.87	b	.338		.238	a	.030	
	16/8	.332	a	34.35		10.67	a	.399		.220		.049	
F-pure	2	.360	a	-		-		.246		.394		-	
	4	.386		-		-		.283		.331		-	
	8	.423	b	-		-		.288	a	.289	a	-	
	16	.411		-		-		.304		.284		-	
F-mixed	2/1	.419		-		-		.270		.311		-	
	4/2	.432	a	-		-		.250	a	.318	a	-	
	8/4	.443		-		-		.259		.298		-	
	16/8	.412		-		-		.315		.273		-	

* For fir, the SLA averaged 9.02 $\pm$ 0.22 mm^2 mg^{-1} leaf with density and treatment.

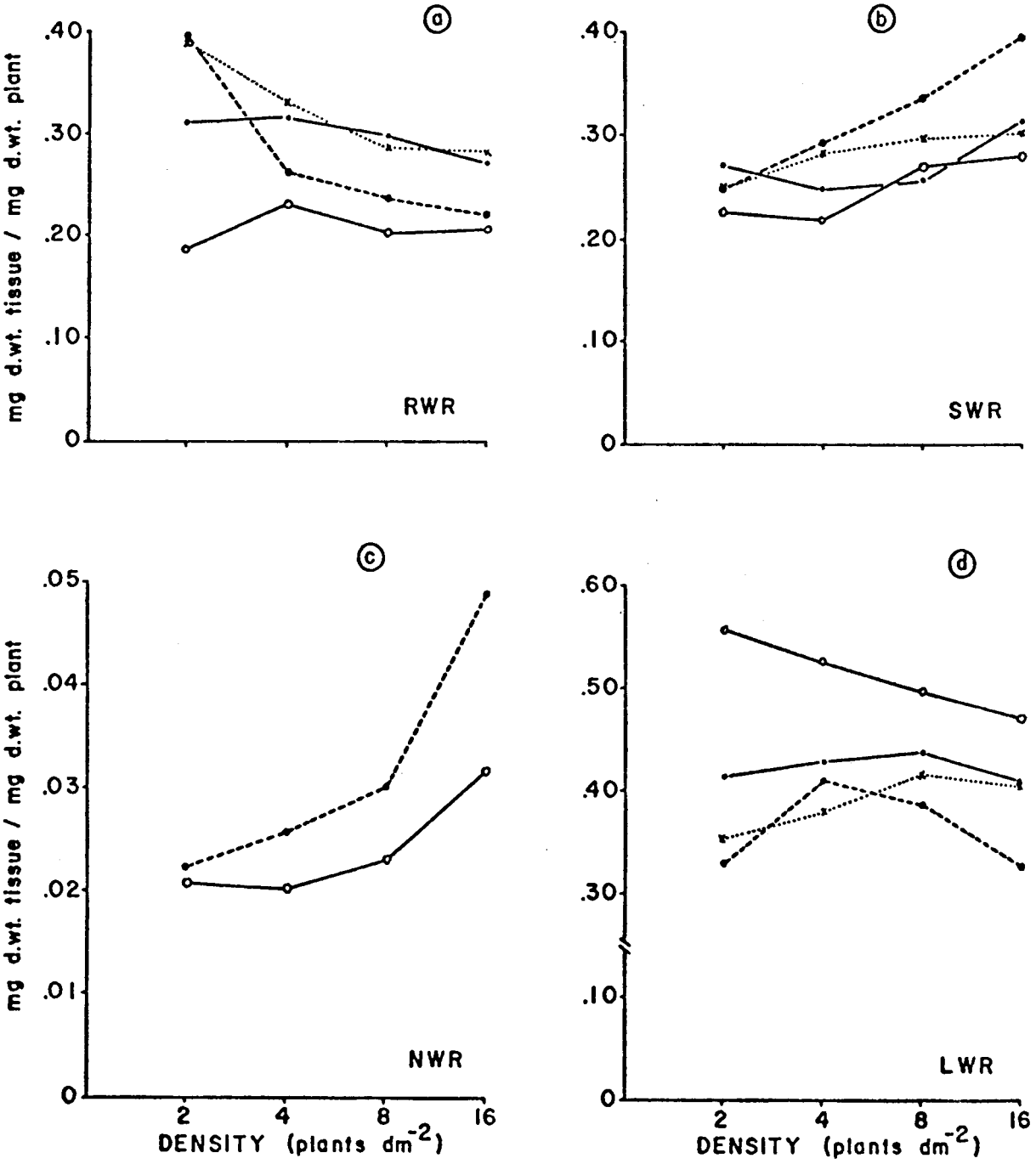


Figure 17. Proportion of total plant biomass devoted to (a) roots (RWR), (b) stems (SWR), (c) nodules (NWR) and (d) leaves (LWR) in A-pure o——o , A-mixed •-----• , F-pure x·····x and F-mixed •——• seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2}. (Data from Table 11).

stress by increasing the proportion of total plant biomass devoted to leaves, and by decreasing the proportion of biomass devoted to roots. In fir seedlings from the mixed treatment, differences in leaf weight ratio and root weight ratio with density were not significant (Table 11).

Between treatment differences in the proportion of total plant biomass devoted to plant components in alder were significant ($P<0.05$), with alder seedlings from the pure treatment placing more of their biomass into leaves, but less into roots, stems and nodules than alder seedlings from the mixed treatment (Table 11). In fir seedlings, there were no significant differences in leaf, stem and root weight ratios between treatments.

In the pure treatments, alder seedlings generally placed more of their biomass into leaves, but less into roots than fir seedlings (Table 11). Differences in RWR and LWR between alder and fir in the pure treatments were most pronounced at the lower densities. At density 2, alder placed almost 25 percent more of its total plant biomass into leaves than fir, but at density 16 only showed 7 percent greater ($P=0.04$) leaf weight ratio. Similarly, at density 2, alder seedlings placed about 20 percent of their total plant biomass into root production as compared to 40 percent in fir seedlings (Fig.17). In the mixed treatment, alder seedlings had lower RWR (except at density 2) and lower LWR (except at density 4) than fir seedlings (Fig.17). Differences in stem weight ratio were not significant between alder and fir seedlings in either the mixed or the pure treatments (Table 11).

In alder seedlings, both the leaf area ratio and the specific leaf area increased with increasing density in the mixed treatment and remained uniform with density in the pure treatment (Table 11). The major effect of density was an almost 60 percent increase in specific leaf area from density 2 to densities 8 and 16 ($P<0.01$) in alder seedlings from AF-mixed treatment (Fig.18). Consequently, alder seedlings from the mixed treatment had significantly greater ($P=0.001$) specific leaf areas than A-pure seedlings at the higher densities (Fig.18). In fir seedlings, the SLA remained essentially uniform (9.02 ± 0.22 mm^2 leaf mg^{-1} leaf) with density and treatment (Table 11).

By definition, the leaf area ratio (LAR) is a product of two components: the leaf weight ratio (LWR) and the specific leaf area (SLA). Any factor which alters the leaf area ratio does so by its positive or negative effects on the leaf weight ratio and/or the specific leaf area (Blackman 1968). In A-pure treatment, the decrease in LWR was balanced by a proportional increase in specific leaf area (Table 11), indicating that density effects on neither the LWR nor the SLA were predominant in giving rise to the uniform LAR pattern found with density (Fig.18). The increase in LAR in alder seedlings from the mixed treatment, however, resulted from a proportionately greater increase (60 percent) in specific leaf area, because the leaf weight ratio decreased (6 percent) with increasing density (Table 12).

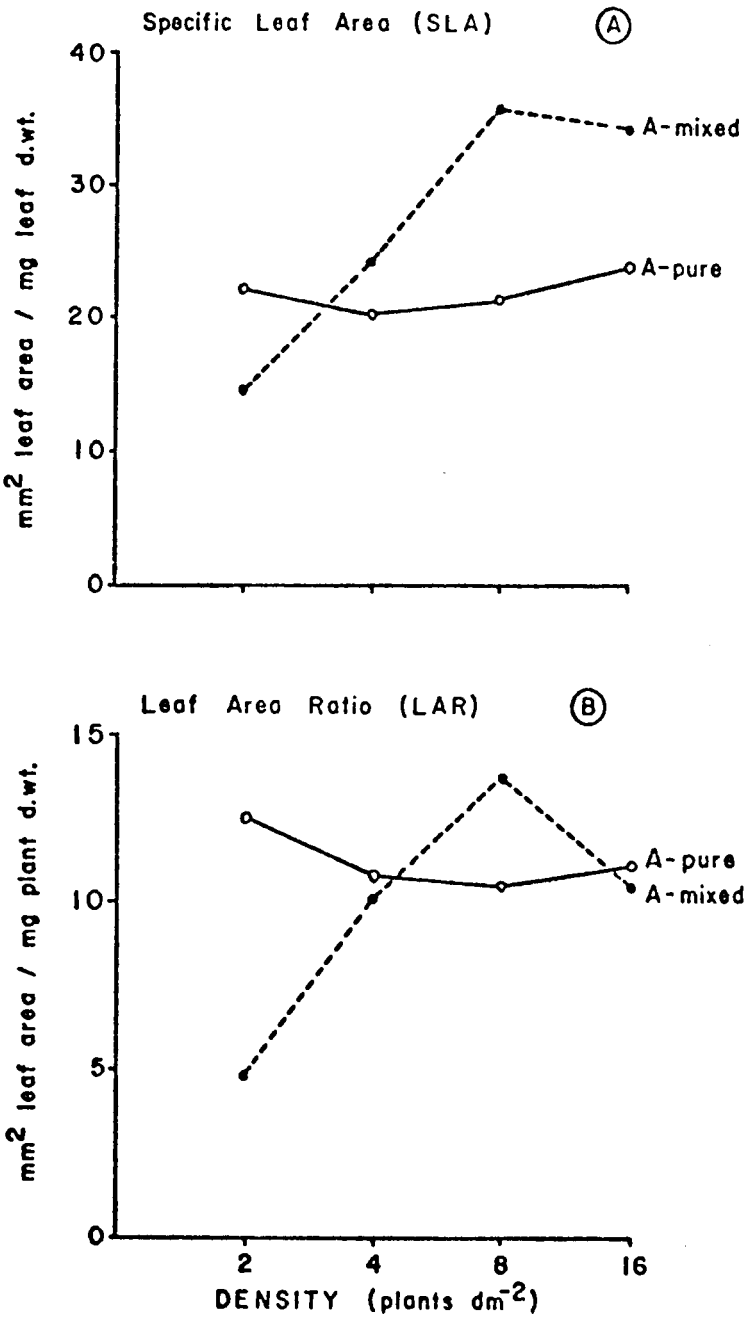


Figure 18. (a) Leaf area to leaf weight ratio (SLA=specific leaf area) and (b) leaf area to plant weight ratio (LAR=leaf area ratio) for alder seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure and AF-mixed treatments (Data from Table 11).

Nitrogen concentration (mg N mg^{-1} d. wt tissue)

Alder seedlings which are provided with a source of nitrogen via nitrogen fixation, showed no consistent trend in nitrogen concentration in the pure treatment; highest values were at density 4 (0.026) and density 16 (0.027). Alder seedlings from AF-mixed treatment, however, showed a progressive increase in plant nitrogen concentration from density 2-8 (Table 12). In the fir treatments, the major effect of increasing density was a reduction in the nitrogen concentration of the fir seedlings (Table 12).

Although no pronounced differences in nitrogen concentration occurred in fir seedlings between treatments, alder seedlings usually showed greater N-concentration in the pure vs. mixed treatment. Alder seedlings also had almost 50 percent higher nitrogen concentration than fir seedlings (Table 12).

In fir seedlings, the highest nitrogen concentration occurred in the leaves, followed by the root and stem. A similar pattern was evident in alder seedlings, except that nodules had nitrogen concentrations intermediate between the leaves and roots. Plant components generally followed a similar nitrogen concentration pattern with density as that shown for seedlings of each species (Table 12).

Growth Analysis

Rate of dry matter production

The rate of dry matter production (Table 13) followed a corresponding pattern with density as that shown for total seedling biomass

Table 12. Nitrogen concentration (mg N mg^{-1} d. wt tissue) in leaf, stem, root and nodules from seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure, AF-mixed and F-pure treatments. Each value is a single measurement at t_2 (1 September). Values at t_o (June 15) are also given.

Treatment	Density (No. plants dm^{-2})	Nitrogen concentration (mg N mg^{-1} d. wt tissue)				
		Leaf	Stem	Root	Nodule	Plant
15 June (t_o)						
Alder	-	.022	.019	.015	.024	.020
Fir	-	.013	.007	.013	-	.011
1 September (t_2)						
A-pure	2	0.029	0.019	0.021	0.022	0.023
	4	0.037	0.018	0.025	0.026	0.026
	8	0.026	0.019	0.020	0.024	0.022
	16	0.035	0.019	0.027	0.027	0.027
A-mixed	2	0.023	0.012	0.021	0.024	0.020
	4	0.027	0.012	0.022	0.024	0.021
	8	0.031	0.017	0.020	0.027	0.024
	16	0.026	0.020	0.019	0.023	0.022
F-pure	2	0.028	0.010	0.013	-	0.017
	4	0.023	0.008	0.012	-	0.014
	8	0.014	0.006	0.011	-	0.010
	16	0.014	0.006	0.011	-	0.010
F-mixed	2	0.026	0.006	0.012	-	0.015
	4	0.024	0.006	0.011	-	0.014
	8	0.012	0.006	0.011	-	0.010
	16	0.014	0.007	0.010	-	0.010

in each treatment (Table 9). In all seedlings from pure cultures and in alder seedlings from AF-mixed treatment, the major effect of density was a marked reduction in Rdmp at the higher densities. Fir seedlings from the mixed treatment, however, showed no significant difference ($P>0.05$) in Rdmp with density (Table 13).

Although alder seedlings had consistently higher ($P<0.001$) Rdmp in the pure vs. mixed treatment, fir seedlings showed no significant differences in rates of dry matter production between treatments (Table 13). Fir seedlings, however, had a much higher Rdmp than alder seedlings owing to their greater initial size at transplanting (Table 9). Because growth is an exponential and cumulative process (Blackman 1919), the rate of production of new material as measured by the dry weight is proportional to the size of the plant and hence, the larger initial size of the fir would predispose a higher Rdmp for fir than for alder seedlings.

Relative growth rate and net assimilation rate

To eliminate the effect of initial biomass differences on the growth rates of alder and fir between successive harvest dates, the relative growth rate (RGR_p) was calculated for seedlings from each density:treatment interaction (Table 13; Fig.19). The RGR_p followed a similar pattern with density as that shown for the Rdmp, with lowest values ($P<0.05$) occurring at densities 8 and/or 16 in seedlings from every treatment (except fir seedlings from the mixed treatment). The greatest effect of density on the RGR_p occurred at density 16 in alder seedlings from

Table 13. Calculated growth analysis data for seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure, AF-mixed and F-pure treatments. Each value is a mean of 3 replicates calculated between t_o (15 June) and t_2 (1 September). Each replicate is based on the mean seedling biomass of each species at the density indicated. Values for each replicate are given in Appendix II, Table 3. Means connected by the same vertical bar and the same letter within each treatment are not significantly different ($P>0.05$).

Treatment	Density (No. plants dm^{-2})	Rdmp (mg d. wt $plant^{-1}$ day^{-1})		RGR_L (mg mg^{-1} day^{-1})	RGR_P (mg mg^{-1} day^{-1})		NAR (mg mg^{-1} leaf day^{-1})	
A-pure	2	3.39	a	.0276	.0250	a	.0476	a
	4	2.86		.0251	.0232		.0460	
	8	1.37		.0169	.0159		.0327	
	16	1.10		.0143	.0139		.0296	
A-mixed	2/1	0.87		.0077	.0120		.0312	
	4/2	1.07	a	.0121	.0137	a	.0314	a
	8/4	1.01		.0109	.0131		.0312	
	16/8	0.03		-.0038	.0006		-.0028	
F-pure	2	25.20	a	.0076	.0135	a	.0309	a
	4	24.38		.0082	.0133		.0291	
	8	12.75	b	.0047	.0085	b	.0177	b
	16	8.60		.0019	.0060		.0102	
F-mixed	2/1	26.59		.0099	.0136		.0288	
	4/2	25.84	a	.0102	.0137	a	.0284	a
	8/4	20.40		.0084	.0117		.0236	
	16/8	10.59		.0032	.0074		.0153	

the mixed treatment, where there was a 95 percent reduction (Fig.19).

Alder seedlings had significantly lower ($P<0.001$) RGR_p in the mixed vs. pure treatment, but fir seedlings showed no significant differences in relative growth rates between treatments (Table 13). Comparison of A-pure and F-pure treatments showed that alder seedlings

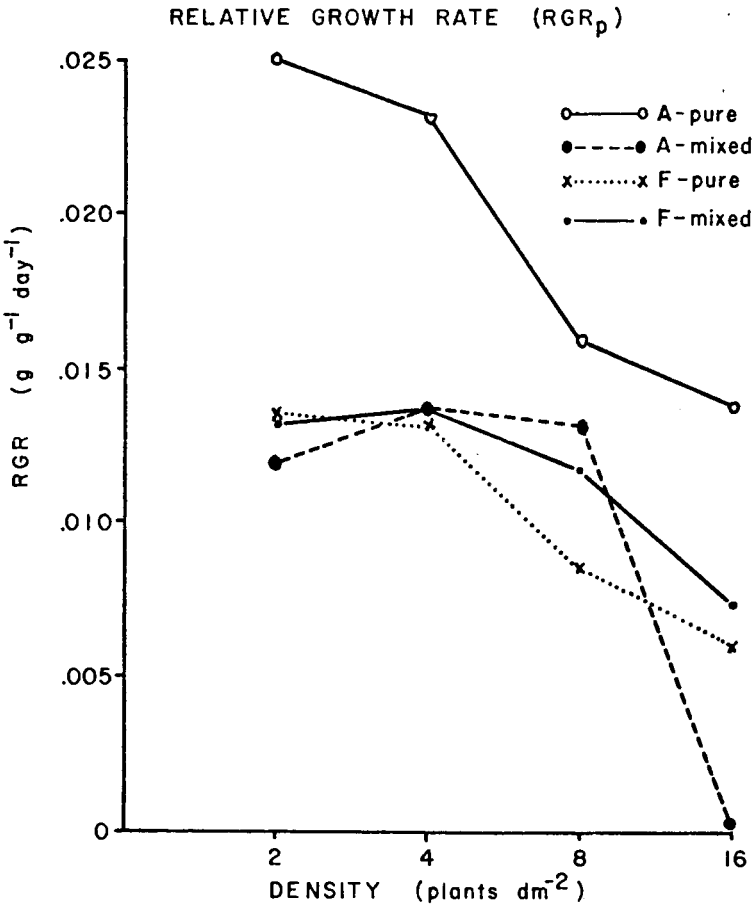


Figure 19. Relative growth rate (RGR_p) of seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure, AF-mixed and F-pure treatments (Data from Table 13).

had significantly higher ($P<0.001$) RGR_p than fir seedlings. The differences in RGR_p between the two species were more pronounced at density 2 ($P=0.005$) than at density 16 ($P=0.024$) (Table 13).

By definition, the relative growth rate (RGR_p) is the product of two components; the net assimilation rate and in this study, the leaf weight ratio ie. RGR_p = NAR x LWR. Any factor which alters the RGR_p, therefore, must do so by its positive or negative effects on either the leaf weight ratio or the net assimilation rate (Blackman 1968). In this study, any reduction in the RGR_p can then be explained in most cases by either (1) a decrease in both NAR and LWR or (2) the decrease in NAR is proportionately greater than the increase in LWR (Figs. 6 and 7). In A-pure treatment, the RGR_p NAR and LWR of alder seedlings all decreased at the higher densities (Table 13). A stronger correlation between RGR_p and NAR ($r = 0.99$) than between RGR_p and LWR ($R = 0.67$) (Table 14) suggested that density effects on the NAR rather than the LWR were of greater importance in giving rise to the decrease in RGR_p at the higher densities in A-pure seedlings. A similar pattern occurred in alder seedlings from the mixed treatment when the negative NAR values at density 16 were omitted (Table 14).

The decrease in NAR at the higher densities in fir treatments was partially offset by an increase in LWR (Table 13). As a result, the reduction in RGR_p in most cases at the higher densities resulted from a decrease in the NAR. In fir seedlings from the pure and mixed treatments, stronger correlations were found between RGR_p and NAR ($r = 0.99$) than between RGR_p and NAR ($r = -0.87; -0.47$) (Table 14).

Table 14. Relationship between RGR_P, RGR_L, NAR and LWR in alder and fir seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure, AF-mixed and F-pure treatments.

Treatment	Growth Parameters	Slope	Y-intercept	Correlation Coefficient (r)
A-pure	RGR_P vs NAR	1.75	0.49	r = 0.98
	RGR_P vs LWR	4.84	41.66	r = 0.67
	RGR_P vs RGR_L	0.86	0.14	r = 0.99
*A-mixed	RGR_P vs NAR	2.00	0.53	r = 0.84
	RGR_P vs LWR	1.30	38.79	r = 0.21
	RGR_P vs RGR_L	0.50	0.78	r = 0.78
F-pure	RGR_P vs NAR	2.46	-0.30	r = 0.99
	RGR_P vs LWR	-6.91	51.92	r =-0.87
	RGR_P vs RGR_L	1.23	0.34	r = 0.95
F-mixed	RGR_P vs NAR	2.21	-0.15	r = 0.99
	RGR_P vs LWR	-2.93	50.26	r =-0.47
	RGR_P vs RGR_L	0.95	0.40	r = 0.97

P = plant
L = leaf
* negative NAR values at density 16 omitted

The negative correlation between RGR_P and LWR indicates that the RGR_P was inversely related to the proportion of total plant biomass devoted to leaf production with increasing density.

The close correlations found between RGR_P and RGR_L in seedlings from the pure treatments and in fir from the mixed treatment (Table 14) also suggest that the relative growth rate of the plant was dependent, in part, on the rate of leaf production. In alder seedlings from the

mixed treatment, the relationship (omitting values for density 16) between RGR_P and RGR_L was not as close (r= 0.70) as that shown for seedlings from the other treatments.

The significantly higher RGR_p found for alder seedlings in pure vs. mixed treatment results from alder's higher ($P<0.001$) NAR (Table 13) and LWR ($P<0.05$) (Table 11) in the pure treatment. Similarly, non-significant differences in NAR and LWR between treatments in fir seedlings resulted in no significant difference in RGR_p.

In the pure treatments, the higher relative growth rate found for alder versus fir seedlings (Table 13) was due to alder's higher NAR ($P<0.001$) and LWR ($P<0.05$). Differences in RGR_p, NAR and LWR between alder and fir were greater at density 2 than at density 16 (Tables 11 and 13). Alder seedlings grown in the mixed treatment with fir had similar relative growth rates as those found for fir seedlings except at density 16, where the RGR_p was markedly reduced in alder (Table 13).

Carbon-dioxide Exchange

Total crop apparent photosynthetic and dark respiration rates in each treatment

Crop apparent photosynthetic (APS) rates at all measurement light intensities decreased with increasing density in every treatment except for A-pure treatment at 500 ft-c (Table 15). At 5000 ft-c, the reduction in crop APS rate from density 2 to 16 was similar for each treatment, averaging about 50 percent (Fig.20). At 500 ft-c, however, the greatest reduction with density occurred in F-pure (96 percent)

Table 15. Leaf areas, apparent photosynthetic (APS) and dark respiration (RS) rates for the total crop grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure, AF-mixed and F-pure treatments. Each value represents the mean of a series of runs for a single crop. Measurements were made between t_2 (1 September) and t_3 (8 October).

Treatment	Density (No. plants dm^{-2})	Total crop *leaf area (dm^2)	APS (mg CO_2 hr^{-1} dm^{-2}) Light intensity (ft-c)			RS (mg CO_2 hr^{-1} dm^{-2})
			5000	1000	500	0
A-pure	2	0.457	18.18	13.17	3.53	2.15
	4	0.920	13.66	11.13	4.34	1.91
	8	2.115	11.89	8.26	2.43	2.28
	16	3.019	9.47	6.08	1.68	1.62
AF-mixed	2	1.479	12.17	8.10	2.43	1.96
	4	3.600	8.81	6.16	2.17	1.40
	8	4.440	8.31	5.54	1.66	1.74
	16	7.936	5.83	3.24	0.57	1.95
F-pure	2	1.786	7.60	5.81	2.53	1.02
	4	2.908	6.81	5.15	1.68	1.64
	8	6.015	4.11	2.62	0.68	1.54
	16	10.451	4.17	2.25	0.09	1.58

*Leaf area given for AF-mixed treatment includes both alder and fir leaf areas.

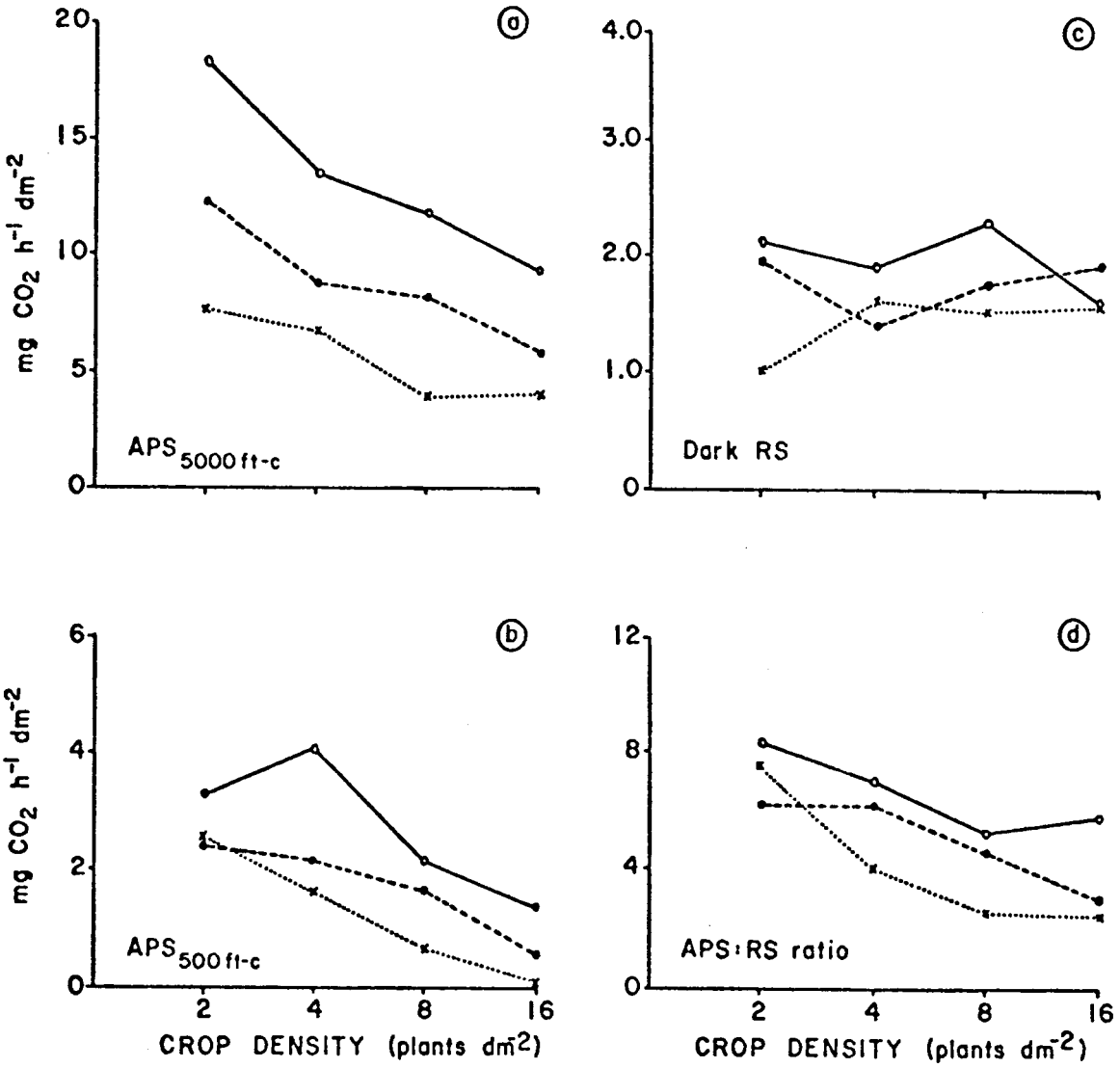


Figure 20. Apparent photosynthetic rates (APS) at (a) 5000 and (b) 500 ft-c, (c) dark respiration rates (RS) and (d) $APS_{5000\ ft\text{-}c}$:RS ratios for seedlings grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure o——o AF-mixed •-----• and F-pure x·····x treatments. (Data from Table 15).

followed by AF-mixed (76 percent) and A-pure (52 percent) treatments (Table 15; Fig.20).

The most pronounced density effect on the total crop dark respiration rates occurred from density 2 to 4 in F-pure and AF-mixed treatments and from density 8 to 16 in A-pure treatment (Fig.20). F-pure showed a sharp increase while AF-mixed showed a comparable decrease in dark RS between densities 2 and 4. In A-pure, there was no consistent RS pattern with increasing density, but in F-pure and AF-mixed treatments the RS rates either remained constant or increased from density 4 to 16 (Table 15).

Between treatments, the highest crop APS rates at all measurement light intensities occurred in A-pure and the lowest in F-pure (Table 15). Alder seedlings (A-pure treatment) showed approximately 2 times greater crop APS rates than fir seedlings (F-pure treatment) at 5000 and 1000 ft-c, and had higher crop RS rates than fir seedlings except at density 16 (Table 15; Fig.20).

The decrease in crop APS combined with either no change or a slight increase in crop dark RS rate resulted in a decrease in crop APS:RS ratio from density 4 to 16 in every treatment (Fig.20). The greatest decrease in this ratio with increasing density and the lowest ratio occurred in F-pure treatment.

Comparison of crop apparent photosynthetic and dark respiration rates in seedlings of each species grown in pure and mixed treatments

Treatment effects on the crop APS and dark RS rates in alder and fir seedlings can be compared in two ways: with regard to 'density'

grown at', and with respect to 'density of plants measured for CO_2 exchange' (see Methods, Part II, p.63). Comparison of the CO_2 exchange rates at the same "measurement density" for seedlings of each species from pure and mixed treatments is shown in Table 16. Alder seedlings grown in pure culture (A-pure) had higher APS rates at 5000 and 1000 ft-c than alder seedlings grown in the mixed treatment (AF-mixed). Differences in crop APS rates at 5000 and 1000 ft-c were more pronounced at the higher densities where alder seedlings grown in pure culture had 4-5 times higher crop APS rates than alder seedlings from the mixed treatment. Crop APS rates at 500 ft-c and dark RS rates in alder seedlings showed no major differences between treatments (Table 16). When CO_2 exchange rates are compared at the same "growth density", however, alder seedlings from AF-mixed treatment showed higher crop APS rates at 500 ft-c and lower crop dark RS rates than alder seedlings from A-pure treatment.

In the fir treatments, fir seedlings from the mixed treatment (AF-mixed) had higher crop APS rates at 5000 ft-c, higher dark RS rates and lower crop APS rates at 500 ft-c than fir seedlings from F-pure treatment (Table 16). At 1000 ft-c, there were no consistent differences in crop APS rates between treatments in fir seedlings.

Comparison of apparent photosynthetic and dark respiration rates between the total crop and a selected individual from the crop in A- and F-pure treatments

In the pure alder treatment, the APS rates of a single seedling at every measurement light intensity followed the same pattern with density

Table 16. Comparison of crop leaf areas, apparent photosynthetic (APS) and dark respiration (RS) rates for alder and fir seedlings grown in pure and mixed treatments at densities 2, 4, 8 and 16 plants dm^{-2}. Each value represents the mean of a series of runs for a single crop. Measurements were made between t_2 (1 September) and t_3 (8 October).

Light Intensity (ft-c)	Density of plants measured (No. plants dm^{-2})	APS or dark RS (mg CO_2 hr^{-1} dm^{-2})			
		A-pure	*A-mixed	F-pure	**F-mixed
5000	1	-	15.33	-	11.59
	2	18.18	13.33	7.60	8.02
	4	13.66	9.36	6.81	7.95
	8	11.89	2.31	4.11	5.99
	16	9.47	-	4.17	-
1000	1	-	11.11	-	7.55
	2	13.17	11.97	5.81	5.15
	4	11.13	5.50	5.15	5.04
	8	8.26	1.73	2.62	3.31
	16	6.08	-	2.25	-
500	1	-	3.79	-	2.18
	2	3.53	5.50	2.53	1.59
	4	4.34	2.93	1.68	1.23
	8	2.43	-	0.68	-
	16	1.68	-	0.09	-
0	1	-	1.84	-	1.62
	2	2.15	1.73	1.02	1.34
	4	1.91	2.00	1.64	1.65
	8	2.28	-	1.54	-
	16	1.62	-	1.58	-
Total Crop Leaf Area (dm^2)	1	-	0.229	-	1.250
	2	0.457	0.536	1.786	3.064
	4	0.920	1.144	2.908	3.300
	8	2.115	0.331	6.015	7.605
	16	3.019	-	10.451	-

*Values for A-mixed represent the crop APS and dark RS rates of the alder component of the AF-mixed treatment following removal of the fir component (see Pt. II, Methods, p.63). Alder seedlings grown at den. 16 in AF-mixed treatment died following measurement of APS at 1000 ft-c.

**Values for F-mixed are calculated by subtracting the CO_2 uptake hr^{-1} (alder component) from the CO_2 uptake hr^{-1} (AF-mixed crop) as described in Pt. II, Methods, p.63.

as that shown for the total crop (Table 17). At both 5000 and 500 ft-c, individual seedling APS rates decreased 30 percent from density 4 to 16 (Fig. 21). APS rates at all measurement light intensities, however, were higher for the individual than for the total crop except at the lower densities (Table 17). This may have been a direct result of marked reduction in mutual shading of foliage during measurement of the individual seedling from the higher densities. Differences in APS rates between the crop and the individual were more pronounced at 500 ft-c than at 5000 ft-c (Table 17).

In the pure fir treatment, APS rates at all measurement light intensities for the individual (Fig.21) followed an opposite pattern with density to that shown for the crop (Fig.20). Individual seedling APS rates increased at all measurement light intensities with increasing crop density, indicating a degree of shade adaptability at the higher crop densities. The greatest increase in individual seedling APS rates with crop density occurred at 500 ft-c.

APS rates at all measurement light intensities were higher in the single fir seedling vs. the total crop, except at the lower densities (Table 17). The greatest difference in APS rates between the individual and the F-pure crop occurred at the higher densities. At 500 ft-c, the APS rate for the individual fir seedling (2.40) was 95 percent higher than the corresponding rate for the crop (0.09) at density 16.

Dark respiration rates for individual alder seedlings also followed a similar pattern with increasing density as that shown for the crop (Table 17). For individual fir seedlings, the dark respiration rate

Table 17. Leaf areas, apparent photosynthetic (APS) and dark respiration (RS) rates for the crop (C) and a selected seedling (I) from that crop grown at densities 2, 4, 8 and 16 plants dm^{-2} in A-pure and F-pure treatments. Each value represents the mean of a series of runs for a single crop or an individual seedling. Measurements were made between t_2 (1 September) and t_3 (8 October).

Treatment	Density (No. plants dm^{-2})	Leaf Area (dm^{-2})		APS (mg CO_2 hr^{-1} dm^{-2}) Light Intensity (ft-c) 5000		1000		500		RS (mg CO_2 hr^{-1} dm^{-2}) 0	
		C	I	C	I	C	I	C	I	C	I
A-pure	2	0.457	-	18.18	-	13.17	-	3.53	-	2.15	-
	4	0.920	0.316	13.66	16.02	11.13	11.82	4.34	4.78	1.91	1.83
	8	2.115	0.290	11.89	11.72	8.26	10.05	2.43	4.20	2.28	2.45
	16	3.019	0.272	9.47	10.89	6.08	8.44	1.68	3.22	1.62	1.82
F-pure	2	1.786	-	7.60	-	5.81	-	2.53	-	1.02	-
	4	2.908	0.738	6.81	5.95	5.15	4.88	1.68	1.42	1.64	1.80
	8	6.015	1.025	4.11	6.43	2.62	5.49	0.68	1.93	1.54	1.45
	16	10.451	1.296	4.17	6.68	2.25	5.55	0.09	2.40	1.58	1.34

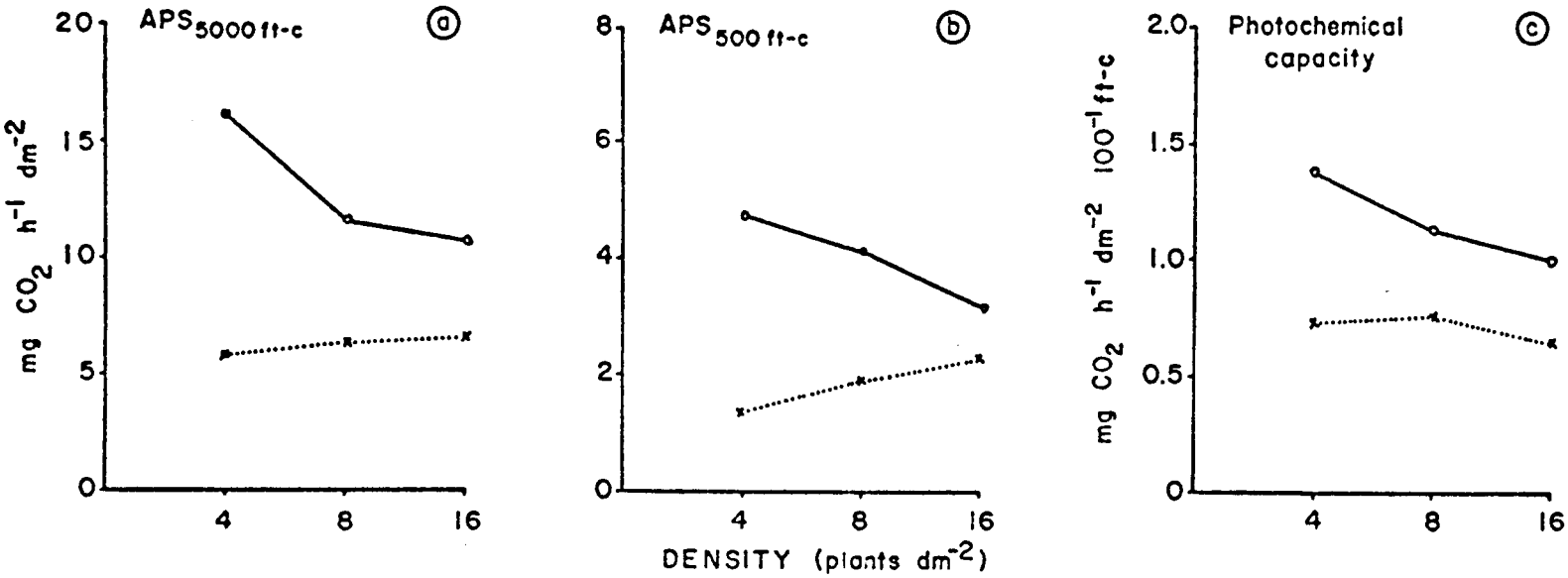


Figure 21. Apparent photosynthetic rates (APS) at (a) 5000 ft-c and (b) 500 ft-c, and (c) photochemical capacity (slope of the rate-intensity curve between 500-1000 ft-c) of a single seedling grown at densities 4, 8 and 16 plants dm^{-2} in A-pure o——o and F-pure x·····x treatments. (APS data from Table 17; photochemical capacity calculated from Table 17).

decreased 25 percent from density 4 to 16 while the dark RS rates for the crop at these densities were similar.

Single alder seedlings from A-pure treatment had higher APS rates than fir seedlings (F-pure treatment) at all measurement light intensities. Although dark RS rates of alder seedlings were higher than those for fir seedlings, the differences were not as marked (Table 17).

The photochemical capacity of an individual alder seedling calculated as

$$\frac{\text{APS rate}_{1000\ \text{ft-c}} - \text{APS rate}_{500\ \text{ft-c}}}{\Delta\ \text{light intensity}} \times 100$$

decreased 46 percent with increasing crop density in the A-pure treatment (Fig.21). For an individual fir seedling from F-pure treatment, however, the photochemical capacity remained essentially constant with increasing crop density. Individual alder seedlings had higher photochemical capacities than fir at every density.

Seasonal Patterns

For comparison of the effect of density on the seasonal growth pattern, only density 2 and 16 (representing the two extremes) were used. Similarly, only seedlings from A-pure and F-pure treatments were used for comparison of species differences during the growing season. Data not included here for each density:treatment interaction are given in Appendix II.

Throughout the growing season, mean seedling biomass increased significantly ($P<0.05$) in alder seedlings at densities 2 and 16, and in fir seedlings from density 2. There was, however, no significant difference ($P>0.05$) in mean fir seedling biomass at density 16 during the season (Fig.22). Growth of both alder and fir seedlings throughout the season was clearly suppressed at density 16 (Fig.22).

Differences in rate of dry matter production (Rdmp) were not significant during the season for either fir or alder seedlings from each density (Table 18). Between September and October, however, growth of fir seedlings dropped off markedly while alder growth was still substantial at both densities. Seasonal differences in RGR_p and NAR were also not significant except for the NAR of alder seedlings grown at density 16. The NAR, in this case, was highest near the end of the growing season.

Total crop APS rates showed a marked seasonal pattern that was closely similar in most cases with the seasonal NAR and RGR_p patterns for each species (Fig.23; Table 18). The greatest changes in APS rates generally occurred in seedlings of each species grown at density 2, with sharp decreases in APS occurring at 5000 and 500 ft-c near the end of the season. APS rates, however, remained essentially uniform during the season in seedlings grown at density 16 (Fig.23).

There were, in general, no major differences in seasonal crop APS and dark RS patterns between alder and fir seedlings. With the exception of fir seedlings from density 2, highest crop APS rates (5000 ft-c) and dark RS rates in alder and fir occurred in early September (Fig.23).

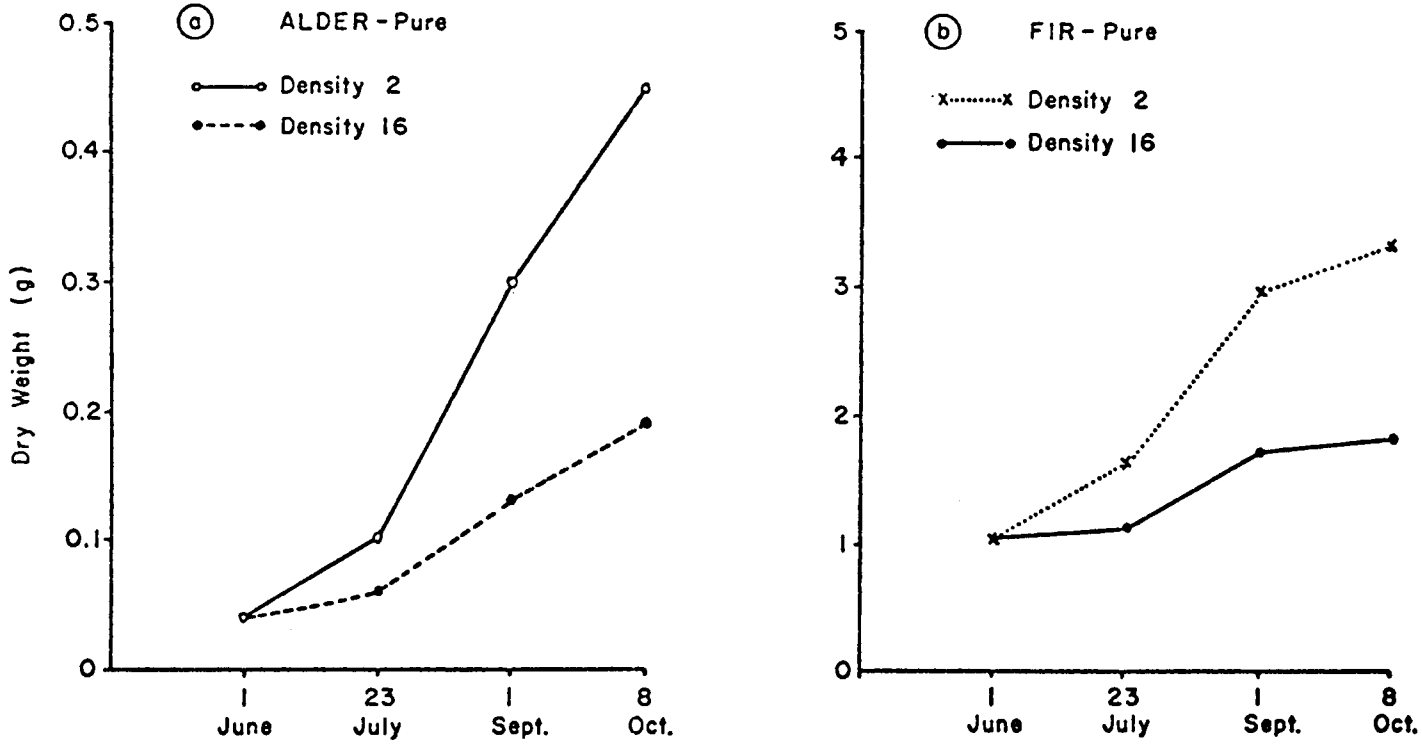


Figure 22. Seasonal biomass pattern for the mean seedling grown at densities 2 and 16 plants dm^{-2} in (a) A-pure and (b) F-pure treatments. Note difference in vertical scale.

Table 18. Calculated seasonal growth analysis data for mean seedling grown at densities 2 and 16 plants dm^{-2} in A-pure and F-pure treatments. Each value is a mean of 3 replicates calculated between t_0 (15 June) and the three successive harvests (t_1, t_2 and t_3). Values for each replicate at each harvest date are given in Appendix II, Table 3. Means connected by the same vertical bar are not significantly different at the 95% level ($P \geq 0.05$) within each treatment.

Treatment	Harvest Period	Rdmp (mg day^{-1})		RGR_p (mg mg^{-1} day^{-1})		NAR (mg mg^{-1} leaf day^{-1})	
		2	16	2	16	2	16
A-pure	15 June-23 July	1.53	0.52	.0217	.0095	.0467	.0204
	15 June-1 Sept.	3.39	1.10	.0250	.0139	.0476	.0296
	15 June-8 Oct.	3.57	1.26	.0203	.0126	.0457	.0327
F-pure	15 June-23 July	14.64	2.13	.0103	*.0041	.0139	.0031
	15 June-1 Sept.	25.20	8.60	.0135	.0060	.0309	.0102
	15 June-8 Oct.	20.00	6.83	.0100	.0047	.0241	.0102

*Mean of 2 replicates only.

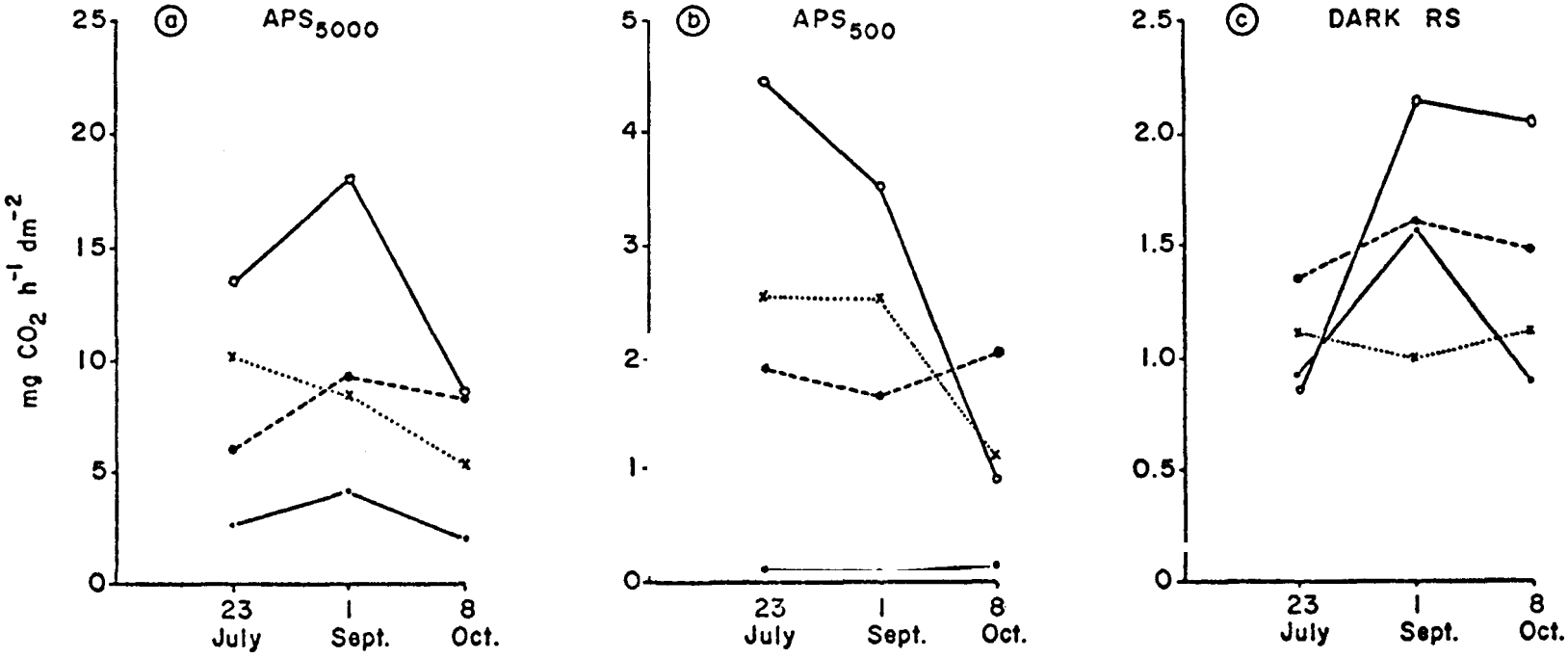


Figure 23. Seasonal crop APS pattern at (a) 5000 and (b) 500 ft-c and (c) dark RS rates for seedlings grown in A-pure (at densities 2 o——o and 16 •-----• plants dm^{-2}) and F-pure (at densities 2 x·····x and 16 •———• plants dm^{-2}) treatments. Note difference in vertical scale. (Data from Appendix II, Table 5).

Differences in the distribution of dry matter within the seedlings were significant ($P<0.05$) for each species grown at densities 2 and 16 during the growing season. The leaf weight ratio showed the most marked differences, with a sharp reduction occurring near the end of the season in both species (Fig.24). In fir seedlings, the leaf weight ratio decreased continuously as the season progressed, but this was not apparent in alder seedlings.

The root weight ratio generally increased near the end of the season in alder seedlings, but remained uniform in fir seedlings. (Fig.24). The most pronounced seasonal effect occurred in fir seedlings between late July and early September where there was a marked increase in root weight ratio. The root weight ratio also began to increase earlier in the growing season in fir seedlings than in alder seedlings.

The stem weight ratio showed less marked differences for each species than the leaf and root weight ratios, and remained quite uniform during the season. In both alder and fir, however, there was a slight increase in SWR at the end of the season and this was associated with a decrease in leaf weight ratio (Fig.24).

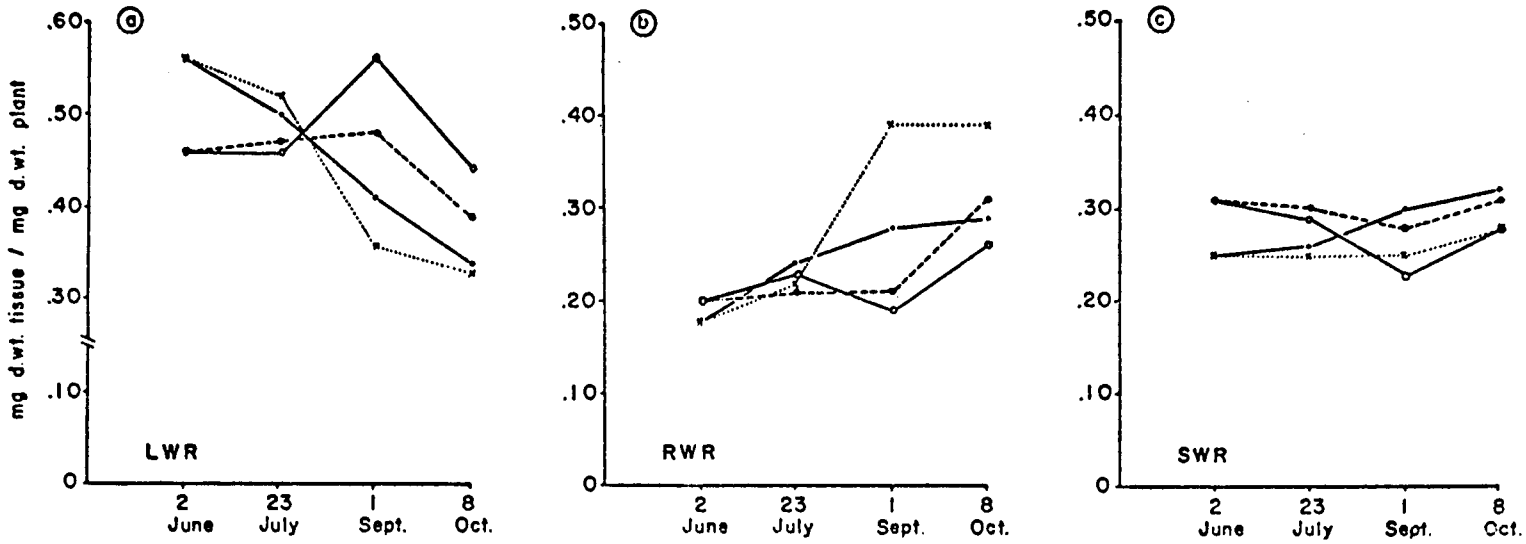


Figure 24. Seasonal (a) leaf weight ratio (LWR), (b) root weight ratio (RWR) and (c) stem weight ratio (SWR) patterns for mean seedling grown in A-pure (at densities 2 o——o and 16 •- - - -• plants dm^{-2}) and F-pure (at densities 2 x·····x and 16 •———• plants dm^{-2}) treatments. Note difference in vertical scale. (Data summarized from Appendix II, Table 2).

DISCUSSION

Density Effects on Plant Growth

Plant competition or interference occurs when the supply of any factor required for growth is inadequate to meet the collective demands of the population (Stern 1965). If one or more factors are limiting in the population, individuals may either 1) die and be eliminated or 2) survive and grow with varying success depending on the degree of adaptability (plasticity) of their physiological and morphological processes to environmental stresses. Two important environmental stresses at higher densities are 1) reduction in light level below the plant canopy and 2) reduction in nutrient levels, both of which may alter the growth response of a plant species.

Differences in the growth response of a plant species to density stress, and particularly shading effects, may therefore be related to the shade tolerance level of the species. The most important criteria for shade tolerance is the ability of a plant to survive and grow successfully in a shaded habitat (Shirley 1945). This requires that the gain of assimilates by photosynthesis is greater than the losses arising through respiration, and will also depend on the ability of the plant to maintain a high photosynthetic surface area for light interception under shaded conditions. Alder is generally acknowledged as a shade intolerant species (Worthington 1965; Baker 1950), although studies have shown that young alder seedlings may be tolerant of shade (Krueger and

Ruth 1969; Ruth 1968). Douglas-fir, on the other hand, is considered more shade tolerant than alder, but less tolerant than Sitka spruce and Western hemlock (Baker 1950).

There are several differences in morphological and physiological responses to shade between shade tolerant and intolerant species. Shade plants usually have lower dark respiration rates, APS rates and hence, slower growth rates in all environments than shade intolerant species (Littell 1972; Loach 1967; Grime 1965; Bourdeau and Laverick 1958). They also show less variation in growth under different light intensities (Krueger and Ruth 1969; Grime 1965). Shade intolerant species show reduced leaf weight ratios but have a greater capacity for increasing their leaf area ratio and specific leaf area with increasing shade (Krueger and Ruth 1969; Brix 1967; Jarvis 1964; Kuroiwa et al. 1964) although there are some exceptions (Loach 1970). Furthermore, shade intolerant species usually have greater leaf weight ratios, leaf area ratios and specific leaf area than shade tolerant species (Littell 1972; Krueger and Ruth 1969). Changes in stem biomass under different growth light intensities appear to be less pronounced than changes in the root and foliage components for both shade tolerant and intolerant species (Loach 1970; Jarvis 1964).

Differences in growth response to density stress in alder and fir seedlings followed, in most cases, previously reported patterns for shade tolerant and intolerant species grown under different light intensities (Table 19). The most noticeable modification was a reduction in mean seedling biomass and relative growth rate of each species, except

Table 19. Summary of Density Effects on Alder and Fir Seedlings

Parameter	Alder	Fir
Mean seedling biomass	Decrease	Decrease or no change
Rdmp	Decrease	Decrease or no change
RGR	Decrease	Decrease or no change
NAR	Decrease	Decrease or no change
Crop APS:RS	Decrease	Decrease
LWR	Decrease	Increase or no change
LAR	Increase or no change	Increase or change
SLA	Increase or no change	No change
SWR	Increase	Increase
Stem Height	No change	No change
RWR	Decrease or no change	Decrease or no change
NWR	Increase	-
N-concentration	No change	Decrease
APS sel. seedling	Decrease	Increase
RS sel. seedling	No change	No change
Phot. Cap. sel. seedling	Decrease	No change

Increasing density stress ↓

in fir seedlings grown in the mixed treatment at the higher densities (Table 9 and 13). A reduction in mean seedlng biomass is a common plastic response to density stress in plant populations (Blackman 1968; Stern 1965; Harper 1964). The greater reduction (about 25 percent) in mean seedling biomass with density stress in alder than in fir, suggests, however, that alder is more sensitive to density than Douglas-fir seedlings. This is in general agreement with the shade tolerance level of each species.

The large reduction in growth found for alder and fir seedlings at the higher densities was probably a direct result of reduced light levels arising from increased mutual shading of foliage. Evidence for mutual shading was shown in Table 17 where a large difference in APS rates at 500 ft-c occurred between the crop and individual seedlings of fir and alder at the higher densities. Furthermore, the APS:RS ratio of the crop decreased with increasing density (particularly in the fir treatments (Fig.20)),where a marked reduction in APS rates occurred with either little or no change in dark respiration rates. This crop APS:RS pattern with increasing density may explain the strong correlation found between RGR and the NAR (Table 14). That is, a reduction in APS arising from mutual shading with no change in dark respiration rate results in a reduced NAR and hence, a reduced relative growth rate. Other studies with herbaceous and forest tree species have shown, in this respect, a strong positive correlation between NAR and the logarithm of relative light intensity (Brix 1967; Blackman and Black 1959; Blackman and Wilson 1951), although in some

cases there may be a reduced NAR under full light conditions (Van den Driessche 1971; Loach 1970). The reduction in NAR which occurred with increasing density in this study may also be attributed in part to reduced CO_2 concentrations during plant growth. Studies with crop plants have shown that CO_2 concentrations may become limiting for normal growth under dense canopies (Loomis and Williams 1963; Watson 1958).

Reduced nitrogen levels, and hence increased root competition in seedlings may have affected growth and net assimilation rate at the higher densities, although Blackman (1968) has indicated that the NAR is only reduced when nitrogen shortages are extreme. In fir seedlings, the progressive decrease in nitrogen concentration within the plant tissues (Table 12) suggested that nitrogen levels in the root medium were reduced and that root competition was active. Root competition has been shown to induce nitrogen shortages in plant tissues (Litav and Wolovitch 1971). In alder seedlings, however, there was no major difference in nitrogen concentration with density. The higher nodule weight ratios found at the higher densities (Table 11) suggested that nitrogen fixation in the root nodules acted as a compensatory mechanism for reduced nitrogen levels in the root medium. Bond et al. (1954) found that greatest nodule weight ratios occur in seedlings grown under low nitrogen levels and Quispel (1954) noted that the presence of combined nitrogen in the rooting medium inhibits the formation of root nodules.

Differences in the proportion of total plant biomass devoted to

leaves, root and stem also occurred with increasing density in fir and alder seedlings (Table 11). The increasing proportion of biomass found in the leaves in fir seedlings grown in the pure treatment (Fig.19) can be considered a favourable response to density, in that proportionately more photosynthetic tissue per plant is produced under conditions where light may be limiting. Although alder had a reduced LWR at the higher densities in the mixed treatment, it still maintained a high photosynthetic surface area per plant (leaf area ratio) by increasing its specific leaf area (Table 11). In the pure treatment, the reduction in LWR was not associated with an increase in LAR or SLA at the higher densities, probably because the reduction in light levels in the canopy was not as extreme as in the mixed treatment. Douglas-fir, in this respect, showed little difference in specific leaf area for all density: treatment interactions (Table 11). With increasing density stress, therefore, alder showed greater shade adaptability than the more shade tolerant Douglas-fir in regards to potential for LAR and SLA increase as the level of shade is increased. This means, in a sense, that alder can maintain a higher photosynthetic surface area per plant under shaded conditions while at the same time conserving available assimilates by not diverting these into greater leaf biomass (leaf weight ratio).

Alder seedlings from the mixed treatment and fir seedlings from the pure treatment showed a marked reduction in root weight ratio at the higher densities which was usually associated with an increase in stem weight ratio (Table 11). A similar root growth pattern has been reported by many workers, ... plants grown in shade have proportionately

smaller root systems than those grown under full light conditions (Loach 1970; Krueger and Ruth 1969; Jarvis 1964; Ashby 1961; Bourdeau and Laverick 1958; Baker 1945; Shirley 1929). Reduced root systems in shade grown plants has been interpreted as an adaptation to divert more available assimilates into the production of above ground components both to outgrow associated species and to capture more light (Davidson 1969; Grime and Jeffrey 1965). The adaptive value of an increased SWR at the higher densities in this study (Table 11) was not apparent however, as there was no corresponding increase in stem height in either fir or alder (Table 9).

The large reduction in RWR in alder seedlings from the mixed treatment and in F-pure seedlings (Table 11) also suggests that light competition was of greater importance than root competition in reducing growth of these seedlings. A reduction in nitrogen levels within the rooting medium usually results in a marked increase in root weight ratio when plants are grown free from shading effects (Bouma 1970a; Wilkinson and Ohlrogge 1964; see Discussion Pt. 1; p.35). If competition for nutrients was greater than competition for light, therefore, one would expect an increase rather than a decline in root weight ratio. This was not the case in this study.

Density Effects on Photosynthesis and Dark Respiration

Differences between shade tolerant and intolerant species on the basis of physiological differences under different growth light intensities are not entirely clear-cut (Loach 1970). Shade tolerant species usually have higher APS rates after growth in heavy shade than in full

daylight (Acer macrophyllum, Littell 1972; sugar maple, Logan and Krotkov 1969; Quercus petraea, Jarvis 1964) while shade intolerant species follow an opposite APS pattern (red alder, Littell 1972; yellow birch, Logan 1970). In many cases, however, no significant differences in APS rates following growth in different light levels have been reported (Tsuga heterophylla, Krueger and Ruth 1969; Douglas-fir, Brix 1967; Tsuga canadensis, Bourdeau and Laverick 1958). In the opposite extreme, Bourdeau and Laverick (1958) have reported higher APS rates in the shade intolerant Pinus resinosa after growth in shade than in full sun.

In general, the photochemical capacity (the initial slope of the APS rate vs. light intensity curve) is usually higher in shade-grown than in sun-grown plants for both shade tolerant and intolerant species (Littell 1972; Loach 1967; Bjorkman and Holmgren 1963). The least variation in photochemical capacity with shade usually occurs in shade tolerant species (Krueger and Ruth 1969; Bourdeau and Laverick 1958). Dark respiration rates also tend to remain either constant or decrease after growth in heavy shade for both shade tolerant (Acer macrophyllum, Littell 1972; Tsuga canadensis, Bourdeau and Laverick 1958) and shade intolerant (red alder, Littell 1972; yellow birch, Logan 1970) species. In Ailanthus altissima, however, Bourdeau and Laverick (1958) have reported highest dark RS rates after growth in heavy shade.

Douglas-fir generally showed greater shade adaptability than alder seedlings in APS rates, photochemical capacity and dark respiration rates (Table 17). The greater APS adaptability of fir compared to alder

is shown by its increased APS rates at all light intensities after growth at the higher densities (Fig.21). Alder, on the other hand, had lower APS rates after growth at higher than at lower densities. The APS pattern found for fir represents a favourable adaptation, in that available light utilization is more efficient in seedlings growing under conditions where light may be limiting for growth. The above APS pattern for alder and the more shade tolerant Douglas-fir is in agreement with previously reported patterns for shade tolerant and intolerant species. Alders poor shade adaptability with regard to photochemical capacity as the density increased (Fig.21), however, was not predictable from previously reported patterns. Here, plants generally have higher photochemical capacity after growth in shade than in full light irregardless of shade tolerance (Bjorkman and Holmgren 1963).

As growth is essentially the outcome of whether a plant can maintain a favourable APS:RS ratio, a reduction in dark RS under shaded conditions may be considered an adaptive response by the plant to minimize losses of assimilates via respiration. The uniform crop dark RS pattern shown for fir between densities 4 and 16 in the pure treatment (Fig.20) suggests that dark RS rates do not vary markedly with different light levels in fir. In the case of selected seedlings, however, a 25 percent decrease in dark RS occurred between density 4 and 16 (Table 17), suggesting that fir exhibits some shade adaptability with regard to dark RS rates. In alder seedlings there was no consistent dark RS pattern with increasing density stress (Fig.20).

Comparison of Growth, Apparent Photosynthesis and Dark Respiration Rates in Alder and Fir

The higher growth rates reported for alder than for fir seedlings in exposed habitats under natural conditions (Ruth 1968; Worthington 1965) was predictable from the results of this study. Here, the higher growth rate shown for alder vs. fir in pure treatment (Table 13) was a direct result of the higher NAR (Table 13) combined with higher leaf weight ratios (Table 11) for the alder seedlings. Differences in the NAR and the shade tolerance level of Douglas-fir and alder were reflected in the APS and dark RS rates of the seedlings (Table 15). At 5000 ft-c, APS rates for alder were almost twice as great as the respective rates found for Douglas-fir seedlings at density 2. APS rates were also similar to rates reported for these species by other workers (Littell 1972; Krueger and Ruth 1969) and were similar to the maximum reported rates for temperate zone evergreen conifers (5-10 mg CO_2 hr^{-1} dm^{-2}) and temperate zone deciduous broad-leafed trees (10-20 mg CO_2 hr^{-1} dm^{-2}) (Jarvis and Jarvis 1964). Furthermore, although fir showed greater shade adaptability with regard to photochemical capacity, alder was still capable of utilizing low light intensities more efficiently than Douglas-fir after growth at all densities (Fig.21). As a result, the greater shade tolerance of fir vs. alder cannot be explained by differences in photosynthetic efficiency under low light levels. Loach (1970) reported similar less steep slopes (lower photochemical capacity) in shade tolerant than in shade intolerant species.

Treatment Effects on Plant Growth

Using reduction in mean seedling biomass as a measure of competition in this study, it was concluded that competition (or interference) was greater for alder seedlings in the mixed vs. pure treatment, and greater for fir seedlings in pure vs. mixed treatment (Table 10). The lower fir seedling biomass in the pure vs. mixed treatment supports the theoretical proposition that plant competition is more extreme in monocultures where the basic requirements of the individuals are similar (Harper 1967). This was not the case for alder.

Comparison of the growth responses of each species between treatments showed trends that were related to the level of interference within each treatment (Table 20). The higher RGR, NAR and hence, biomass found in fir seedlings from mixed versus pure treatment in this study (Table 9 and 13) resulted from greater root and shoot competition in the pure treatment. Greater root competition in the pure vs. mixed treatment would be expected from the greater total root biomass in the F-pure crop at the higher densities. Evidence for greater light competition between the fir treatments was shown, in part, by the greater self-thinning of needles which occurred in the pure treatment. Increased self-thinning may result from an unfavourable APS:RS balance in leaves spending more time below than above the light compensation point in shaded habitats (Donald 1961).

Extreme shading of alder seedlings beneath the fir canopy at the higher densities probably gave rise to their large reduction in biomass

Table 20. Summary of Treatment Effects on Seedling Growth

Seedling biomass	F-mixed>F-pure (ns)°	A-pure>A-mixed*
Leaf biomass	F-mixed>F-pure*	A-pure>A-mixed*
Stem biomass	F-mixed>F-pure (ns)	A-pure>A-mixed*
Root biomass	F-mixed>F-pure (ns)	A-pure>A-mixed*
Nodule biomass	-	A-pure>A-mixed*
Stem height	F-mixed>F-pure (ns)	A-pure>A-mixed (ns)
Dist. to lst g.needle	F-pure>F-mixed*	-
LWR	F-mixed>F-pure (ns)	A-pure>A-mixed*
SWR	F-mixed>F-pure (ns)	A-mixed>A-pure*
RWR	F-mixed>F-pure (ns)	A-mixed>A-pure*
NWR	-	A-mixed>A-pure*
LAR	-	A-pure>A-mixed*
SLA	-	A-mixed>A-pure*
N concentration (plant)	F-pure>F-mixed	A-pure>A-mixed
Rdmp	F-mixed>F-pure (ns)	A-pure>A-mixed*
RGR	F-mixed>F-pure (ns)	A-pure>A-mixed*
NAR	F-mixed>F-pure (ns)	A-pure>A-mixed*

° ns = not significant ($P > 0.05$)

* = significant ($P \leq 0.05$)

in the mixed treatment (Table 9). Reduced leaf dry weights from leaf fall and leaf respiration losses below the dense fir canopy also results in higher ratios for root, stem and nodules as a proportion of total plant weight in alder seedlings from the mixed vs. pure treatment (Table 11).

A characteristic growth response under low light levels is the greater increase in the leaf area ratio and specific leaf area at the higher densities in alder seedlings from the mixed vs. pure treatment. Thinner, broader leaves under low levels of shade would permit greater light transmission and greater photosynthetic surface area for light interception without utilizing valuable assimilates which may be limiting for normal growth.

The large difference in mean seedling biomass between alder seedlings from the pure and the mixed treatment at the lower densities (Table 9) could not be explained by competition for light as there was little interaction between leaves in seedlings at the lower densities (Fig.15). The large root systems of the fir seedlings, however, may have added to this difference in mean biomass by a greater reduction of the moisture levels in the AF-mixed versus the A-pure treatment.

APS and dark RS patterns between treatments were related to the level of interference in each treatment. At 5000 ft-c, highest APS rates occurred in A-pure and F-mixed seedlings (Table 15), or those seedlings from each treatment showing the lowest level of interference (Table 10). This trend was reversed at 500 ft-c, where seedlings from treatments showing the highest level of interference (and mutual shading)

for each species had the highest APS rates. It is clear then that both species have a level of adaptability which facilitates efficient utilization of low light intensities under shaded conditions.

Shade adaptability is further indicated by changes in the dark RS rates (Table 15). For both species, dark RS rates were slightly lower in treatments showing the highest level of interference. This pattern would tend to conserve available assimilates by reducing their losses via dark respiration under shaded conditions.

Seasonal Patterns

The increase in the proportion of total plant biomass devoted to woody tissue (roots and stems) in alder and fir seedlings near the end of the season (Fig.24) was similar to the increases found for alder in Part 1 (Fig. 6; p.19), and has been reported for many species (Littell 1972; Newhouse and Madgwick 1968; Lister et al. 1967; Kozlowski and Keller 1966). In alder, the increase in the RWR resulted from a reduction in leaf biomass arising, in part, from leaf fall near the end of season. This probably gave rise to the decline in LWR of alder from early September to the end of the growing season (Fig.24). A decline in LWR near the end of the season was also reported for alder and broadleaf maple by Littell (1972). The decline in LWR in fir seedlings as the season progressed (Fig.24) indicates a reduction in the ratio of photosynthetic to non-photosynthetic tissue. A similar LWR pattern with time was shown for sycamore, birch, poplar and larch (Pollard and Wareing 1968). For Pinus radiata and Pinus contorta, however, Sweet

and Wareing (1968 a) reported no difference in LWR between June and October.

In general, many variations occur in the relationships between RGR_p, NAR and LWR both in response to environmental parameters and as factors explaining differences in growth rates of plant populations and species (Eagles 1971; Sweet and Wareing 1968 a; 1968 b; Watson 1952; Heath and Gregory 1938). In fir, the decline in LWR as the season progressed was associated with a non-significant difference in NAR and RGR_p (Table 18). As a result, differences in RGR_p during the growing season were more closely paralleled by changes in NAR than LWR in fir seedlings. Changes in RGR_p with time in alder seedlings were also more closely related to differences in NAR than LWR (Fig.24; Table 18). Similar patterns for a variety of hardwoods and conifers have been previously reported by Pollard and Wareing (1968).

Changes in net assimilation rate were similar in most cases to differences in crop APS rates during the season, with highest values for each usually occurring around September (Table 18; Fig.23). The large decrease in APS rates (particularly at density 2) which occurred near the end of the season in alder and fir was similar to the APS reduction found for alder in Part 1 (Fig.9 p.28). The higher APS rates at 500 ft-c found for alder seedlings at density 16 vs. density 2 late in the season indicates a level of shade adaptability in alder; ie. seedlings grown under the shaded conditions of higher density were capable of utilizing low light levels more efficiently than seedlings grown at the lower densities. Shade adaptability was also evident in

crop dark RS rates which were lower in alder and fir seedlings grown at density 16 vs. density 2 at the end of the season.

During the growing season, the major effect of density stress was to reduce growth (Fig.22) and the seasonal growth and CO_2 exchange differences ie. although the pattern was basically similar in most cases, changes in growth and CO_2 exchange were less variable in seedlings grown at the high vs. low density. This may have been the result of shading effects modifying the impact of seasonal environmental stresses on the individual in the population.

The large time period (38 days) between successive harvests of alder and fir seedlings in this study did not permit comparison of growth periodicity between high and low density plants. Winget and Kozlowski (1964) have reported, however, that growth may begin later and cease earlier in suppressed vs. dominant trees in a conifer-hardwood stand during a growing season.

SUMMARY

1) Seedlings of red alder and Douglas-fir were grown in pure and mixed cultures at densities 2, 4, 8 and 16 plants dm^{-2} and harvested at three successive intervals during a growing season. Morphological and physiological responses of the seedlings to density stress were examined by combining growth analysis measurements with measurements of apparent photosynthesis (APS) and dark respiration (RS) on the crop and selected individuals from the crop.

2) In most combinations, the major effect of increasing density was to suppress growth of the seedlings throughout the season. The general reduction in growth at the higher densities was attributed mainly to light competition on the basis of:

(a) No change or a reduction in root-weight ratios with increasing density in alder and fir. If root competition was the major factor limiting growth then one would expect a much higher root weight ratio under the shaded conditions of higher densities (Stern 1965). This was not the case in this study.

(b) A marked decrease in crop APS rates for both alder and fir with increasing density. This reduction in crop APS rates probably resulted from increased mutual shading of foliage during the APS measurements. APS rates of single seedlings from the crop did not show

a marked reduction at the higher densities and in some cases, increased.

3) An important adaptation for growth under low light levels was shown for both alder and fir seedlings at the higher densities. In fir seedlings, proportionately more photosynthetic tissue per plant was produced under the shaded conditions of higher densities in the pure treatment. Alder, however, showed either no change or a reduction in leaf weight ratio, but was still able to maintain a high photosynthetic surface area per plant (leaf area ratio) by increasing its specific leaf area in the mixed treatment. For a given weight of leaf tissue alder was capable of maintaining a greater leaf area (ie. a higher specific leaf area) than fir. This is an important growth response for alder in that a high photosynthetic surface area is possible without diverting available assimilates (which may be limiting for growth) into greater leaf biomass (leaf weight ratio).

4) Between fir treatments, there was no significant difference in mean seedling biomass, RGR_p, NAR, RWR, SWR and LWR in fir seedlings. Alder seedlings grown in the mixed treatment, however, had lower mean seedling biomass, RGR_p, NAR, LWR and LAR but greater RWR, SWR and NWR than alder seedlings from the pure treatments. This large difference in growth response between A-pure and A-mixed seedlings was attributed to a marked reduction in light levels below the dense fir canopy in the mixed treatment.

5) Comparison of alder and fir responses in the pure treatments showed that alder had a higher RGR_p than fir seedlings. This was

explained by alder's higher net assimilation rate (NAR) and leaf weight ratio (LWR) at every density. Furthermore, alder usually showed higher APS rates, dark respiration rates and photochemical capacities than Douglas-fir seedlings at every growth density.

6) The supposed shade intolerance of alder was not explained on the basis of photosynthetic efficiency or on the size of the leaf system with increasing density, and hence, shading. Alder did, however, exhibit some characteristics of shade intolerance; 1) a low root weight ratio combined with a high LAR at the higher densities, 2) high dark RS rates, and 3) a marked flexibility in growth response under different levels of density. Fir, on the other hand, showed much higher RWR and proportionately lower LWR, lower dark RS rates and exhibited a less variable growth response to density stress than alder.

7) Nitrogen concentration within the plant tissues in alder showed no consistent trend with density, but the higher NWR in alder at the higher densities suggested that nodules via their nitrogen-fixing capacity acted as a compensatory mechanism for reduced nitrogen levels in the root medium. Fir, however, showed reduced nitrogen concentration at the higher densities, indicating that reduced soil nitrogen levels arising from root competition may have induced nitrogen shortages in the plant tissues.

EPILOGUE

As Baker (1945) indicated, the only reasonable criteria in separating plants into shade tolerance categories is the ability of a plant to survive and grow successfully under shaded conditions. The apparent inability of alder seedlings to establish themselves below dense shaded canopies under natural conditions, and hence their shade intolerance, was not explained on the basis of photosynthetic efficiency under either high or low light intensities. Alder's shade intolerance may, therefore, arise in later stages of growth (Krueger and Ruth 1969; Worthington 1965). In their second year of growth, however, alder seedlings (Part II) were capable of utilizing low light intensities more efficiently (ie. higher photochemical capacity) than the more shade tolerant Douglas-fir. Furthermore, alder was able to maintain a higher leaf weight ratio and leaf area ratio than fir seedlings under low levels of light, and this represents a favourable adaption by the plant for greater light interception under shaded conditions. The ability of alder seedlings to utilize high light intensities efficiently (high light saturation level) may be advantageous on the forest floor where high irradiance of sunflecks provides a significant percentage of the below canopy light level (Krueger and Ruth 1969).

Loach (1970) has suggested that the respiration rate rather than the photosynthetic efficiency under low light levels may be the most important criteria for success or failure of a plant species under

shaded conditions. Although alder had much higher dark respiration rates than Douglas-fir, it still maintained a higher APS:RS ratio, and hence NAR than Douglas-fir under all light intensities in the competition study. Furthermore, alder has been shown to outgrow the more shade tolerant Sitka spruce and Western hemlock seedlings under 10 percent total radiation below a forest canopy (Ruth 1967; cf. Krueger and Ruth 1969) which suggests that alder seedlings once established may grow successfully in a shaded habitat. The inability of alder to survive in shade may be more pronounced, however, immediately following seedling establishment early in the season, where there is a high APS:RS ratio (Table 4).

The ability of alder seedlings to use low light intensities efficiently and to grow successfully once established below a shaded canopy suggests, in part, that the shade intolerance may be related more to seed germination and seedling establishment on the forest floor. Ruth (1968) has reported a very low level of alder establishment under a forest canopy (one seedling per 31 viable seeds), and suggested that this may be a result of unfavourable soil conditions. In general, best germination of alder seeds is found on bare mineral soils (Newton et al. 1968). McVean (1954) found depressed germination of Alnus glutinosa seeds in the presence of toxic substances, probably tannins in unweathered alder litter, and that almost any amount of organic matter or litter on the soil surface creates micro-environments too dry for alder seedlings to tolerate. The smaller root systems of alder seedlings combined with its higher leaf area ratio at the higher

densities in this study suggests that alder seedlings are more susceptible to drought on the forest floor than Douglas-fir seedlings. During initial seedling establishment, seedlings possessing a proportionately greater root system would have a definite advantage as their roots could penetrate the litter surface more and be less affected by evapo-transpiration losses than seedlings with small root systems. The high nitrogen concentration found in alder leaf litter (Mikola 1958) combined with low light levels would also suppress the development of a root system in seedlings trying to establish themselves below an alder stand.

The importance of red alder in vegetation succession was evident in Part 1 of this study, where alder seedling root nodules fixed appreciable amounts of nitrogen for growth (almost 1.50 mg plant^{-1} · day^{-1} in late August). In field studies, alder is recognized as an important species by its capacity to enrich soils with nitrogen (Tarrant and Trappe 1971). Dense stands of alder in their first 20 years of growth may fix nitrogen at an annual rate of more than 300 kg per hectare on nitrogen deficient soils (Newton et al. 1968; Zavitovski and Newton 1968). Furthermore, other forest tree species may benefit from the nitrogen-fixing properties of red alder (Wollum and Youngberg 1964; Tarrant 1961). Most of the nitrogen from alder is added to the soil by leaf fall (Mikola 1958) although Virtanen (1957) suggested that direct secretion of nitrogen from nodules to the soil may occur and benefit associated plants. This study was not able to determine whether fir received any benefit from nitrogen fixed in red alder root nodules

in the mixed treatment owing to the large differences in light levels between fir treatments.

Based upon patterns of growth, nitrogen fixation and apparent photosynthesis, it is possible to briefly outline a few theoretical changes which may occur in the above parameters with increasing stand development in alder (Fig.25). In general, the highest relative growth rates (arising from a high NAR and a high LWR) and relative nitrogen fixation rates (from a high APS rate combined with a low soil nitrogen level) would initially occur in alder seedlings established in exposed habitats with low soil nitrogen levels, which, in many cases, characterize pioneer sites in vegetation succession. Alder via its nitrogen fixation would also be able to establish and outgrow many associated species in areas deficient in soil nitrogen. Tarrant (1968) has suggested in this respect, that alder is more effective as a nitrogen fixing plant when soil nitrogen is low. Nodule efficiency would also be maximum in the early stages of stand development in alder. As the nodules age and grow they develop a greater percentage of inactive tissue which reduces nodule efficiency (Stewart 1962). The lack of soil nitrogen combined with high light levels in the early stages of stand development would similarly give rise to a high root-weight ratio. As shown in the competition study (Part II), an increase in light level would also result in a corresponding reduction in SWR, LAR and SLA, and an increase in LWR.

With time, decreasing light levels (via shading effects) and increasing soil nitrogen levels (from alder leaf litter) would even-

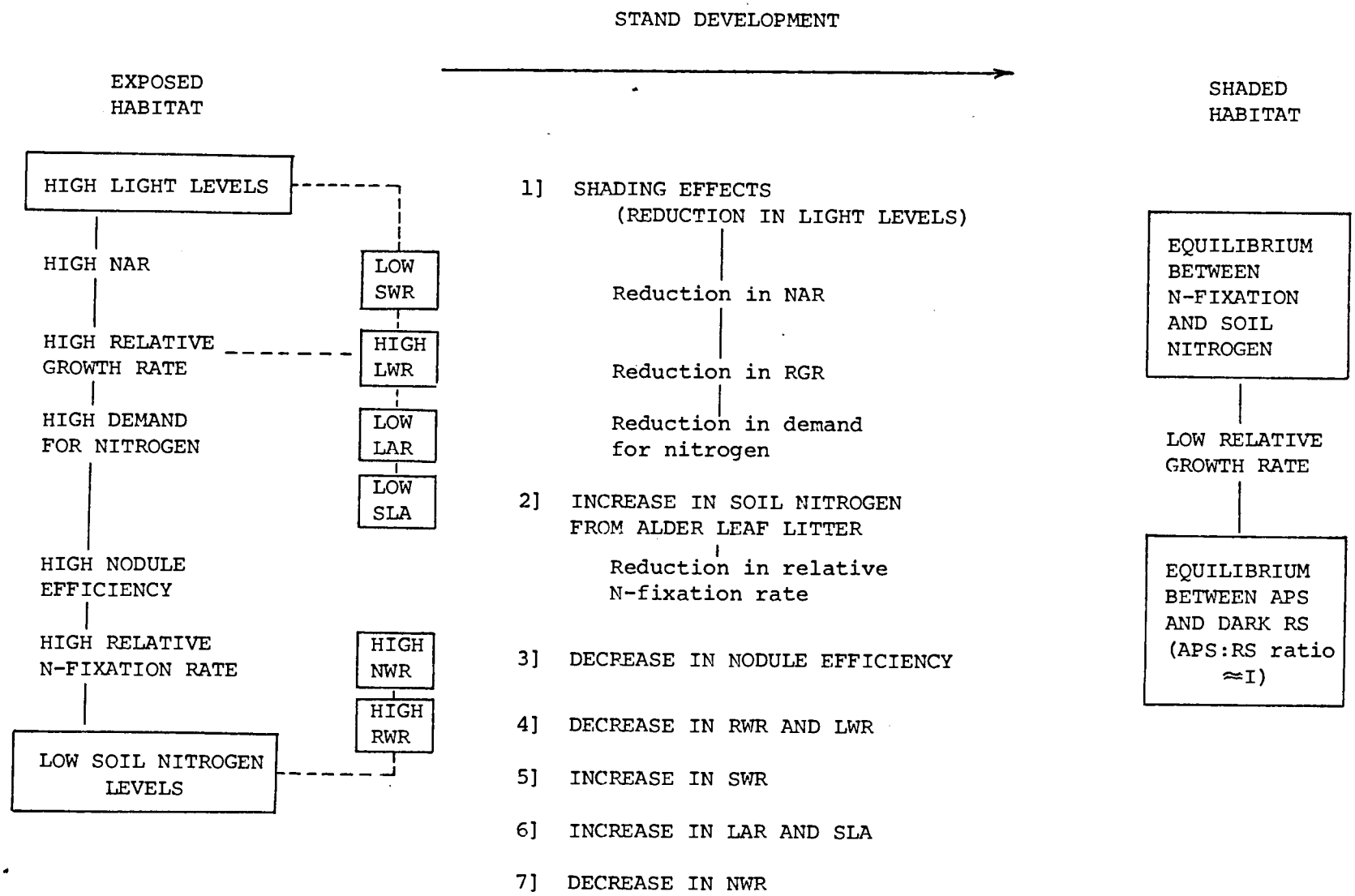


Figure 25. Theoretical changes in growth of alder with increasing soil nitrogen levels and shade.

tually result in a decrease in relative growth and nitrogen fixation rates, a decrease in RWR and an increase in SWR until an equilibrium is established between nitrogen fixation and soil nitrogen and between APS and dark respiration. Newton et al. (1968) have suggested that equilibration of nitrogen fixation with soil nitrogen occurs before the age of 20 years, after which contributions from nitrogen fixation are small.

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APPENDIX I

Table 1. Energy (μ watts cm^{-2}) for 10 nm intervals provided by the 500 watt Dicrolite lamps at light intensities used for the apparent photosynthesis measurements. Energy was measured at the top of the plant chamber.

Spectral region (nm)	Light intensity (ft-c)									
	5000	4000	3000	2500	2000	1500	1000	750	500*	250*
400	8.0	6.0	3.1	2.5	1.0	1.2	0.4	1.1	0.6	0.4
10	9.0	6.0	4.5	4.0	3.2	2.5	1.8	1.9	1.1	0.4
20	12.0	9.0	5.9	4.6	3.6	2.9	1.6	2.1	1.4	0.5
30	13.0	12.0	7.0	5.6	4.2	3.5	2.8	2.8	1.9	0.7
40	19.0	13.0	10.0	7.5	6.3	5.0	3.5	3.8	2.6	0.9
450	23.0	17.0	11.4	9.3	6.8	5.7	3.9	4.1	2.9	1.1
60	28.0	22.0	13.8	12.5	8.7	7.4	5.1	5.1	3.5	1.3
70	34.0	25.0	16.2	13.7	10.3	8.3	5.9	5.9	3.8	1.6
80	39.0	28.0	18.6	15.8	12.1	9.7	6.5	6.4	4.5	1.8
90	40.0	31.0	19.4	17.4	13.3	10.7	6.8	6.7	4.5	1.8
500	46.0	36.0	22.5	19.9	13.9	12.1	7.8	7.8	5.2	2.1
10	48.0	38.0	23.2	20.8	15.2	12.6	7.8	7.7	5.3	2.1
20	55.0	46.0	27.4	25.1	16.7	14.4	9.1	9.3	6.4	2.7
30	63.0	48.0	31.2	27.7	21.0	16.8	10.5	10.2	6.8	2.7
40	61.0	49.0	30.5	27.0	20.4	16.3	10.5	10.4	7.2	2.9
550	72.0	58.0	36.0	32.0	24.0	19.5	12.6	12.3	8.3	3.2
60	72.0	55.0	34.4	32.8	26.6	20.0	13.6	10.9	7.7	3.0
70	68.0	55.0	34.1	29.1	20.3	18.5	11.2	12.6	7.7	3.6
80	92.0	74.0	45.5	41.6	26.6	24.7	16.2	15.6	10.5	4.1
90	98.0	78.0	49.4	46.4	43.3	28.1	18.2	14.6	10.7	3.8
600	83.0	72.0	42.3	35.8	30.0	21.5	14.6	15.7	9.9	3.8
10	106.0	82.0	49.6	45.3	27.3	26.7	17.4	16.7	11.3	4.5
20	90.0	72.0	44.3	41.3	39.0	27.0	16.5	13.5	9.7	3.6
30	106.0	84.0	52.0	44.9	29.9	25.8	17.7	16.9	11.4	4.5
40	89.0	73.0	43.4	40.3	31.0	23.6	15.6	13.9	9.7	3.7
650	69.0	62.0	33.5	32.0	29.8	20.1	13.4	10.3	7.4	2.8
60	69.0	50.0	32.2	27.3	18.0	16.1	10.5	11.2	7.3	2.8
70	67.0	56.0	32.2	29.1	24.1	17.4	11.3	9.3	6.9	2.6
80	54.0	46.0	27.0	24.0	19.2	14.4	9.2	7.9	5.6	2.2
90	43.0	36.0	21.4	19.0	16.1	11.3	7.1	5.7	3.9	1.6
700	34.0	27.0	16.6	14.9	12.0	8.6	5.7	4.8	3.4	1.3
10	29.0	24.0	14.7	13.0	10.2	7.3	4.9	4.1	2.9	1.1
20	25.0	21.0	12.2	11.6	8.7	6.5	4.3	3.8	2.6	1.0
30	23.0	20.0	11.9	10.7	8.3	6.1	4.0	3.4	2.5	1.0
40	23.0	18.0	11.4	10.2	7.8	6.0	3.0	3.4	2.3	0.9
750	23.0	17.0	11.3	10.1	7.7	5.9	3.0	3.4	2.3	0.9

* For the 500 ft-c measurement, one screen was placed on top of the ISCO sensor, and for the 250 ft-c measurement, three neutral gray fibreglas screens were placed on top of the sensor.

APPENDIX I

Table 2. Seasonal pattern of mean dry weight distribution for nodulated (+) and non-nodulated (-) alder seedlings. Values given at successive harvests throughout the growing season include standard errors; n = 8 for nodulated plants, and n = 4 for non-nodulated plants.

Harvest date	Plants	LWR Leaf weight ratio	SWR Stem weight ratio	RWR Root weight ratio	NWR Nodule weight ratio
		(mg d. wt plant component / mg d. wt plant $x10^2$)			
2 June	+	54.48 ± 1.57	17.65 ± 2.02	24.42 ± 3.04	3.78 ± 0.66
	-	47.21 ± 3.77	19.76 ± 2.15	33.02 ± 3.05	
16 June	+	58.38 ± 1.12	18.63 ± 0.97	21.16 ± 1.42	1.79 ± 0.24
	-	44.80 ± 1.91	18.20 ± 0.76	37.07 ± 1.81	
*30 June	+	62.18 ± 1.07	16.47 ± 1.03	17.97 ± 0.83	3.38 ± 0.40
	-	37.79 ± 2.32	16.60 ± 1.59	45.59 ± 3.20	
14 July	+	62.18 ± 0.73	16.23 ± 0.63	15.63 ± 0.92	5.94 ± 0.29
28 July	+	62.54 ± 0.96	16.50 ± 0.74	15.07 ± 0.66	5.86 ± 0.52
11 Aug.	+	61.80 ± 0.84	20.58 ± 1.34	11.93 ± 0.98	5.64 ± 0.36
25 Aug.	+	57.56 ± 1.50	22.16 ± 0.78	14.38 ± 1.05	5.57 ± 0.21
8 Sept.	+	50.32 ± 1.35	26.35 ± 0.77	18.94 ± 1.53	4.37 ± 0.33
22 Sept.	+	47.14 ± 2.16	27.73 ± 1.92	20.62 ± 2.01	4.50 ± 0.46
6 Oct.	+	42.09 ± 1.83	30.53 ± 0.97	22.09 ± 1.28	5.26 ± 0.33

* Non-nodulated seedlings died following this harvest date.

Table 3. Mean apparent photosynthesis (APS) and dark respiration rates (mg CO_2 h^{-1} dm^{-2} single surface) for nodulated (+) and non-nodulated (-) alder seedlings at successive harvest dates throughout the growing season. Each value is a mean of 2 or 3 measurements (runs) for each plant.

Harvest date	Plant	Light intensity (ft-c)									Dark resp.
		5000	4000	3000	2500	2000	1500	1000	750	500	
2 June	+	.	.	13.79	14.27	14.27	14.74	.	.	.	5.70
	+	.	.	18.84	19.64	17.60	.	.	.	.	7.36
	-	.	.	18.84	.	17.59	.	.	.	.	8.44
16 June	+	28.75	28.52	26.30	25.01	22.85	19.41	14.45	11.21	6.04	3.74
	+	25.11	25.36	27.97	27.09	24.98	21.89	17.25	.	8.29	6.08
	+	.	.	24.86	25.12	23.85	.	.	.	.	4.09
	-	.	9.61	9.85	9.85	9.85	8.79	7.99	5.59	4.28	4.41
	-	.	.	8.84	8.84	8.58	8.58	7.54	6.49	.	3.73
30 June	+	24.02	24.08	23.53	23.01	20.22	17.17	13.83	9.25	5.87	4.18
	+	.	.	.	.	.	.	.	.	6.92	3.83
	-	.	.	3.73	3.73	3.73	.	2.90	.	.	2.49
14 July	+	18.12	17.48	16.63	14.61	15.78	10.92	8.01	3.49	1.83	3.35
	+	15.87	16.17	15.60	17.02	13.16	.	.	.	.	4.79
	+	20.24	19.31	19.19	.	.	.	.	.	.	.
28 July	+	14.47	14.09	14.50	13.47	12.47	10.97	7.16	3.83	2.47	2.43
	+	.	14.04	13.66	12.42	11.40	10.44	7.92	3.75	2.48	2.05
	+	.	13.20	13.16	12.02	11.28	10.70	7.06	4.08	2.76	2.04
11 Aug.	+	10.64	10.78	10.49	10.03	9.37	8.14	5.30	2.97	1.80	1.72
	+	12.62	12.84	12.38	11.89	10.94	10.15	6.71	.	.	1.15
	+	12.54	12.75	12.60	12.10	11.58	.	.	.	.	2.12
25 Aug.	+	10.82	10.76	9.82	9.58	9.02	7.68	4.99	2.75	1.75	1.66
	+	12.02	13.15	12.88	11.63	10.93	9.16	6.13	.	.	2.11
	+	11.59	11.69	11.74	11.20	10.48	8.65	5.17	.	.	1.84
8 Sept.	+	12.37	12.89	12.56	12.41	10.97	9.66	6.06	3.04	1.84	1.93
	+	10.59	11.79	11.64	10.91	9.86	8.23	5.43	.	.	1.78
	+	10.88	11.18	11.10	10.78	9.70	8.14	.	.	.	1.68
22 Sept.	+	8.27	8.20	7.64	7.33	6.91	5.91	.	.	.	1.25
	+	8.45	8.40	7.92	7.42	6.84	7.01	.	.	.	1.73
	+	11.10	10.85	9.98	9.54	8.39	.	.	.	.	2.11
8 Oct.	+	.	7.78	7.46	7.35	7.00	.	.	.	.	1.31

Table 4. Mean nitrogen content per unit dry weight of plant component for nodulated (+) and non-nodulated (-) alder seedlings at successive harvests throughout the growing season. Values given include standard errors; n = 8 for nodulated seedlings, and n = 4 for non-nodulated seedlings.

Harvest date	Plants	Leaf	Stem	Root	Nodule	Plant
		(mg tissue N / mg d. wt tissue x10^2)				
2 June	+	2.47 ± .12	2.15 ± .12	1.74 ± .21	1.90 ± .23	2.20 ± .09
	-	1.60 ± .22	1.25 ± .17	1.60 ± .08		1.53 ± .14
16 June	+	1.92 ± .10	1.04 ± .03	1.69 ± .09	3.19 ± .31	1.74 ± .08
	-	0.86 ± .04	0.54 ± .02	1.12 ± .08		0.89 ± .04
*30 June	+	1.82 ± .15	1.37 ± .05	1.66 ± .09	3.44 ± .10	1.84 ± .09
	-	0.67 ± .02	0.52 ± .05	0.68 ± .08		0.64 ± .03
14 July	+	2.33 ± .11	1.44 ± .05	1.54 ± .06	3.23 ± .09	2.11 ± .08
28 July	+	2.32 ± .10	1.28 ± .05	1.34 ± .10	3.08 ± .15	2.04 ± .06
11 Aug.	+	2.39 ± .10	1.24 ± .07	1.76 ± .04	3.07 ± .12	2.11 ± .08
25 Aug.	+	2.74 ± .06	1.35 ± .08	1.71 ± .04	2.80 ± .09	2.28 ± .04
8 Sept.	+	2.96 ± .06	0.96 ± .05	1.44 ± .06	2.97 ± .10	2.14 ± .04
22 Sept.	+	2.67 ± .11	1.09 ± .06	1.69 ± .08	2.61 ± .06	2.03 ± .07
6 Oct.	+	2.57 ± .06	1.18 ± .06	1.76 ± .07	2.22 ± .12	1.94 ± .06

* Non-nodulated seedlings died following this harvest.

APPENDIX II

Table 1. Primary growth and dry weight measurements at three successive harvest dates (t_1= 23 July, t_2= 1 September, and t_3= 8 October) during the growing season for the mean seedling grown at densities of 2, 4, 8 and 16 plants dm^{-2} in Alder-pure, Alder-Fir mixed, and Fir-pure treatments

HARVEST 1

Treatment	Density (plants per dm^2)	Sample No.	Stem ht. (cm)	Leaf area (mm^2)	Leaf	Stem	Root	Nodule	Plant
					(dry weight in mg)				
A-pure	2	1	7.2	983	58.43	37.23	30.05	3.01	128.72
		2	5.3	915	42.40	26.21	20.54	1.20	90.35
		3	6.0	811	41.76	25.08	20.04	1.56	88.44
	4	1	6.5	955	50.55	29.22	23.56	1.39	104.72
		2	5.5	834	47.21	30.45	24.56	1.46	103.68
		3	6.6	919	48.78	26.84	21.17	1.62	98.41
	8	1	5.8	643	33.62	18.33	16.16	1.80	69.91
		2	6.1	601	29.02	19.54	9.79	1.10	59.45
		3	5.6	673	34.62	17.37	18.66	1.32	71.97
	16	1	5.6	431	25.11	16.38	12.06	1.12	54.67
		2	6.0	696	34.98	21.29	12.16	1.10	69.53
		3	6.2	574	29.26	19.44	16.45	1.91	67.06
A-mixed	2/1	1	6.6	1123	51.01	20.16	28.18	1.93	101.28
		2	6.3	890	44.41	19.68	28.14	1.68	93.91
		3	5.7	859	48.24	22.48	26.68	1.05	98.45
	4/2	1	4.7	598	27.50	20.44	18.57	1.06	67.57
		2	5.4	650	31.20	22.44	20.57	1.38	75.59
		3	5.9	570	29.35	27.36	14.69	1.41	72.81
	8/4	1	8.6	1103	34.99	24.74	16.05	2.25	78.03
		2	7.3	947	34.21	21.91	12.84	1.46	70.42
		3	6.4	704	20.17	20.50	14.78	1.75	57.20
	16/8	1	5.4	434	11.54	9.00	6.63	1.39	28.56
		2	6.6	731	18.22	19.35	15.26	3.16	55.99
		3	7.2	803	31.03	30.06	18.66	3.39	83.14

* For the mixed treatments, 2/ indicates the number of seedlings of both species grown in the crop, and /1 indicates the seedling number of one species grown in the crop.

APPENDIX II

Table 1 (continued)

HARVEST 1

Treatment	Density (plants per dm^2)	Sample No.	Leader extens. (cm)	Stem ht. (cm)	Distance 1st needle (cm)	Needle	Stem	Root	Plant
						(dry weight in mg)			
F-pure	2	1	9.0	17.0	4.2	600.2	297.1	335.5	1232.7
		2	8.8	18.2	3.8	776.5	381.2	310.3	1468.0
		3	10.9	22.8	4.5	1163.5	552.5	446.1	2162.2
	4	1	10.0	19.3	4.0	960.2	467.7	457.5	1885.5
		2	9.5	18.5	3.7	871.7	446.3	342.5	1660.5
		3	9.8	20.7	4.0	1107.5	528.2	494.8	2130.5
	8	1	8.9	18.0	3.3	758.0	355.3	371.0	1484.2
		2	11.6	21.2	3.1	824.7	454.3	405.0	1684.0
		3	10.8	22.1	4.2	930.3	497.8	405.3	1833.4
	16	1	9.5	18.1	4.2	603.6	309.5	294.0	1207.1
		2	10.1	18.2	3.6	461.2	237.5	234.5	933.2
		3	12.0	21.1	4.0	662.9	353.9	279.6	1296.4
F-mixed	2/1	1	11.5	21.8	3.0	1163.0	613.0	298.9	2074.9
		2	10.6	22.0	3.4	981.4	454.4	218.7	1654.5
		3	12.5	21.5	4.2	858.6	409.5	370.1	1638.2
	4/2	1	13.0	19.0	5.1	1204.4	600.7	492.6	2297.6
		2	8.0	16.6	3.4	1146.0	456.5	301.0	1903.5
		3	10.0	22.0	4.6	1048.0	475.7	227.6	1751.4
	8/4	1	9.7	20.4	3.3	1200.6	544.4	521.2	2266.2
		2	10.5	20.6	3.6	1023.3	465.7	311.4	1800.4
		3	11.8	21.6	3.6	1012.6	508.6	439.9	1961.2
	16/8	1	10.4	21.0	3.9	767.1	451.4	324.8	1543.4
		2	12.7	21.8	4.4	833.0	427.5	341.7	1602.2
		3	11.2	21.6	3.5	1037.3	522.8	493.9	2054.0

APPENDIX II

Table 1 (continued)

HARVEST 2

Treatment	Density (plants per dm^2)	Sample No.	Stem ht. (cm)	Leaf area (mm^2)	Leaf	Stem	Root	Nodule	Plant
					(dry weight in mg)				
A-pure	2	1	8.2	3718	170.74	83.28	59.49	7.34	320.85
		2	9.2	4646	207.28	78.22	66.86	7.51	359.87
		3	8.6	3025	131.96	44.98	43.23	4.06	224.23
	4	1	6.8	2476	117.00	44.12	39.24	2.84	203.20
		2	8.8	3187	156.16	71.06	66.96	5.98	300.16
		3	8.3	2788	143.73	56.01	74.92	7.12	281.78
	8	1	7.1	1246	72.68	41.31	31.24	3.76	148.99
		2	7.3	1601	66.06	39.08	30.04	3.40	138.58
		3	8.4	1980	85.61	40.48	29.27	3.20	158.56
	16	1	7.1	1234	56.30	33.48	28.56	3.99	122.33
		2	7.8	1627	65.10	35.36	22.19	4.09	126.74
		3	8.4	1468	61.77	39.47	28.62	4.16	134.02
A-mixed	2/1	1	6.7	514	38.97	29.35	45.10	2.04	115.46
		2	5.3	480	37.67	25.28	39.13	3.26	105.34
		3	3.7	612	34.02	27.07	47.43	2.08	110.60
	4/2	1	7.4	1118	47.86	32.12	29.34	3.00	112.32
		2	7.8	1651	59.72	40.08	34.18	2.93	136.91
		3	7.2	1043	48.45	39.10	34.63	3.80	125.98
	8/4	1	7.7	1446	44.15	45.87	33.29	4.46	127.77(1)*
		2	9.7	1707	57.61	47.23	29.09	3.48	137.41(1)
		3	6.9	1709	40.95	29.67	24.08	2.97	97.67(1)
	16/8	1	7.1	506	15.56	19.87	13.13	2.40	50.96(2)
		2	9.3	465	16.08	18.59	9.24	2.61	46.52(3)
		3	6.5	573	14.51	17.07	8.29	1.84	41.71(1)

*( ) represents the number of dead seedlings in each sample.

APPENDIX II

Table 1 (continued)

HARVEST 2

Treatment	Density (plants per dm^2)	Sample No.	Leader extens. (cm)	Stem ht. (cm)	Distance 1st needle (cm)	Needle (dry weight in mg)	Stem (dry weight in mg)	Root (dry weight in mg)	Plant (dry weight in mg)
F-pure	2	1	8.4	20.5	3.4	1188.3	781.2	1195.2	3164.7
		2	10.2	17.2	4.0	948.5	733.5	1216.5	2898.5
		3	9.0	18.8	4.1	1079.4	686.3	1110.0	2875.7
	4	1	11.2	21.7	3.8	1074.9	797.6	954.7	2827.2
		2	10.6	20.4	4.2	1167.1	848.9	977.0	2993.0
		3	11.0	21.2	3.3	1134.2	831.6	967.0	2932.8
	8	1	12.7	21.5	3.6	827.2	561.6	554.8	1943.5
		2	11.2	19.2	3.8	862.6	565.2	561.5	1989.2
		3	12.9	22.2	4.2	890.2	630.4	648.5	2169.1
	16	1	12.9	21.2	4.2	532.7	355.3	335.7	1223.6
		2	13.3	22.8	4.9	807.6	565.7	580.9	1954.1
		3	10.9	21.7	5.4	780.8	648.4	549.0	1978.2
F-mixed	2/1	1	10.8	20.0	3.5	1104.4	694.3	481.2	2279.8
		2	13.1	20.9	3.2	1239.6	857.2	901.5	2998.5
		3	10.2	19.3	3.1	1531.6	951.4	1495.4	3978.4
	4/2	1	12.7	20.6	3.0	1357.1	840.3	1026.8	3224.2
		2	10.4	21.4	4.0	1314.4	708.8	935.1	2958.4
		3	11.4	22.8	3.2	1252.9	722.0	929.1	2904.0
	8/4	1	10.6	22.0	3.5	1485.5	876.8	836.8	3199.0
		2	11.4	20.9	2.7	1055.3	621.6	856.6	2533.6
		3	10.7	19.6	3.4	937.5	531.6	644.0	2113.1(1)*
	16/8	1	11.1	21.1	3.8	739.3	564.3	489.5	1793.1
		2	11.4	21.4	5.1	678.1	518.0	441.6	1637.7
		3	12.8	22.9	4.3	893.8	685.6	597.8	2177.2(1)

* ( ) represents the number of dead seedlings in each sample.

APPENDIX II

Table 1 (continued)

HARVEST 3

Treatment	Density (plants per dm^2)	Sample No.	Stem ht. (cm)	Leaf area (mm^2)	Leaf	Stem	Root	Nodule	Plant
					(dry weight in mg)				
A-pure	2	1	8.9	-	203.4	156.9	158.6	14.0	533.0
		2	9.2	-	225.4	123.7	96.8	9.5	455.3
		3	7.6	2934	160.1	93.9	96.6	12.9	363.5
	4	1	9.1	-	171.2	132.2	104.4	9.0	416.8
		2	6.2	-	121.8	87.6	93.7	8.8	312.0
		3	9.4	3313	151.2	84.4	85.3	8.5	329.3
	8	1	7.1	-	82.4	66.0	66.7	4.4	219.4
		2	6.9	-	76.3	57.8	70.6	5.6	210.3
		3	7.4	1892	100.4	62.6	75.5	8.5	246.9
	16	1	10.4	-	55.4	53.4	54.6	4.9	168.3
		2	9.3	-	53.0	51.0	54.5	5.8	164.3
		3	11.9	1844	84.2	72.5	65.9	8.5	231.0
A-mixed	2/1	1	6.6	-	64.7	64.5	56.5	8.4	194.1
		2	5.5	-	49.3	46.0	47.5	3.1	145.9
		3	6.6	1460	73.3	44.3	61.0	7.0	185.5
	4/2	1	6.1	-	66.2	59.3	74.3	7.0	206.7
		2	8.0	-	70.3	78.8	58.8	7.6	215.4
		3	7.6	1770	60.4	59.5	49.0	8.3	177.2
	8/4	1	8.0	-	91.4	88.9	62.9	8.0	251.2
		2	7.4	-	68.2	92.0	73.3	8.4	241.8
		3	8.6	1864	56.9	70.3	66.8	6.9	200.9
	16/8	1	6.7	-	23.6	32.0	22.7	3.2	81.4
		2	7.2	-	16.4	20.8	10.6	2.4	50.2
		3	5.9	880	28.3	29.2	13.4	2.5	73.4

APPENDIX II

Table 1 (continued)

HARVEST 3

Treatment	Density (plants per dm^2)	Sample No.	Leader extens. (cm)	Stem ht. (cm)	Distance 1st needle (cm)	Needle (dry weight in mg)	Stem (dry weight in mg)	Root (dry weight in mg)	Plant (dry weight in mg)
F-pure	2	1	11.2	19.4	3.3	1029.6	906.9	1247.8	3184.3
		2	10.0	19.6	3.2	1272.7	950.4	1376.9	3600.0
		3	12.2	22.0	3.6	1047.6	939.0	1262.5	3249.0
	4	1	11.4	22.0	3.5	1140.4	956.4	1275.0	3371.8
		2	12.2	20.2	3.4	1108.7	879.6	1223.5	3211.8
		3	10.7	20.2	4.4	1097.1	812.6	1109.1	3018.8
	8	1	13.4	23.2	4.9	856.2	715.5	637.0	2208.7
		2	12.2	21.9	4.8	1030.8	765.3	824.7	2620.8
		3	13.0	22.3	4.2	930.4	671.8	715.7	2317.9
	16	1	13.0	22.9	6.0	707.5	616.2	522.6	1846.2
		2	12.1	21.1	5.2	846.8	650.3	640.3	2137.4
		3	12.0	21.2	4.7	609.8	491.4	445.7	1546.8
F-mixed	2/1	1	13.0	20.3	2.7	1199.3	1179.8	1513.0	3892.1
		2	10.2	20.6	2.5	1260.6	1164.3	1553.0	3977.9
		3	11.8	24.4	3.7	967.8	1042.1	1555.0	3564.9
	4/2	1	10.6	18.4	2.6	1321.8	964.6	1434.4	3720.8
		2	12.2	21.4	4.3	1085.9	748.0	1069.0	2902.9
		3	13.5	22.5	4.6	951.0	841.1	1290.5	3082.6
	8/4	1	10.2	20.4	3.1	1141.4	833.8	1290.2	3265.3
		2	11.2	21.2	3.8	1014.23	874.2	1173.8	3062.2
		3	12.2	20.8	4.0	1013.7	799.1	879.5	2692.3
	16/8	1	13.1	21.6	4.6	992.2	770.0	757.2	2519.5
		2	12.3	23.7	6.2	862.4	689.2	650.8	2202.4
		3	9.5	19.3	4.9	595.0	489.1	518.8	1602.9

APPENDIX II.

Table 2. Proportion of total biomass present in leaves (LWR), stem (SWR), root (RWR), nodules (NWR), leaf area ratio (LAR) and specific leaf area (SLA) at three successive harvest dates (t_1= 23 July, t_2= 1 September, and t_3= 8 October) during the growing season for the mean seedling grown at densities of 2, 4, 8 and 16 plants dm^{-2} in Alder-pure, Alder-Fir mixed, and Fir-pure treatments.

Treatment	Density (plants per dm^2)	Sample No.	LWR	SWR	RWR	NWR	LAR	SLA
			HARVEST 1					
A-pure	2	1	.454	.289	.233	.023	7.64	16.82
		2	.469	.290	.227	.013	10.13	21.58
		3	.472	.284	.227	.018	9.17	19.58
	4	1	.483	.279	.225	.013	9.12	18.89
		2	.455	.294	.237	.014	8.04	17.67
		3	.478	.300	.205	.017	8.92	18.87
	8	1	.481	.262	.231	.026	9.10	19.12
		2	.488	.329	.165	.018	10.11	20.71
		3	.481	.241	.259	.018	9.27	19.71
	16	1	.459	.300	.221	.020	9.71	21.15
		2	.503	.306	.175	.016	10.01	19.90
		3	.436	.290	.245	.028	8.25	20.08
A-mixed	2/1	1	.504	.199	.278	.019	11.09	22.02
		2	.473	.210	.300	.018	9.48	20.04
		3	.490	.228	.271	.011	8.72	17.81
	4/2	1	.407	.302	.275	.016	8.85	21.74
		2	.413	.297	.268	.018	8.60	20.83
		3	.403	.376	.202	.019	8.78	19.58
	8/4	1	.448	.317	.206	.019	14.14	31.52
		2	.486	.311	.182	.021	13.45	27.68
		3	.353	.358	.258	.031	12.36	35.64
	16/8	1	.404	.315	.232	.049	15.20	37.61
		2	.325	.346	.273	.056	13.06	40.12
		3	.369	.357	.222	.040	11.66	36.23

Treatment	Density (plants per dm^2)	Sample No.	LWR	SWR	RWR
			HARVEST 1		
F-pure	2	1	.487	.241	.272
		2	.529	.260	.211
		3	.538	.256	.206
	4	1	.509	.248	.243
		2	.525	.269	.206
		3	.520	.248	.232
	8	1	.511	.239	.250
		2	.490	.270	.240
		3	.507	.272	.221
	16	1	.500	.256	.243
		2	.494	.254	.251
		3	.511	.273	.216
F-mixed	2/1	1	.560	.295	.144
		2	.593	.275	.132
		3	.524	.250	.226
	4/2	1	.524	.261	.214
		2	.602	.240	.158
		3	.598	.272	.130
	8/4	1	.530	.240	.230
		2	.568	.259	.173
		3	.516	.259	.224
	16/8	1	.497	.292	.210
		2	.520	.267	.213
		3	.505	.254	.240

APPENDIX II

Table 2 (continued)

Treatment	Density (plants per dm^2)	Sample No.	LWR	SWR	RWR	NWR	LAR	SLA
			HARVEST 2					
A-pure	2	1	.532	.260	.185	.023	11.59	21.80
		2	.576	.217	.186	.021	12.91	22.41
		3	.588	.201	.193	.018	13.25	22.66
	4	1	.576	.217	.193	.014	12.18	21.16
		2	.520	.237	.223	.020	10.62	20.41
		3	.510	.199	.266	.025	9.78	19.54
	8	1	.488	.277	.210	.025	8.36	17.14
		2	.477	.282	.217	.024	11.55	24.23
		3	.540	.255	.185	.020	12.14	22.91
	16	1	.460	.274	.234	.033	10.09	21.92
		2	.514	.279	.175	.032	12.83	24.99
		3	.461	.294	.214	.031	10.51	24.63
A-mixed	2/1	1	.338	.254	.391	.018	4.45	13.19
		2	.358	.240	.372	.031	4.56	12.74
		3	.308	.245	.429	.019	5.53	17.99
	4/2	1	.426	.286	.261	.027	9.96	23.37
		2	.436	.293	.250	.021	12.06	27.64
		3	.385	.310	.275	.030	8.29	21.53
	8/4	1	.345	.359	.260	.035	11.32	32.76
		2	.419	.344	.212	.025	12.42	29.62
		3	.419	.304	.246	.030	17.87	44.96
	16/8	1	.305	.390	.258	.047	9.92	32.49
		2	.346	.400	.199	.056	10.00	28.93
		3	.348	.409	.199	.044	12.10	41.64

Treatment	Density (plants per dm^2)	Sample No.	LWR	SWR	RWR
		HARVEST 2			
F-pure	2	1	.376	.247	.378
		2	.327	.253	.420
		3	.375	.239	.386
	4	1	.380	.282	.338
		2	.390	.284	.326
		3	.387	.284	.330
	8	1	.426	.289	.286
		2	.434	.284	.282
		3	.410	.291	.299
	16	1	.435	.290	.274
		2	.413	.290	.297
		3	.395	.328	.278
F-mixed	2/1	1	.484	.304	.211
		2	.414	.286	.301
		3	.385	.239	.376
	4/2	1	.421	.261	.318
		2	.444	.240	.316
		3	.431	.249	.320
	8/4	1	.464	.274	.262
		2	.416	.245	.338
		3	.444	.252	.305
	16/8	1	.412	.315	.273
		2	.414	.316	.270
		3	.410	.315	.275

APPENDIX II

Table 2 (continued)

Treatment	Density (plants per dm^2)	Sample No.	LWR	SWR	RWR	NWR	LAR	SLA
			HARVEST 3					
A-pure	2	1	.382	.294	.298	.026	-	-
		2	.495	.272	.213	.021	-	-
		3	.440	.258	.266	.035	8.36	18.54
	4	1	.411	.317	.250	.022	-	-
		2	.390	.281	.300	.028	-	-
		3	.459	.256	.259	.026	10.63	21.91
	8	1	.376	.301	.304	.020	-	-
		2	.363	.275	.336	.026	-	-
		3	.407	.254	.306	.034	7.57	18.92
	16	1	.329	.317	.324	.029	-	-
		2	.323	.310	.332	.035	-	-
		3	.364	.314	.285	.037	7.94	21.98
A-mixed	2/1	1	.333	.332	.291	.043	-	-
		2	.338	.315	.326	.021	-	-
		3	.395	.239	.329	.038	7.87	19.93
	4/2	1	.320	.287	.359	.034	-	-
		2	.326	.366	.273	.035	-	-
		3	.340	.336	.277	.047	10.25	29.62
	8/4	1	.364	.354	.250	.032	-	-
		2	.282	.380	.303	.035	-	-
		3	.283	.350	.332	.034	9.56	33.54
	16/8	1	.289	.392	.279	.039	-	-
		2	.326	.415	.212	.047	-	-
		3	.386	.398	.183	.034	12.09	31.07

Treatment	Density (plants per dm^2)	Sample No.	LWR	SWR	RWR
		HARVEST 3			
F-pure	2	1	.323	.285	.392
		2	.354	.264	.382
		3	.322	.289	.389
	4	1	.338	.284	.378
		2	.345	.274	.381
		3	.363	.269	.367
	8	1	.388	.324	.288
		2	.393	.292	.315
		3	.401	.290	.309
	16	1	.383	.334	.283
		2	.396	.304	.300
		3	.394	.318	.288
F-mixed	2/1	1	.308	.303	.389
		2	.317	.293	.390
		3	.271	.292	.436
	4/2	1	.355	.259	.386
		2	.374	.258	.368
		3	.308	.273	.419
	8/4	1	.350	.255	.395
		2	.331	.286	.383
		3	.376	.297	.327
	16/8	1	.394	.306	.301
		2	.392	.313	.296
		3	.371	.305	.324

APPENDIX II

Table 3. Calculated growth analysis data between successive harvest periods ($t_0 - t_1$, $t_0 - t_2$, and $t_0 - t_3$) for the mean seedling grown at densities 2, 4, 8 and 16 plants dm^{-2} in Alder-pure, Alder-Fir mixed, and Fir-pure treatments during the growing season.

Treatment	Density (plants per dm^2)	Sample No.	Rdmp	RGR	NAR
			HARVEST 1		
A-pure	2	1	2.22	.0281	.0612
		2	1.21	.0189	.0401
		3	1.16	.0182	.0387
	4	1	1.59	.0228	.0477
		2	1.56	.0223	.0486
		3	0.83	.0140	.0302
	8	1	0.68	.0120	.0256
		2	0.40	.0078	.0164
		3	0.73	.0129	.0272
	16	1	0.28	.0055	.0122
		2	0.67	.0120	.0246
		3	0.60	.0110	.0244
A-mixed	2/1	1	1.50	.0219	.0447
		2	1.31	.0198	.0424
		3	1.43	.0212	.0440
	4/2	1	0.62	.0110	.0260
		2	0.83	.0140	.0325
		3	0.75	.0131	.0304
	8/4	1	0.89	.0150	.0327
		2	0.69	.0122	.0258
		3	0.34	.0067	-.0165
	16/8	1	-0.41	-.0115	-.0262
		2	0.31	.0062	-.0161
		3	1.02	.0166	.0401
F-pure	2	1	4.42	.0039	-.0074
		2	10.61	.0085	.0154
		3	28.88	.0186	.0338
	4	1	21.60	.0150	.0281
		2	15.68	.0117	.0214
		3	28.05	.0170	.0338
	8	1	11.04	.0085	.0164
		2	16.30	.0120	.0230
		3	20.23	.0143	.0267
	16	1	3.75	.0032	.0060
		2	-3.45	-	-.0064
		3	6.10	.0051	.0097
F-mixed	2/1	1	26.59	.0177	.0313
		2	15.52	.0115	.0200
		3	15.09	.0113	.0210
	4/2	1	32.44	.0203	.0373
		2	22.07	.0152	.0260
		3	18.07	.0131	.0226
	8/4	1	31.62	.0198	.0364
		2	19.36	.0138	.0244
		3	23.59	.0161	.0299
	16/8	1	12.60	.0097	.0184
		2	14.15	.0108	.0198
		3	26.03	.0173	.0325

APPENDIX II

Table 3 (continued)

Treatment	Density (plants per dm^2)	Sample No.	Rdmp	RGR	NAR
			HARVEST 2		
A-pure	2	1	3.64	.0260	.0514
		2	4.15	.0276	.0514
		3	2.37	.0214	.0400
	4	1	2.09	.0200	.0378
		2	3.37	.0251	.0505
		3	3.13	.0244	.0496
	8	1	1.38	.0159	.0334
		2	1.24	.0150	.0318
		3	1.50	.0168	.0329
	16	1	1.03	.0134	.0290
		2	1.09	.0138	.0281
		3	1.18	.0145	.0316
A-mixed	2/1	1	0.94	.0126	.0327
		2	0.80	.0115	.0283
		3	0.87	.0120	.0325
	4/2	1	0.90	.0122	.0279
		2	1.22	.0150	.0332
		3	1.08	.0138	.0332
	8/4	1	1.10	.0140	.0357
		2	1.23	.0150	.0343
		3	0.70	.0104	.0237
	16/8	1	0.09	.0018	-.0051
		2	0.03	.0007	-.0016
		3	-0.03	-.0007	-.0018

Treatment	Density (plants per dm^2)	Sample No.	Rdmp	RGR	NAR
			HARVEST 2		
F-pure	2	1	27.63	.0143	.0320
		2	24.13	.0131	.0318
		3	23.83	.0131	.0290
	4	1	23.19	.0129	.0283
		2	23.57	.0136	.0297
		3	24.58	.0134	.0292
	8	1	11.56	.0078	.0164
		2	12.16	.0083	.0168
		3	14.53	.0094	.0198
	16	1	2.09	.0018	-.0037
		2	11.70	.0081	.0168
		3	12.02	.0081	.0175
F-mixed	2/1	1	15.99	.0099	.0193
		2	25.44	.0136	.0288
		3	38.34	.0173	.0384
	4/2	1	28.41	.0145	.0306
		2	24.92	.0134	.0274
		3	24.20	.0131	.0272
	8/4	1	28.08	.0145	.0288
		2	19.33	.0115	.0239
		3	13.80	.0090	.0182
	16/8	1	9.58	.0069	.0143
		2	7.54	.0058	.0117
		3	14.64	.0094	.0198

APPENDIX II

Table 3 (continued)

Treatment	Density (plants per dm^2)	Sample No.	Rdmp	RGR	NAR
			HARVEST 3		
A-pure	2	1	4.29	.0219	.0539
		2	3.61	.0205	.0421
		3	2.80	.0184	.0412
	4	1	3.27	.0196	.0460
		2	2.35	.0170	.0414
		3	2.50	.0175	.0382
	8	1	1.54	.0140	.0345
		2	1.46	.0136	.0343
		3	1.78	.0152	.0355
	16	1	1.09	.0117	.0311
		2	1.05	.0115	.0306
		3	1.64	.0145	.0364
A-mixed	2/1	1	1.31	.0129	.0341
		2	0.89	.0104	.0272
		3	1.24	.0127	.0276
	4/2	1	1.43	.0136	.0366
		2	1.50	.0138	.0371
		3	1.17	.0122	.0318
	8/4	1	1.82	.0152	.0382
		2	1.73	.0150	.0435
		3	1.37	.0134	.0384
	16/8	1	0.33	.0053	.0147
		2	0.05	.0012	-.0028
		3	0.26	.0044	.0106
F-pure	2	1	18.59	.0097	.0233
		2	22.24	.0106	.0249
		3	19.16	.0097	.0240
	4	1	20.24	.0101	.0240
		2	18.83	.0097	.0237
		3	17.14	.0092	.0207
	8	1	10.04	.0064	.0138
		2	13.65	.0078	.0170
		3	10.99	.0069	.0145
	16	1	6.86	.0048	.0106
		2	9.41	.0060	.0131
		3	4.23	.0032	.0069
F-mixed	2/1	1	24.80	.0113	.0286
		2	25.55	.0115	.0288
		3	21.93	.0106	.0286
	4/2	1	23.30	.0110	.0256
		2	16.12	.0088	.0196
		3	17.70	.0092	.0233
	8/4	1	19.30	.0099	.0228
		2	17.52	.0092	.0221
		3	14.28	.0081	.0182
	16/8	1	12.76	.0076	.0164
		2	9.98	.0064	.0138
		3	4.72	.0037	-.0078

APPENDIX II.

Table 4. Dry weight and leaf area of plants used for APS measurements at three successive harvest dates (t_1 = 23 July, t_2 = 1 September, and t_3 = 8 October) for the crop and selected individual(s) from the crop grown at densities of 2, 4, 8 and 16 plants dm^{-2} in Alder-pure, Alder-Fir mixed, and Fir-pure treatments. Each value is a single measurement.

Treatment	Density (plants per dm^2)	Leaf area (dm^2)	Total Crop					Individual(s)*					
			Leaf	Stem	Root	Nodule	Plants	Leaf area (dm^2)	Leaf	Stem	Root	Nodule	Plant(s)
				(dry weight, g)						(dry weight, g)			
							Harvest I						
A-pure	2	0.2634	0.12	0.06	0.08	0.01	0.27	-	-	-	-	-	-
	4	0.4357	0.23	0.14	0.14	0.03	0.54	0.1005	0.05	0.03	0.03	0.01	0.12
	8	1.2973	0.69	0.33	0.31	0.03	1.36	0.1552	0.09	0.04	0.03	0.01	0.17
	16	2.0387	1.05	0.51	0.52	0.06	2.14	0.1170	0.07	0.03	0.03	t	0.13
A-mixed**	2/1***	1.0965	1.15	0.57	0.73	t	2.45	0.1547	0.10	0.05	0.06	t	0.21
	4/2	2.6632	2.77	1.33	2.01	0.01	6.12	0.2917	0.13	0.08	0.07	0.01	0.29
	8/4	4.3699	4.38	2.51	2.96	0.01	9.86	0.6625	0.26	0.19	0.16	0.01	0.62
	16/8"	7.5533	7.83	4.53	4.89	0.02	17.27	0.7711	0.29	0.21	0.16	0.02	0.68
F-pure	2	1.7342	1.93	1.26	1.52	-	4.71	-	-	-	-	-	-
	4	3.5568	3.95	2.23	2.82	-	9.00	0.9471	1.05	0.65	0.79	-	2.49
	8	8.6832	9.65	5.01	4.91	-	19.57	0.7481	0.83	0.54	0.50	-	1.87
	16	11.7204	13.02	7.73	7.11	-	27.86	0.9054	1.01	0.62	0.46	-	2.09
F-mixed**	2/1***	1.0965	1.15	0.57	0.73	t	2.45	0.9418	1.05	0.52	0.67	-	2.24
	4/2	2.6632	2.77	1.33	2.01	0.01	6.12	2.3715	2.64	1.25	1.94	-	5.83
	8/4	4.3699	4.38	2.51	2.96	0.01	9.86	3.7074	4.12	2.32	2.80	-	9.24
	16/8	7.5533	7.83	4.53	4.89	0.02	17.27	6.7822	7.54	4.32	4.73	-	16.59

* For the pure treatments, values for individual(s) represent a single seedling; for the mixed treatments, values for the individual(s) represent the total species crop (ie. A-mixed + F-mixed individuals = A-mixed or F-mixed total crop).

** Crop values for A-mixed and F-mixed are the same.

*** 2/ represents total crop density of both species, and /1 represents the crop density of one species.

" Only 6 alder seedlings survived in this treatment

t Trace

APPENDIX II.

Table 4 (continued)

Treatment	Density (plants per dm^2)	Leaf area (dm^2)	Total Crop: Leaf	Stem (dry weight, g)	Root (dry weight, g)	Nodule (dry weight, g)	Plants	Individual(s): Leaf area (dm^2)	Leaf (dry weight, g)	Stem (dry weight, g)	Root (dry weight, g)	Nodule (dry weight, g)	Plant(s)
						Harvest 2							
A-pure	2	0.4573	0.24	0.13	0.11	0.01	0.49	-	-	-	-	-	-
	4	0.9200	0.48	0.21	0.24	0.03	0.96	0.3164	0.18	0.07	0.10	0.01	0.36
	8	2.1151	1.01	0.50	0.63	0.07	2.21	0.2901	0.15	0.08	0.11	0.01	0.35
	16	3.0193	1.61	0.95	1.02	0.10	3.68	0.2719	0.16	0.09	0.12	0.01	0.38
A-mixed	2/1	1.4788	1.51	1.13	1.58	0.01	4.23	0.2293	0.12	0.06	0.11	0.01	0.30
	4/2	3.6002	3.61	1.93	2.65	0.02	8.21	0.5363	0.21	0.21	0.18	0.02	0.62
	8/4	4.4401	4.04	3.31	3.51	0.03	10.88	1.1443	0.38	0.37	0.23	0.03	1.00
	16/8*	7.9360	8.53	6.70	6.46	0.01	21.70	0.3308	0.09	0.12	0.06	0.01	0.28
F-pure	2	1.7855	1.98	1.52	1.84	-	5.34	-	-	-	-	-	-
	4	2.9084	3.23	2.27	2.41	-	7.91	0.7382	0.82	0.50	0.54	-	1.86
	8	6.0146	6.68	4.50	4.30	-	15.48	1.0251	1.14	0.58	0.52	-	2.24
	16	10.4513	11.60	7.58	7.35	-	26.53	1.2961	0.72	0.33	0.52	-	1.57
F-mixed	2/1	1.4788	1.51	1.13	1.58	0.01	4.23	1.2495	1.39	1.07	1.47	-	3.93
	4/2	3.6002	3.61	1.93	2.65	0.02	8.21	3.0639	3.40	1.72	2.47	-	7.59
	8/4	4.4401	4.04	3.31	3.51	0.03	10.88	3.2958	3.66	2.94	3.28	-	9.88
	16/8	7.9360	8.53	6.70	6.46	0.01	21.70	7.6052	8.44	6.58	6.40	-	21.42

* Only 5 alder seedlings survived in this treatment.

APPENDIX II.

Table 4 (continued)

Treatment	Density (plants per dm^2)	Leaf area (dm^2)	Total Crop (dry weight, g) Leaf	Stem	Root	Nodule	Plant	Harvest 3	Leaf area (dm^2)	Individual(s) (dry weight, g) Leaf	Stem	Root	Nodule	Plant(s)
A-pure	2	0.2904	0.20	0.16	0.26	0.02	0.64		0.1686	0.10	0.08	0.16	0.01	0.35
	*4	0.5131	0.37	0.30	0.35	0.03	1.05		0.1577	0.09	0.10	0.12	0.01	0.32
	**8	0.5370	0.31	0.45	0.58	0.05	1.39		0.2426	0.14	0.18	0.23	0.02	0.57
	+16	1.8961	1.04	1.00	1.21	0.14	3.39		0.3553	0.20	0.20	0.27	0.02	0.69
A-mixed	2/1	1.3910	1.31	0.96	1.72	0.01	4.00		0.0598	0.04	0.10	0.10	0.01	0.25
	4/2	2.2752	2.06	1.58	2.66	0.02	6.32		0.2672	0.14	0.24	0.23	0.02	0.63
	8/4	5.6142	4.96	3.79	4.67	0.04	13.46		0.6538	0.23	0.35	0.42	0.04	1.04
	"16/8	7.1129	6.66	4.60	5.11	0.01	17.38		0.1783	0.04	0.11	0.06	0.01	0.22
F-pure	2	2.2595	2.16	1.78	3.33	-	7.27		1.0338	0.99	0.82	1.78	-	3.59
	4	3.6777	3.51	3.34	4.51	-	11.36		0.6007	0.57	0.78	0.99	-	2.34
	8	8.0019	7.64	6.04	5.42	-	19.10		0.9644	0.92	0.53	0.45	-	1.90
	16	12.0065	11.45	9.17	9.61	-	30.23		0.8511	0.81	0.66	0.48	-	1.95
F-mixed	2/1	1.3910	1.31	0.96	1.72	0.01	4.00		1.3392	1.27	0.86	1.62	-	3.75
	4/2	2.2752	2.06	1.58	2.66	0.02	6.32		2.0080	1.92	1.34	2.43	-	5.69
	8/4	5.6142	4.96	3.79	4.67	0.04	13.46		4.9604	4.73	3.44	4.25	-	12.42
	16/8	7.1129	6.66	5.60	5.11	0.01	17.38		6.9346	6.62	5.49	5.05	-	17.16

* Only 3 alder seedlings survived in this treatment (1 dead)

** Only 5 alder seedlings survived in this treatment

\+ Only 15 seedlings survived in this treatment

" Only one seedling from this treatment (alder) was measured for CO_2 exchange

APPENDIX II.

Table 5. Apparent photosynthesis and dark respiration rates at three successive harvest dates (t_1 = 23 July, t_2 = 1 September, and t_3 = 8 October) for the total crop and individual(s) from the crop grown at densities of 2, 4, 8 and 16 plants dm^{-2} in Alder-pure, Alder-Fir mixed, and Fir-pure treatments. Each value is the mean of 3 separate 'runs' at each light intensity.

Harvest 1

Treatment	Light intensity (ft-c)	Density →	CO_2 uptake or release h^{-1} (mg CO_2 plant(s)$^{-1}$ or crop^{-1})								CO_2 uptake or release h^{-1} (mg CO_2 dm^{-2})							
			2		4		8		16		2		4		8		16	
			Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.
'A-pure	5000		3.54	-	3.78	1.25	14.19	1.46	12.42	0.33	13.45	-	8.69	12.42	10.94	9.39	6.09	2.84
	1000		2.65	-	3.16	1.04	9.21	1.09	9.91	0.22	10.07	-	7.25	10.40	7.10	7.03	4.86	1.87
	500		1.17	-	1.26	0.42	3.15	0.33	3.87	0.17	4.46	-	2.89	4.23	2.43	2.14	1.90	1.48
	0		0.23	-	0.48	0.10	1.94	0.43	2.79	0.22	0.87	-	1.09	0.95	1.50	2.80	1.37	1.86
**A-mixed	5000		6.11	1.23	22.22	3.44	26.00	4.96	31.60*	3.28*	5.57	7.94	8.34	11.81	5.95	7.49	4.18*	4.25*
	1000		4.85	1.10	13.82	3.06	17.48	4.33	20.82*	3.16*	4.42	7.07	5.19	10.50	4.00	6.53	2.76*	4.10*
	500		1.45	0.48	3.37	1.50	5.29	1.88	6.65*	0.92*	1.32	3.08	1.27	5.16	1.21	2.84	0.88*	1.19*
	0		1.67	0.23	3.10	0.30	4.76	0.85	5.79*	1.44*	1.52	1.46	1.16	1.03	1.09	1.27	0.77*	1.87*
'F-pure	5000		17.58	-	26.59	9.81	38.19	5.29	31.98	6.81	10.14	-	7.48	10.36	4.40	7.07	2.73	7.53
	1000		11.56	-	18.11	6.90	21.25	4.44	18.76	5.08	6.67	-	5.09	7.29	2.45	5.94	1.60	5.61
	500		4.43	-	6.08	2.16	3.47	1.19	1.16	1.72	2.55	-	1.71	2.28	0.40	1.59	0.10	1.90
	0		1.97	-	4.10	1.15	9.62	1.39	11.02	1.06	1.14	-	1.15	1.21	1.11	1.87	0.94	1.17
"F-mixed	5000		6.11	4.88	22.22	18.78	26.00	21.06	31.60	28.35	5.57	5.18	8.34	7.92	5.95	5.68	4.18	4.18
	1000		4.85	3.75	13.82	10.77	17.48	12.90	20.82	17.63	4.42	3.98	5.19	4.54	4.00	3.48	2.76	2.60
	500		1.45	0.97	3.37	1.87	5.29	3.41	6.65	5.70	1.32	1.03	1.27	0.79	1.21	0.92	0.88	0.84
	0		1.67	1.44	3.10	2.80	4.76	3.89	5.79	4.34	1.52	1.53	1.16	1.18	1.09	1.05	0.77	0.64

* Only 6 alder seedlings survived in the crop for this treatment and density.

** Crop values for A-mixed and F-mixed are the same. Ind. values for the A-mixed and F-mixed treatments represent the total species crop for one species only.

' Ind. values for A-pure and F-pure represent measurements of a single selected seedling in the treatment and density.

" Ind. values for F-mixed are crude estimates only determined by subtracting the CO_2 uptake or release (total alder component) from the - total crop CO_2 uptake or release (Crop measurement). Consequently, the estimate does not account for increased light intensity reaching the foliage of fir if the alder seedlings had been removed rather than the fir seedlings.

APPENDIX II.
Table 5 (continued)

Harvest 3

Treatment	Light intensity (ft-c)	Density →	CO_2 uptake or release h^{-1} (mg CO_2 plant(s)$^{-1}$ or crop^{-1})								CO_2 uptake or release h^{-1} (mg CO_2 dm^{-2})							
			2		4		8		16		2		4		8		16	
			Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.	Crop	Ind.
A-pure	5000		2.50	1.62	4.11*	1.05	4.53**	1.72	16.11"	3.44	8.61	9.59	8.01*	6.66	8.44**	7.12	8.50"	9.69
	1000		1.69	1.29	3.17*	1.00	3.70**	1.64	11.50"	2.95	5.83	7.62	6.18*	6.36	6.89**	6.75	6.06"	8.31
	500		0.26	0.16	0.78*	0.48	1.01**	0.91	3.89"	1.14	0.90	0.98	1.52*	3.01	1.87**	3.75	2.05"	3.21
	0		0.60	0.38	1.10*	0.36	1.06**	0.47	2.81"	0.75	2.07	2.26	2.14*	2.28	1.99**	1.93	1.49"	2.11
A-mixed	5000		7.23	0.33	7.89	0.70	14.87	1.35	21.72	-	5.20	5.53	3.47	2.62	2.65	2.07	3.05	-
	1000		6.19	0.29	6.56	0.66	11.83	1.40	12.83	-	4.45	4.87	2.88	2.43	2.11	2.14	1.80	-
	500		2.73	0.15	2.43	0.32	3.43	0.30	2.02	-	1.97	2.47	1.07	1.22	0.61	0.45	0.28	-
	0		1.26	0.12	2.81	0.44	6.25	1.49	8.62	-	0.91	2.00	1.24	1.67	1.12	2.27	1.21	-
F-pure	5000		12.17	6.59	17.90	3.53	26.17	2.31	26.21	3.96	5.39	6.37	4.87	5.87	3.27	2.39	2.18	4.65
	1000		9.04	5.07	13.34	2.97	17.39	2.16	15.83	3.12	4.00	4.90	3.63	4.95	2.17	2.24	1.32	3.67
	500		2.53	1.99	4.88	0.92	4.31	1.27	1.69	0.94	1.12	1.93	1.33	1.52	0.54	1.32	0.14	1.11
	0		2.55	1.18	3.17	0.82	9.10	1.09	10.93	1.09	1.13	1.15	0.86	1.37	1.14	1.13	0.91	1.28
F-mixed	5000		7.23	6.90	7.89	7.19	14.87	13.54	21.72	-	5.20	5.18	3.47	3.58	2.65	2.73	3.05	-
	1000		6.19	5.90	6.56	5.90	11.83	10.42	12.83	-	4.45	4.43	2.88	2.94	2.11	2.10	1.80	-
	500		2.73	2.58	2.43	2.11	3.43	3.12	2.02	-	1.97	1.94	1.07	1.05	0.61	0.63	0.28	-
	0		1.26	1.14	2.81	2.37	6.25	4.76	8.62	-	0.91	0.86	1.24	1.18	1.12	0.96	1.21	-

* Only 3 alder seedlings survived in this treatment and density
** Only 5 alder seedlings survived in this treatment and density
" Only 15 alder seedlings survived in this treatment and density

APPENDIX II.
Table 5 (continued)

Harvest 2

Treatment	Light intensity (ft-c)	Density →	CO_2 uptake or release h^{-1} (mg CO_2 plant(s)$^{-1}$ or crop^{-1}) 2 Crop	2 Ind.	4 Crop	4 Ind.	8 Crop	8 Ind.	16 Crop	16 Ind.	CO_2 uptake or release h^{-1} (mg CO_2 dm^{-2}) 2 Crop	2 Ind.	4 Crop	4 Ind.	8 Crop	8 Ind.	16 Crop	16 Ind.
A-pure	5000		8.31	-	12.57	5.07	25.15	3.40	28.59	2.96	18.18	-	13.66	16.02	11.89	11.72	9.47	10.89
	1000		6.02	-	10.23	3.74	17.47	2.92	18.36	2.29	13.17	-	11.13	11.82	8.26	10.05	6.08	8.44
	500		1.62	-	4.00	1.51	5.14	1.22	5.09	0.88	3.53	-	4.34	4.78	2.43	4.20	1.68	3.22
	0		0.98	-	1.75	0.58	4.83	0.71	4.90	0.49	2.15	-	1.91	1.83	2.28	2.45	1.62	1.82
A-mixed	5000		18.00	3.52	31.71	7.15	36.90	10.71	46.30*	0.76*	12.17	15.33	8.81	13.33	8.31	9.36	5.83*	2.31*
	1000		11.98	2.55	22.18	6.41	24.59	7.97	25.72*	0.58*	8.10	11.11	6.16	11.97	5.54	6.97	3.24*	1.78*
	500		3.59	0.87	7.83	2.95	7.39	3.35	4.51*	1.40*	2.43	3.79	2.17	5.50	1.66	2.93	0.57*	4.21*
	0		2.90	0.88	5.03	0.92	7.73	2.28	15.51*	-	1.96	3.84	1.40	1.73	1.74	2.00	1.95*	-
F-pure	5000		13.58	-	19.80	4.40	24.73	6.58	43.53	8.65	7.60	-	6.81	5.95	4.11	6.43	4.17	6.68
	1000		10.38	-	14.97	3.60	15.74	5.62	23.56	7.19	5.81	-	5.15	4.88	2.62	5.49	2.25	5.55
	500		4.52	-	4.90	1.05	4.07	1.98	0.93	3.11	2.53	-	1.68	1.42	0.68	1.93	0.09	2.40
	0		1.83	-	4.78	1.33	9.27	1.48	16.52	1.74	1.02	-	1.64	1.80	1.54	1.45	1.58	1.34
F-mixed	5000		18.00	14.48	31.71	24.57	36.90	26.20	46.30	45.56	12.17	11.59	8.81	8.02	8.31	7.95	5.83	5.99
	1000		11.98	9.43	22.18	15.78	24.59	16.61	25.72	25.17	8.10	7.55	6.16	5.15	5.54	5.04	3.24	3.31
	500		3.59	2.72	7.83	4.87	7.39	4.05	4.51	3.12	2.43	2.18	2.17	1.59	1.66	1.23	0.57	3.12
	0		2.90	2.02	5.03	4.10	7.73	5.44	15.51	-	1.96	1.62	1.40	1.34	1.74	1.65	1.95	-

* Only 5 alder seedlings survived in this treatment and density.

LIST OF ABBREVIATIONS USED IN THE TEXT

APS..... APPARENT PHOTOSYNTHESIS

Dark RS... DARK RESPIRATION

APS:RS.... Ratio of apparent photosynthesis to dark respiration

Rdmp..... RATE OF DRY MATTER PRODUCTION (weight of plant produced $unit^{-1}$ time).

RGR_P..... RELATIVE GROWTH RATE OF THE PLANT (weight of plant produced·$weight^{-1}$plant·$time^{-1}$)

RGR_L..... RELATIVE GROWTH RATE OF THE LEAVES (weight of leaves produced·$weight^{-1}$ leaves·$time^{-1}$)

RGR_R..... RELATIVE GROWTH RATE OF THE ROOTS (weight of roots produced·$weight^{-1}$ roots·$time^{-1}$)

NAR..... NET ASSIMILATION RATE (weight of plant produced·$unit^{-1}$ leaf·$time^{-1}$)

LWR..... LEAF WEIGHT RATIO.... ratio of leaf weight to plant weight (mg leaf·mg^{-1} plant)

SWR..... STEM WEIGHT RATIO.... ratio of stem weight to plant weight (mg stem·mg^{-1} plant)

RWR..... ROOT WEIGHT RATIO.... ratio of root weight to plant weight (mg root·mg^{-1} plant)

NWR..... NODULE WEIGHT RATIO... ratio of nodule weight to plant weight (mg nodule·mg^{-1} plant)

LAR..... LEAF AREA RATIO..... ratio of leaf area to plant weight (mm^2 leaf·mg^{-1} plant)

SLA..... SPECIFIC LEAF AREA.... ratio of leaf area to leaf weight (mm^2 leaf·mg^{-1} leaf)

CURRICULUM VITAE

Alan Michael Williams

Personal History

Place of birth : Vancouver, British Columbia

Date of birth : August 2, 1947

Marital Status : Single

Educational Background

Graduated from Windsor Secondary, 1965.

Degrees

B.Sc. (Hons), Simon Fraser University, August 1968.

Awards

British Columbia Government Scholarships : Summer and Spring 1968; Fall, 1966 and 1967.

Simon Fraser University President's Research Grant, Spring 1971.

Teaching Experience

Teaching Assistant, Simon Fraser University:

BISC 101 - BISC 102, Introduction to Biology
BISC 300, Physics and Chemistry of the Environment
BISC 305, Comparative Animal Physiology
BISC 404, Plant Ecology
BISC 428, Modern Laboratory techniques

Graduate Courses Taken

BISC 804 - Ecology
BISC 825 - Forest Physiology
BISC 879 - Special Topics III : Modern Forestry Practices
BISC 806 - Adaptation and adaptability