COMPARATIVE GROWTH AND CARBON DIOXIDE EXCHANGE PATTERNS IN FIRST-YEAR RED ALDER AND BROADLEAF MAPLE SEEDLINGS GROWN UNDER DIFFERENT LIGHT INTENSITIES

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ABSTRACT

First-year seedlings of red alder (Alnus rubra Bong.) and broadleaf maple (Acer macrophyllum Pursh) were grown in 100, 56 and 22 percent of natural light. Growth analysis, apparent photosynthesis (APS) and dark respiration rate measurements, and chlorophyll content analysis were carried out on the two species at five harvest periods spaced approximately 30 days apart throughout the first growing season.

Biomass production of alder was significantly higher than that of maple. This difference may be accounted for by alder APS rates approximately four times those of maple. Alder shows higher growth rates and continues to increase in biomass to the end of the season, whereas the growth rate of maple declines after the first harvest in early summer and there is little biomass increment from mid-summer to end of the growing season. For both species, biomass increase and relative growth rates (RGR) were not significantly different within species among full-light (100 percent) control plants and those given shade treatments. These results are due to high respiration rates and low APS rates at low light intensities in the full-light alders in contrast to the low respiration rates and higher APS rates at low light intensities in the shade-grown alders. The shaded maples displayed higher APS rates at all light intensities in all but the first harvest period. Both species showed significantly higher chlorophyll contents in the shade-grown plants. Differences of all other factors among treatments in both species were negligible.

The significantly higher growth rates and APS rates give the alder a competitive advantage in occupying forest habitats disturbed by logging or fire in the Pacific Coast Mesothermal Forest area.

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INTRODUCTION

Broadleaf maple (Acer macrophyllum Pursh) and red alder (Alnus rubra Bong.) are common associates in the Pacific Coast Mesothermal Forest area. They are early invaders following logging or fire, and germinate well on mineral soil. They need full light to germinate and to establish seedlings (Sabhasri and Ferrel, 1960). Both species are acclimatized to the superhumid climates of the Pacific coast; they are limited primarily in their ranges by low moisture, particularly the alder, which requires at least 60 cm of rain per year (Worthington, 1965). Northern limits of both species are determined by low temperatures; alder cannot withstand temperatures below -18°C, or extended periods of low temperatures.

Maple is considered more shade tolerant, at least in comparison with conifers (Ruth and Muerle, 1965), but alder grows very rapidly on mineral soil with adequate light. Because of these high initial growth rates, either species can crowd out conifers, and thus become the initial successor species following elimination of conifer cover by fire or logging. Although considered a 'weed' tree in the coastal British Columbia area, the alder does perform an important function in fixing nitrogen through root nodules and fallen-leaf duff containing a high percentage of nitrogen (Tarrant et al, 1969). These two sources are estimated to add about 43 kilograms of nitrogen per hectare per year (Crocker and Major, 1955).

Maple if established first may shade out alder, but the reverse is also true. Thus they are not precisely competitive, but seem to have approximately the same biogeocoenotic requirements for establishment and growth.

There have been a number of studies on various eastern species of coniferous and broadleafed seedlings in relation to light requirements (Logan, 1965, 1966a, 1966b; Logan and Krotkov, 1969; Newhouse and Madgwick, 1968; Loach, 1967, 1970). Little experimental research has been done on broadleaf maple and

red alder. Most research reported has to do with their commercial uses or silviculture (survey of Forestry Abstracts).

Growth (biomass added) depends on how well the plant makes use of its environmental inputs: water, nutrients, and light, particularly the latter. Measurement of apparent photosynthesis (APS) rates and biomass accumulation in relation to the light regimens under which the plants were grown, should therefore indicate how the two species respond to light at different intensity levels. From these data, we may get some clues about their relative ecological roles in succession and about their distribution patterns.

Since growth is most rapid during the first seasons of a plant's life, and varies as the growing season progresses, a study of growth patterns from the seedling stage to the end of the first growing period should provide useful information.

As pointed out by Loach (1970), shade influences plant morphology as well and one must consider changes in the size and arrangement of the photosynthetic system as the APS rate is measured. Blackman (1968) together with his co-workers, showed that the effects of shade on gross morphology may be at least as important in growth response as changes in leaf physiology. For these reasons, although APS rates are considered primarily in this paper, growth analysis and the relative growth rate (RGR), root:shoot ratios, and leaf area ratios (LAR) are compared for the two species and the three treatments described below.

Formally stated, the null hypothesis for the experimental series was: Plants grown for their first season under differing degrees of shading will exhibit significant differences in growth, development, and function, and these differences will vary according to the species.

EXPERIMENTAL DESIGN AND PROCEDURE

Plant Material and Establishment

Two species of local interest were chosen: red alder (Alnus rubra Bong.) and broadleaf maple (Acer macrophyllum Pursh.). In April 1969, one hundred eight first-year seedlings of each species were collected at an approximate age of six weeks. An attempt was made to select uniform plants of median size.

The collection site was a southwest-facing slope on Burnaby Mountain, at an altitude of approximately 350 m. The slope was partially shaded by mature alders and western hemlock. Seedlings were taken from an area that received a moderate amount of shade, but was neither in full sun or in almost continual shade. The soil used in transplanting was taken from this general area, and was skimmed from the top 6 - 10 cm of the surface after it was cleared of duff. Effectively, this was the same type of mineral soil bed on which the alders had germinated. The maple seedlings were collected on the same slope, a short distance to the east along a roadside bank.

Seedlings were replanted in 400-ml plastic beakers that had been perforated on their bottoms with eight 1-mm holes to provide free drainage. After the soil had been screened through a 0.5-cm mesh screen to remove rocks and wood fragments, it was sifted through and over the seedling roots and packed uniformly to approach natural density. The plants were watered to saturation and placed on greenhouse benches under artificial light. The lights consisted of two banks, each containing six 96-in. G. E. Cool-white fluorescent 100-watt tubes and six 60-watt incandescent bulbs. At a distance of 75 - 80 cm, the plants received about 1000 ft-c of illumination, as measured with a Brockway Sekonic Studio Exposure Meter, Model S. A 12-hour photoperiod was used for the plants in the greenhouse.

Growing Conditions and Light Treatments

Following a stabilizing period of several days, moribund plants were replaced with healthy standby specimens. After another 10 days, the plants were divided randomly into three lots of thirty-six each of the two species and numbered for later random sampling (Fig. 1). One block was left uncovered (as control), and the second and third blocks were shaded by one and three layers of fibreglas 1-mm mesh screen to give 56 percent (partial shade) and 22 percent (full shade) of ambient light respectively. The screens were supported on frames that held the surface 20 cm above the 'canopy' of

1	2	3	4	5	6
7	8	9	10	11	12
13	14	15	16	17	18
19	20	21	22	23	24
25	26	27	28	29	30
31	32	33	34	35	36

Figure 1. Arrangement of plants in all treatments prior to random shifting to avoid edge effects.

the plants. In addition, the sides of the screen frames were covered with 6-in. strips of one- and three-layer screening to prevent side edge effects and to provide uniform illumination. The light intensities were 1000, 540 and 260 ft-c on the control, 1-layer shade, and 3-layer shade blocks respectively. There was no ambient light in the greenhouse, as windows were covered with black plastic sheeting. A hygrothermostat system maintained humidity at 60 - 70 percent, and air temperature at 21°C. Plants were watered each morning sufficiently to keep the surface of the soil just moist. Thus, the environment was relatively well controlled with light as the major experimental variable.

By the end of the third week, it was clear that light intensity was too low. Plants were becoming etiolated and some showed symptoms of damping off. During the fourth week, about 16 percent of the alder seedlings were replaced from the original source and all plants were moved to an exposed

walkway beside the greenhouse. The groups were oriented in a north-south row with the control treatments (100 percent ambient light) occupying the southern end and the highest shade treatment (22 percent ambient light) occupying the northern end (Fig. 2).

a)

North

b)

Shade: 22 percent ambient light

Maple

Alder

Shade: 56 percent ambient light

Maple

Alder

No shade: 100 percent ambient light (control)

Maple

Alder

South

Figure 2. Arrangement of the light treatments for the alder and maple seedlings, a) uncovered, and b) screen covered for shade. Foliage of maple seedlings is easily visible.

Light

Ambient light intensities varied widely for the plants throughout the season with the minimum for the control plants being 480 ft-c on a completely overcast day. Light intensity measurements made at noon and averaged over a number of cloudy and clear days throughout the season were as follows:

	Control (100 percent light)	Partial shade (56 percent light)	Full shade (22 percent light)
Clear day	8000 ft-c	4500	2000
Cloudy day	3000 ft-c	1600	700

Thus, the measurements consistently gave ratios of about 100:56:22 percent of the ambient light received by the control, partial shade, and full shade plants respectively.

Since the plants were grown in ambient light, they all received a similar spectral distribution of energy. The effect of the neutral gray fibrelas screen was simply to reduce the radiation intensity received at the leaves, the so-called 'iris effect'.

Temperature

As temperature control was lost by moving the plants outside the greenhouse, periodic air and soil temperatures were measured at noon to determine differences caused by differential shading. Representative temperatures measured were:

	Control (100 percent light)	Partial shade (56 percent light)	Full shade (22 percent light)
Ambient air at canopy level	19°C	21°C	20.5°C
Soil temperature, -1 cm			
Maple	24.5	21.5	20.5
Alder	29.0	24.0	24.0

Highest ambient air temperature occurred in the partial-shade treatment. The extra shade of the full-shade treatment apparently offsets the restricted air flow, whereas the partial shade treatment both restricts air flow and lets more radiation through.

Differences in soil temperature between species can be accounted for by the greater leaf area index of maple during early summer which effectively shaded much of the soil surface. Apparently this was also sufficient to bring both partial- and full-shade maple soil temperatures close together.

It was not possible to separate the effect of temperature differences from light treatment on growth of the alder and maple seedlings.

Humidity

From the appearance of mildew on the full-shade maple plants during mid-summer, it was deduced that relative humidity may be higher than under other treatments. Lower temperature under this treatment may also account for mildew growth. Thus, on humid days, side screens were lifted away from the sides to provide freer air movement over the plants.

Mildew was removed from most of the leaves by mopping affected spots with 70 percent ethanol. Following this treatment, no more mildew developed. Treated and untreated maple seedlings could not be distinguished in their photosynthetic response.

Water

All plants received natural precipitation. This was supplemented by periodic watering to minimize desiccation from warm winds which swept across the site and during prolonged dry periods. Because of their exposure, control (100 percent light) plants were supplemented with water more often than either the partial- or full-shade plants. Soil moisture gauges (Soil Moisture Equipment Corp., Santa Barbara, Calif.) were used to ensure that soil moisture would be comparatively uniform among the three light treatments. Gauge cups inserted 4 cm into a pot at the center of each block of plants showed when plants needed water to maintain soil moisture at 20 centibars (about 80 percent saturation) among all treatments. To prevent differential drying or edge effects, pots were rotated every two weeks. The inner nine pots were brought to the outer corners and replaced by those from outer rows.

Seasonal temperature and precipitation pattern

Daily temperature and precipitation patterns during the course of the season were obtained from the nearby Burnaby Mountain weather station (Fig. 3).

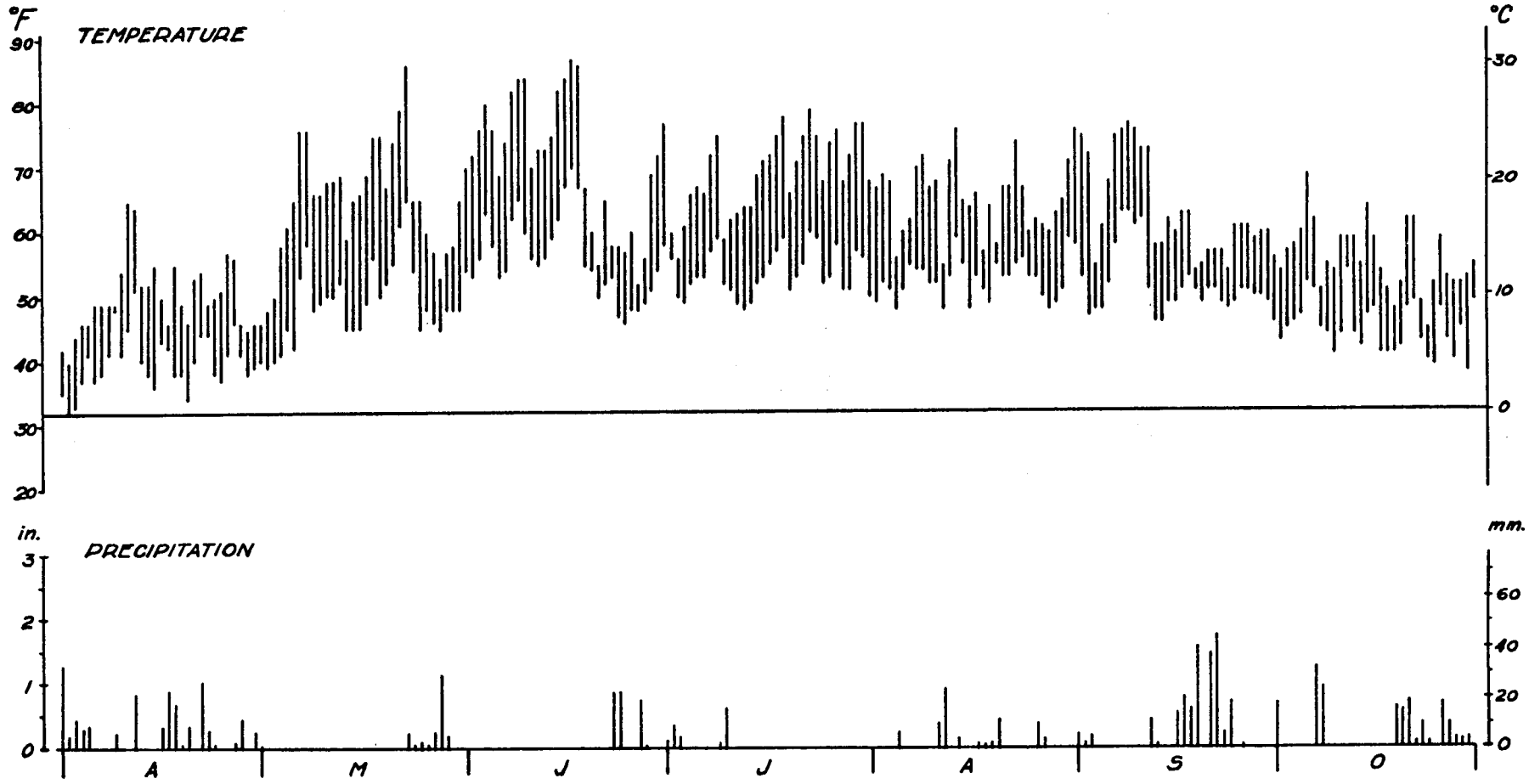


Figure 3. Seasonal temperature and precipitation pattern, Burnaby Mountain climatic station (Canada, Dept. of Transport. 1969).

Harvest Schedules

The first harvest and measurement of seedlings was designed originally to occur in early May. However, some seedling mortality and movement outside from the greenhouse delayed measurement. A final transplanting of three or four alders in each treatment and several maples occurred shortly after moving the seedlings outdoors. These transplants were obtained from the original source area but as they could not be preconditioned by the shade treatment for the same time as original seedlings, an attempt was made to obtain seedlings from corresponding levels of shade along the forest border. First harvest, as a result, did not occur until late May with subsequent harvests within the major harvest sections at approximately monthly intervals (Table 1).

Table 1. Harvest schedule.

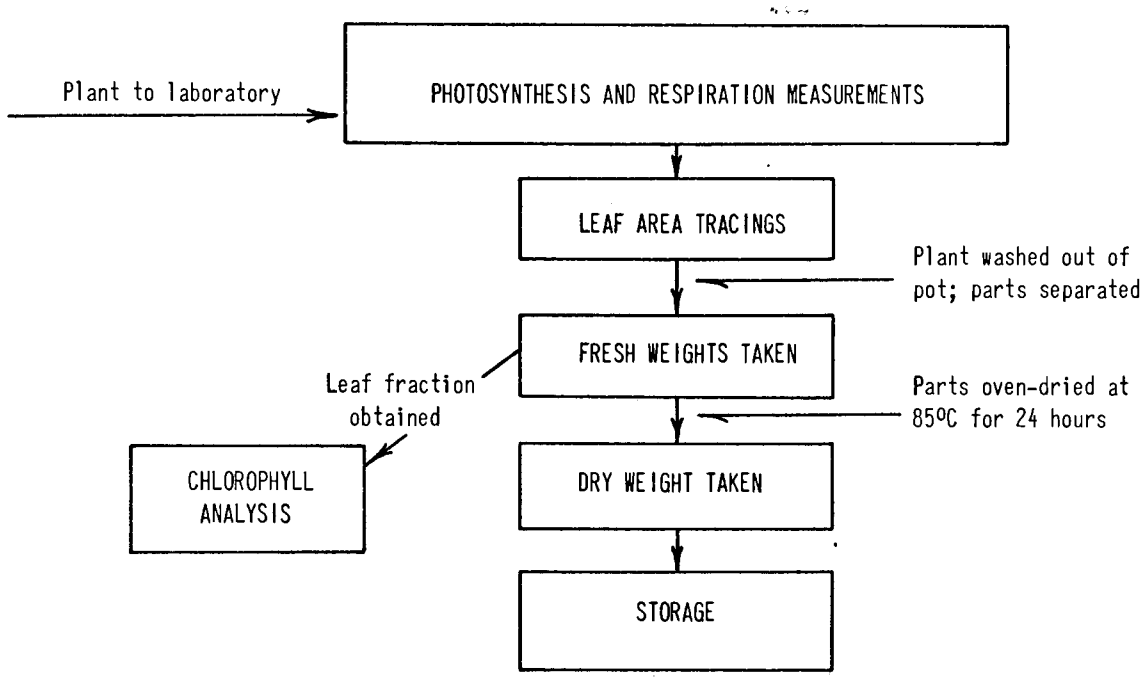
Harvest	Season	Section A		Section B	
		Long Run*	Days from planting**	Short Run	Days from planting
1	Late Spring (May - June)	27 May - 2 June 4 Maple 4 Alder	31 - 37	11 - 16 June 6 Maple 5 Alder	45 - 50
2	Early Summer (June - July)	23 - 27 June 3 Maple 3 Alder	57 - 61	7 - 11 July 4 Maple 5 Alder	71 - 75
3	Mid-summer (July - Aug.)	21 - 26 July 4 Maple 3 Alder	85 - 90	4 - 9 August 5 Maple 7 Alder	99 - 108
4	Late Summer (Aug.- Sept.)	18 - 23 August 3 Maple 3 Alder	113 - 118	1 - 8 September 6 Maple 6 Alder	126 - 133
5	Early Fall (Sept.- Oct.)	Nil		29 Sept.- 10 Oct.	166 - 177

*Long and Short Run refer to apparent photosynthesis measurements at several light intensities or at a standard but more limited series of light intensity.
**Days from planting are calculated from a base date of 26 - 29 April.

Sampling and Measurement Protocol

Plants were selected for measurement and harvest using random number tables (Moses and Oakford, 1963). For the CO_2 exchange measurements, plants were brought to the laboratory 24 hours

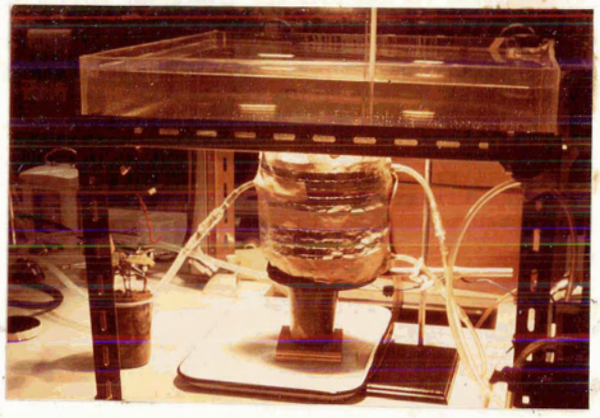
prior to the analyses. During preparation of the equipment and calibration of the infra-red analyzer, the test plant was exposed to a light intensity of approximately 3000 ft-c. The sampling and measurement sequence was as follows:



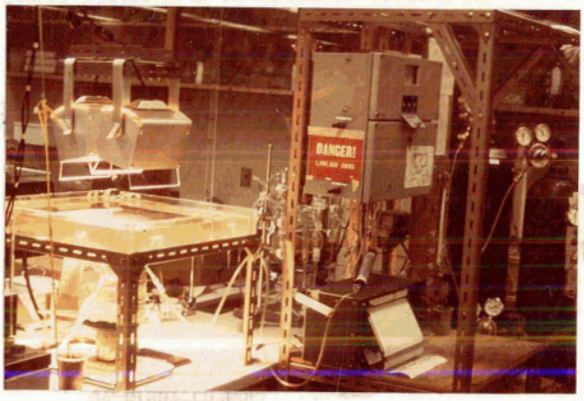
Photosynthesis and respiration measurements

A closed system was used for the apparent photosynthesis and respiration measurements. The measuring system consisted of a URAS II (Hartmann & Braun AG) infra-red gas analyzer, flow meter, mercury manometer, pump, desiccator and interchangeable plant chambers of various sizes. The components were interconnected with Tygon tubing and signal output from the analyzer was recorded on a Moseley 7100B Strip chart Recorder (Hewlett Packard) (Fig. 4). Volume of the measuring system excluding the plant chamber was approximately 530 cc; including the plant chamber, total volume of the system ranged from approximately 575 cc to 4330 cc. Small chambers were used during the initial harvest and larger ones near the end of the growing season.

The smallest chambers were square and constructed from clear 3 mm Plexiglas; the base was grooved to facilitate sealing the chamber with Apiezon Q and also contained the air inlet and outlet connections. The largest chambers were brass cylinders painted white on the inside and fitted with a



a



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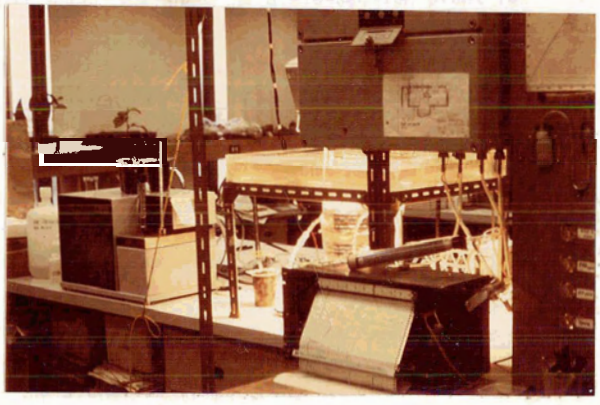


c

Figure 4. Equipment used for measuring apparent photosynthesis and dark respiration rates; a) insulated, cooled chamber under illumination, b) and c) lights, heat filter (water), URAS II infra-red gas analyzer and recorder.

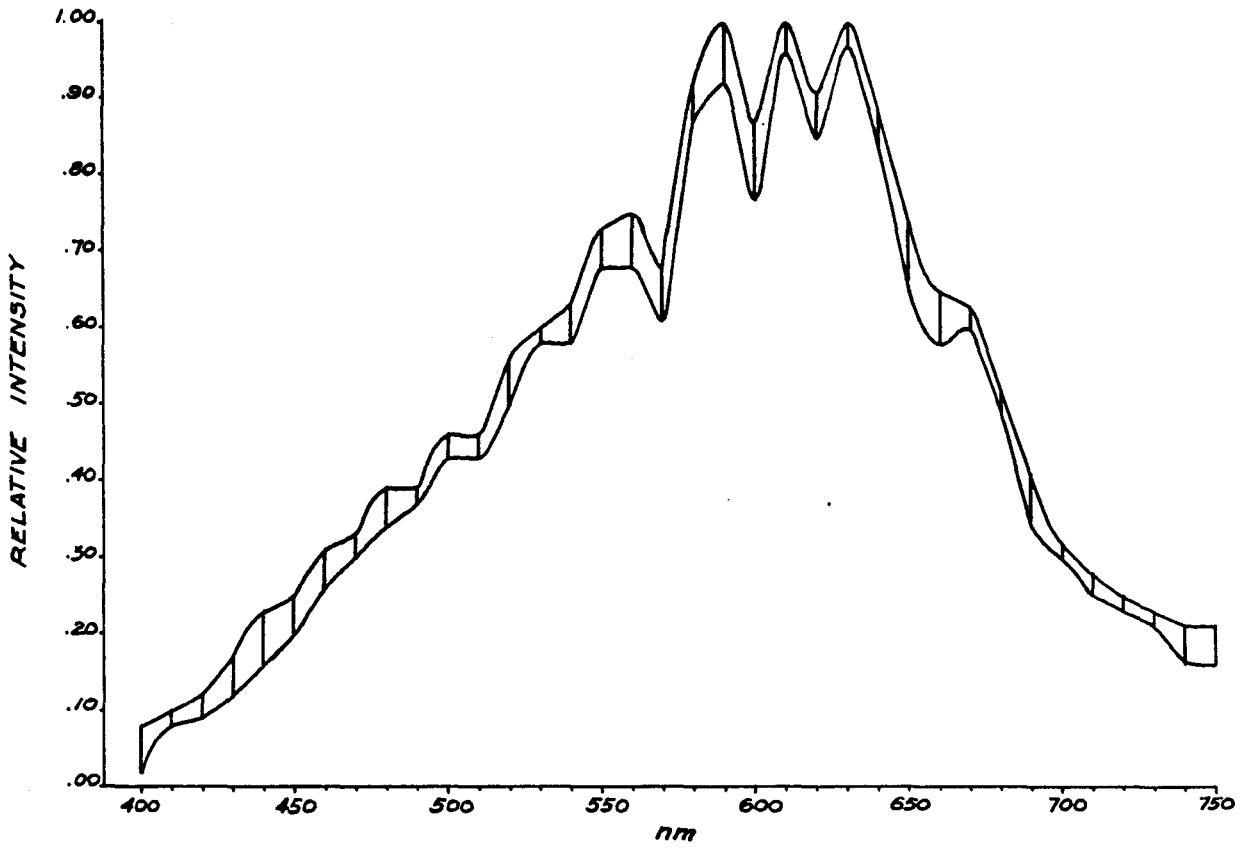
clear 3mm Plexiglas closure plate at one end. The cylinder was fitted with an air inlet and outlet. Base plates were grooved to accept the cylinder and for sealing and the plate slotted to receive the plant stem.

A flow rate of 1 liter per minute was used for all measurements. As a time lag occurs between the moment of CO_2 concentration change at the plant chamber and its indication at the analyzer, a 'circulation time' for the gas stream based on volume of the circuit components can be approximated. The 'circulation time' for the largest chamber used was approximately 1 1/2 minutes; for the smaller chambers it was proportionately lower. Smoke tests indicated sufficient turbulence of air flow within the chamber without the use of a fan or mixing device.

Illumination for the plant was provided by two 500-watt Dicrolite quartz-iodine lamps (3300°K emitted temperature) fitted with infra-red reflecting 'hot mirror' assemblies. Light intensity was controlled by raising or lowering the position of the lamps above the plant chamber. For the lowest light intensities used, the surface of the plant chamber was covered with neutral gray Fibreglas screening. Light intensity received by the canopy surface of the plant was measured with a Brockway Sekonic Exposure Meter. The spectral distribution of energy (400 - 750 nm) received by the plant under various experimental conditions was measured with an ISCO Model SRR spectroradiometer and is given in Figure 5.

Air temperature in the plant chamber was measured with a 24-gauge copper-constantan thermocouple which was located under the shade of a mid-section plant leaf but not touching it. For comparable experiments with adequate air flow, Salisbury and Spooner (1964) have shown that air temperature measured in this manner approximates plant leaf temperature.

Temperature control in the plant chamber was effected by various means. The infra-red reflecting 'hot mirror' assemblies reduced the heat component at the illumination source in part. The infra-red component was further reduced by placing a filter of circulating water 5 cm deep between the plant chamber and the Dicrolite lamps (Fig. 4). The base of the water filter was located in a fixed position 1 dm above the top of the plant chamber. At high light intensities, however, these means were insufficient to maintain a constant air temperature within the plant chamber. For the small chambers used during the first two harvests, additional temperature control was achieved with limited success by



Total energy (μw cm^{-2}) provided by the Dicrolite lamps at light intensities used for APS measurements

Light (ft-c)	Spectral region (nm) V 400-420	B 420-490	G 490-580	Y 580-590	O 590-650	R 650-700	FR 700-750	Total	0.5λ (nm)*
5000	184.6	1813.3	5508.3	948.4	5580.5	2840.3	1292.2	18167.7	606.9
2500	74.8	754.4	2441.4	439.8	2466.2	1228.9	579.9	7985.4	606.9
1000	28.2	318.5	946.1	172.4	975.9	477.6	205.4	3124.2	605.9
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

Figure 5. Spectral distribution of energy (400 - 750 nm) received by the plant under experimental conditions for APS measurements. Graph shows absolute range in relative intensity between 5000 and 500 ft-c.

using a cheesecloth jacket and ice-water spray or thermal tubing with circulating cold water. Excellent temperature control was achieved for the last three harvest periods using a Lauda K-2R controlled temperature water bath which circulated cool water through copper coils fixed on the outside of the brass plant chambers. Chamber air temperatures with this control could be maintained at 20 ± 0.5°C at all illumination intensities and lamp positions.

Relative humidity of the air stream at the plant chamber outlet was measured periodically with a wet- and dry-bulb psychrometer. To reduce moisture added to the air stream by the transpiring plant before reaching the water-vapour sensitive sensors of the infra-red analyzer, a desiccator consisting of a 200 cc flask chilled with dry ice was inserted into the air circuit. For the last three harvest measurements, this was replaced with a tube of Drierite (anhydrous $CaSO_4$). The desiccator tube contents were replaced when the color indicator showed that the Drierite was becoming saturated. Relative humidity of the air stream at the plant chamber outlet was maintained at 70 percent with the dry ice-chilled desiccator and 60 percent with the Drierite desiccator.

For the CO_2 exchange measurements, the infra-red analyzer was calibrated at the start and end of each day's measurements. Dry nitrogen was used as the zero standard and circulated through both reference and sample cells of the infra-red 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' through the reference analyzer cell. The zero standard (nitrogen gas) was trickled through the reference cell continuously during the CO_2 exchange measurements.

After the shoot of the test plant had been sealed in the chamber, incorporated into the closed measuring circuit under the illumination source and the circuit checked for air leaks, the change in CO_2 concentration from the fixed volume air stream was monitored. Given the volume of the measuring circuit, the rate of apparent photosynthesis can be calculated per unit plant material from the rate of depletion of carbon dioxide (ppm CO_2 v/v) from the fixed volume. Similarly, the rate of dark respiration can be calculated from the rate of increase in CO_2 concentration from the fixed volume when the plant is placed in complete darkness.

Apparent photosynthesis measurements were made at light intensities ranging from 5000 ft-c to 500 or 250 ft-c at various increments for each plant sampled (see Appendix I for light intensities used at each harvest). Illumination was set to the highest intensity at the beginning of each series of measurements. Each light intensity series consisted of a number of 'runs' between air stream CO_2 concentrations of approximately 375 and 250 ppm v/v. The CO_2 concentration of the air stream was increased to about 375 ppm by blowing carefully over an opened ground glass joint in the measuring circuit. Following closure of the joint, the illuminated plant was allowed to deplete the CO_2 concentration over a period of time until CO_2 in the closed air stream reached about 250 ppm. This process was repeated until two or preferably three consistent runs had been obtained at the given test light intensity level. A similar procedure was followed for each stage of lower light intensities. At each light intensity level, a period of 5 to 10 min. was provided the plant to adjust to the illumination. If an apparent photosynthesis 'run' indicated that a longer period of adjustment was necessary (the slope of the curve traced by the recorder being steeper than subsequent runs), the run was discarded.

Except for the first harvest, when dark respiration measurements were made following each light intensity change, dark respiration was measured only following completion of apparent photosynthesis runs at the lowest light intensity used. For each dark respiration run, CO_2 concentration in the plant chamber was depleted by inserting a CO_2 absorber tube (Indicarb) into the closed system. When the air stream CO_2 concentration reached approximately 300 ppm, the absorber was removed and the measuring system closed until plant dark respiration increased the air stream concentration to about 350 ppm CO_2. The procedure was repeated to obtain several dark respiration runs.

Leaf area and physical measurements

Immediately following completion of the CO_2 exchange measurements, the test plant was removed from the plant chamber and the area of photosynthetic surfaces was determined. Leaves, axillary and apical bud, and terminal green trunk surfaces were outlined and traced onto 1-mm graph paper. A count of the squares and partial squares gave area in square decimeters. Necrotic leaf areas were deducted from the total area for calculation of the CO_2 exchange rates.

Following tracing of the photosynthetic surfaces and recording of number of leaves, measurement of shoot length and an approximate count of alder root nodules, the plant was harvested. Roots were washed carefully to remove soil particles, and the plant separated into root, trunk and leaf components. Excess moisture was removed from the roots and fresh weight (mg) of each component determined.

For the chlorophyll analysis, the second largest leaf was divided along the midrib and the halves were weighed separately for small plants. For the larger plants, four or eight 1-cm discs were punched out from the leaves and half the total weighed for fresh weight prior to the analysis. The remaining half leaf or discs not used in the chlorophyll analysis were oven-dried and used to adjust leaf dry weight by accounting for parts used in the chlorophyll determination.

Chlorophyll content of the leaves was determined following the method of Holden (1967). Leaf halves or discs were macerated in 5-ml of chilled 80 percent acetone, then centrifuged until the supernatant was clear. The supernatant was analyzed in a 1-cm quartz cell with an Hitachi - Perkin Elmer Model 139 Spectrophotometer at 645 and 663 mμ. Readings were converted to mg chlorophyll g^{-1} fresh weight of leaves using the formula of Maclachlan and Zalik (1963):

$$\text{Chlorophyll a (mg g}^{-1}) = \frac{12.3\, D_{663} - 0.86\, D_{645}\, V}{d \times 1000 \times W}$$

$$\text{Chlorophyll b (mg g}^{-1}) = \frac{19.3\, D_{645} - 3.6\, D_{663}\, V}{d \times 1000 \times W}$$

where: V = volume (ml)
D = density reading on spectrophotometer
d = length of light path (cm), and
W = fresh weight (g) of plant material

Dry weight of the plant components was determined following oven-drying at 85 ± 2°C for a minimum of 24 hours. Parts were weighed separately and added to give total dry weight of plant material. Leaf halves or half the leaf discs were weighed and the weight doubled and added to the remainder of the leaf dry weight to account for material used in the chlorophyll determination.

DATA REDUCTION AND STATISTICAL TREATMENT

For calculation of apparent photosynthesis and dark respiration rates from the curves of $[CO_2]$ versus time, the computer program of Bulley (1969) was employed. Data input for the program consisted of $[CO_2]$ppm read from the sloping curve of each 'run' at one minute intervals 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 based on the data set using the least squares method where all data points are given equal weight. Differentiation of this equation yields rate values at specified ambient $[CO_2]$ as computer output. The rate value (ppm CO_2) taken at 325 ppm ambient $[CO_2]$ was then standardized for pressure and temperature differences, and rates expressed as mg CO_2 $dm^{-2}_{1\ surface}$ h^{-1} (mg CO_2 per decimeter of leaf area (one surface) per hour).

Statistical tests were performed on all data to determine whether significant differences existed between species, treatments (control, partial and full shade) or season (harvest). Analysis of variance models (ANOVA) were set up for the data following Sokal and Rohlf (1969) to partition variation contributed by treatment, season and individual plant components. The first model was a three-level hierarchical nested ANOVA testing for significance of different apparent photosynthesis rates at selected light intensity levels between the two species, among treatments, and at different harvest periods (Fig. 6). This model was also used to test for significance of treatment effects on chlorophyll content and biomass measurements. As the first between-species ANOVA for APS rates showed a high level of significance, a second model was constructed which compared differences in APS rates at different light intensities within one species and among treatments (Fig. 7). The third model was a two-level model, essentially similar to the second model, but incorporated only treatment

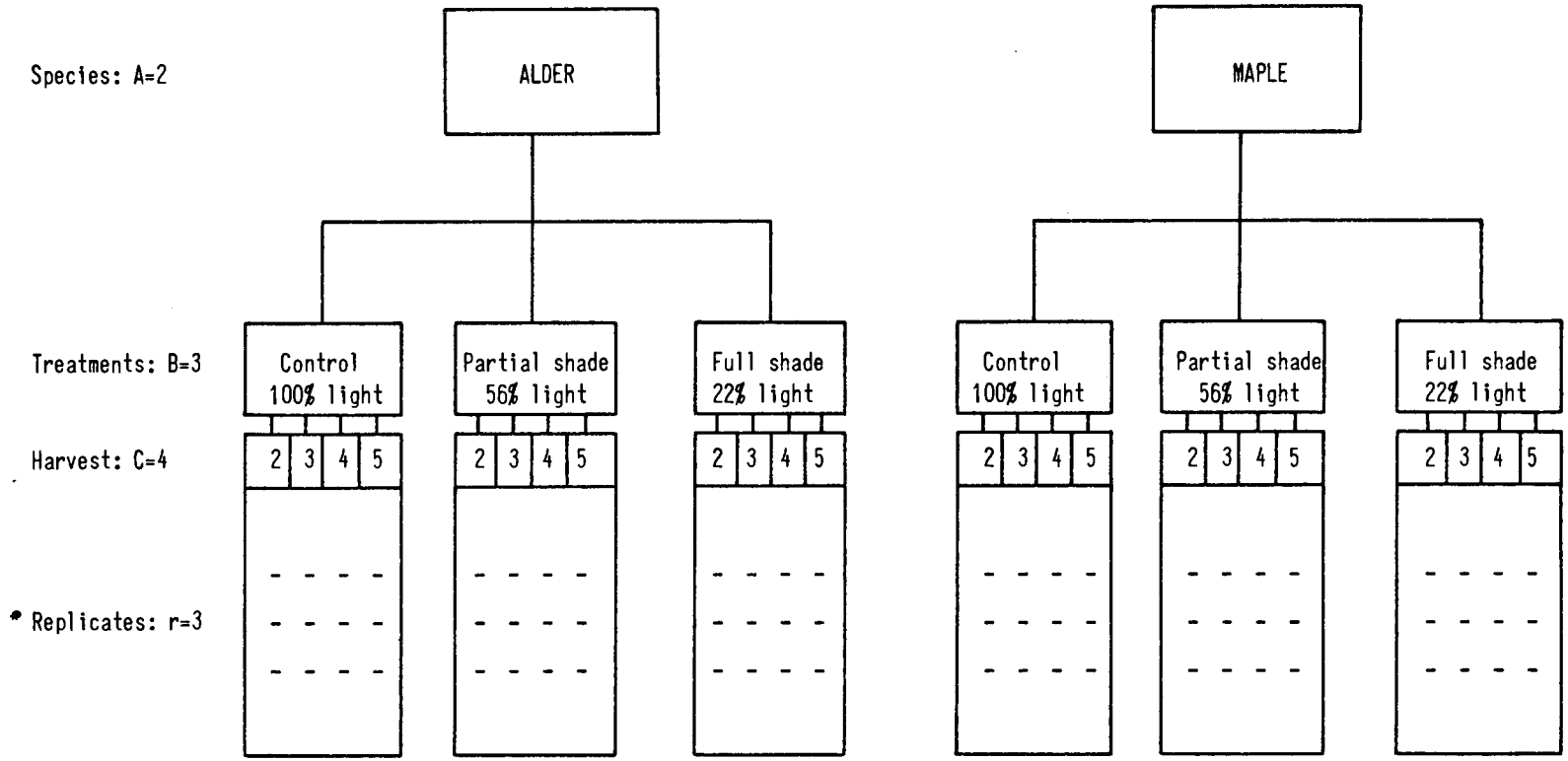


Figure 6. ANOVA model for between species comparison of apparent photosynthesis rates with treatment and season. The model was used for four comparisons at specific light intensities (5000, 2500, 1000 and 500 ft-c).
* Each replicate represents the mean APS rate (3 runs) of an individual plant for a given light intensity.

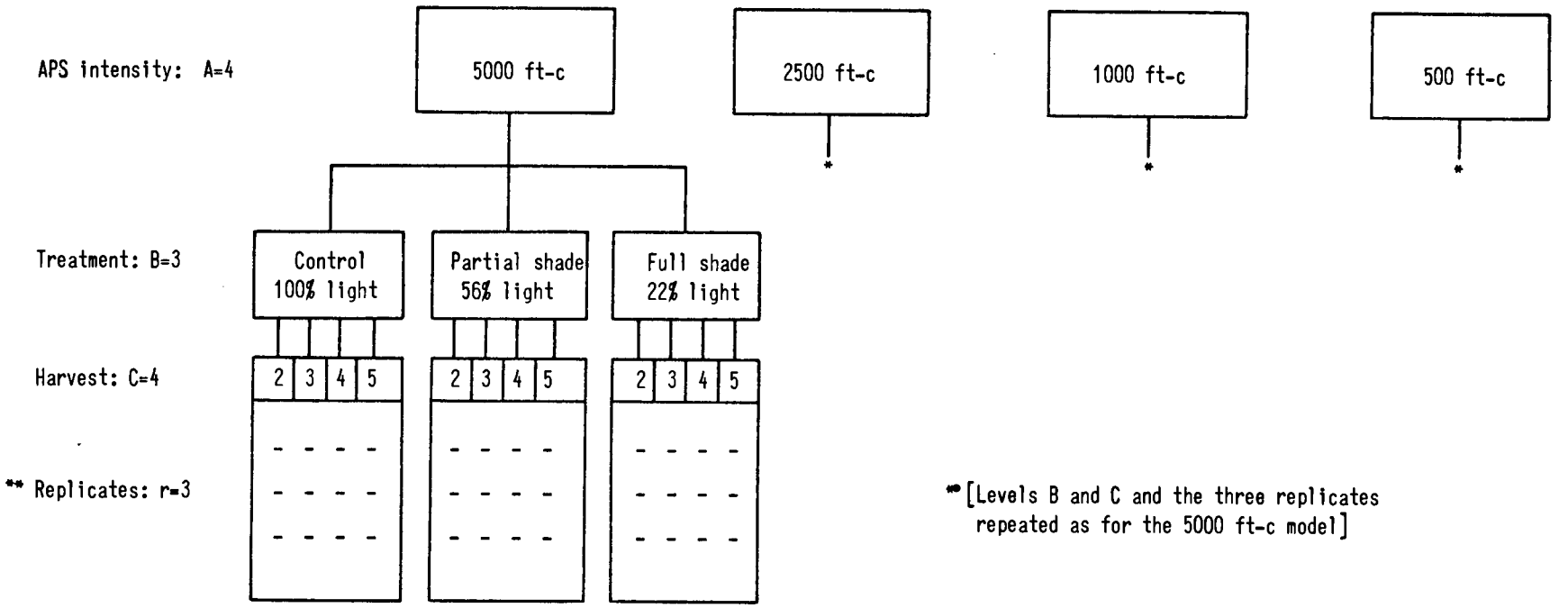


Figure 7. ANOVA model for within-species comparisons of apparent photosynthesis rates with treatment and season at different light intensities. Levels B and C and the replicates were used for the truncated two-level ANOVA. ** Each replicate represents the mean APS rate (3 runs) of an individual plant for a given light intensity.

and harvest parameters within the species. This model was used for comparison of respiration and relative growth rates (RGR) among treatments at different harvests.

In the latter model type, the replicates consist of individual measurements of a plant in a given harvest and treatment. As the majority of harvests consisted of three plants and three 'runs' at each light intensity for the apparent photosynthesis measurements, all values were considered. If missing values occurred (such as only two APS runs rather than three or a missing plant in the chlorophyll measurements), the computer program (SFU AVAR 23) accepts the 'missing cells' and completes the computation adjusting for degrees of freedom. Computed F-ratios are tabulated in the results section as follows:

Source	Degrees of freedom	Mean square	F-ratio	Probability
A) APS light intensity (5000, 2500, 1000 and 500 ft-c)	3	184.17	232.22**	0.0000
B) Treatment (100, 56 and 22 percent light)	2	60.48	76.25**	0.0000
C) Season (Harvest 2, 3, 4 and 5)	3	46.42	58.53**	0.0000
Interaction				
AB (Intensity/Treatment)	6	2.03	2.56 ns	0.0197
AC (Intensity/Harvest)	9	4.80	6.05**	0.0000
BC (Treatment/Harvest)	6	11.35	14.31**	0.0000
ABC (Intensity/Treatment/Harvest)	18	1.50	1.89 ns	0.0164
E(ABC) Within, error term	281	0.79		
Total	328	3.62		

** P=<0.001 and * P=<0.01, difference significant. ns = difference not significant

Critical values of the F-distribution at indicated probability levels are taken from Table S (Rohlf and Sokal, 1969).

RESULTS

The results reported here are presented in three sections. First, the growth habit and appearance of the plants is described, and biomass changes and relationships of major plant components are given. Second, characteristics of the photosynthetic apparatus (leaf area, specific leaf area and chlorophyll contents) are presented, and third, apparent photosynthesis (APS) and dark respiration rates are analyzed by species, season and growth light treatment. Summarized data on which the figures and analyses are based is given in Appendix II.

Plant Growth

As the term is used here, growth habit comprises subjectively descriptive terms such as shape, vigor, succulence, surface texture and color tone. These qualities combine to form a Gestalt that uniquely characterizes plants from the three light treatments (Fig. 8).

Figure 8. Experimental plants in late spring (June 4).

Differences in maple seedlings among the three treatments were sufficiently great to be noticeable at a distance, but were more difficult to distinguish among the alder seedlings. Control (100 percent light) alder plants in late spring (4 June) had a slight bronzed color in the leaves and the leaves had a coarse surface texture and were more stiffly disposed from the stem than alder plants from the shade treatments (Fig. 9). Alder seedlings from the shade treatments (56 and 22 percent light) had soft, almost velvety surfaces and a fragile thin appearance. In contrast, maple seedlings from the three light treatments showed striking differences in color (Fig. 10). Control maples (100 percent light) had a reddish-bronze color which was maintained throughout the season, whereas the full shade plants (22 percent light) were characteristically rich green with a slight bluish cast. Partial shade (56 percent light) maple seedlings were intermediate in color. Chlorophyll content of leaves from the three treatments were different within each species and are discussed later.

Differences in leaf disposition from the stem are also apparent between species and between treatments (Figs. 9 and 10). Alder seedling leaves are more inclined upward (becoming more flatly arranged with increasing shade) than the maple leaves which are inclined slightly downward in full shade and almost vertically disposed in the full light (control) treatment.

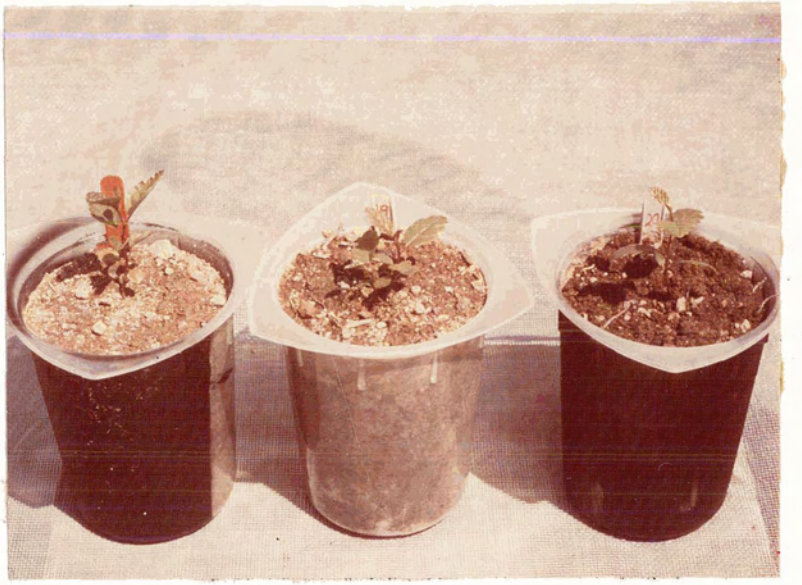


Figure 9. Representative alder seedlings from the three light treatments in late spring (4 June). Control (100 percent light), left; partial shade (56 percent light), middle; full shade (22 percent light), right.

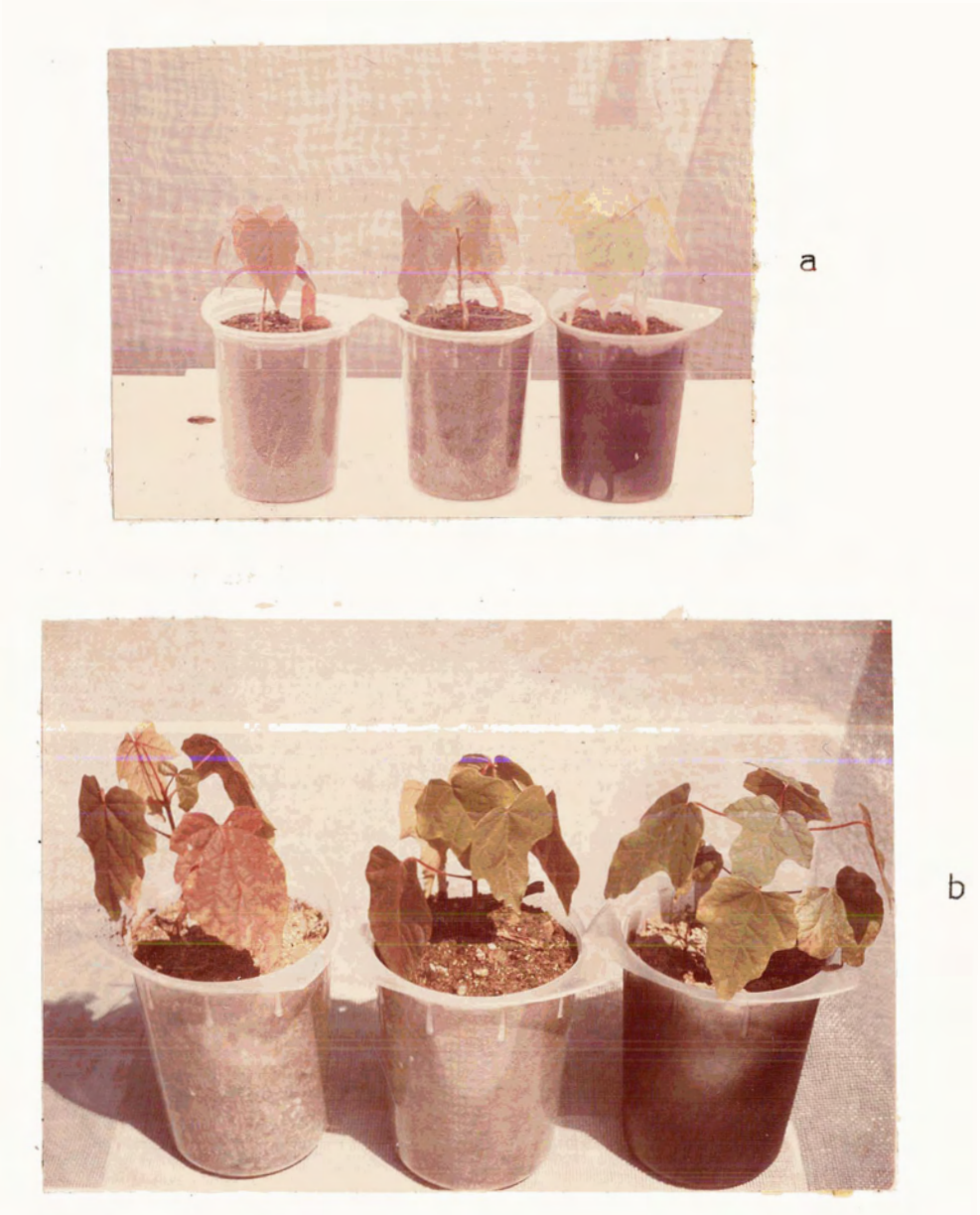


Figure 10. Representative maple seedlings from the three light treatments in a) late spring (4 June) and b) mid-summer (26 July). Control (100 percent light), left; partial shade (56 percent light), middle; and full-shade (22 percent light), right.

Alder and maple growth patterns are strikingly different. From the two-leaf stage in early spring, alder seedlings in all light treatments continue shoot extension with new leaves developing until late summer. Maple seedlings, on the other hand, develop two or four leaves early in the season with very little shoot extension and addition of new leaves from early summer. As a result, maple seedlings were larger plants at the beginning of the harvest schedule but did not maintain as high rate of biomass increase as the alder seedlings later in the season (Fig. 11 and Table 2). For all light treatments, total biomass of the maple seedlings increased about 2.5 to 3 times between harvests 1 and 5, whereas total biomass of the alder seedlings increased about 90 to 110 times. Almost all total biomass increment is attained by maple seedlings by late July - early August. The bulk of biomass increment occurs after late July - early August in the alder seedlings. Total biomass of the seedlings by harvest period (season) and between species was significantly different (Table 3).

Although total plant biomass and biomass of the separated plant components appears different between treatments for both alder and maple seedlings (Fig. 11), considerable variation was present between individual plants within each treatment at the different harvest periods (see Appendix II, Table I). Analysis of total biomass between treatments was not significantly different for either species when tested together (Table 3) or separately (Table 4).

To reduce variation caused by individual plant size within treatments, percent dry weight distribution of the plant components was calculated for both alder and maple seedlings. For both species, stems accounted for an approximately constant amount (16 - 20 percent) of the plant dry weight with a slight increase near the end of the season (Fig. 12). At the end of the harvest schedule, mean dry weight of the maple seedlings roots was 54 - 64 percent of the total, whereas alder roots accounted for only 40 - 46 percent of the total dry weight. For both species, lowest percentages occurred in the full shade (22 percent light) treatment at the end of the season. Although both species have most of their dry matter concentrated in the leaves at the beginning of the season with a decreased amount at the end of the season, the patterns differ between species (Fig. 12). Maple seedlings show a consistent decline in the percent dry matter present in the leaves of all treatments from the initial harvest to the final harvest. Leaves of alder seedlings, however, maintain a high percentage of the total dry weight until

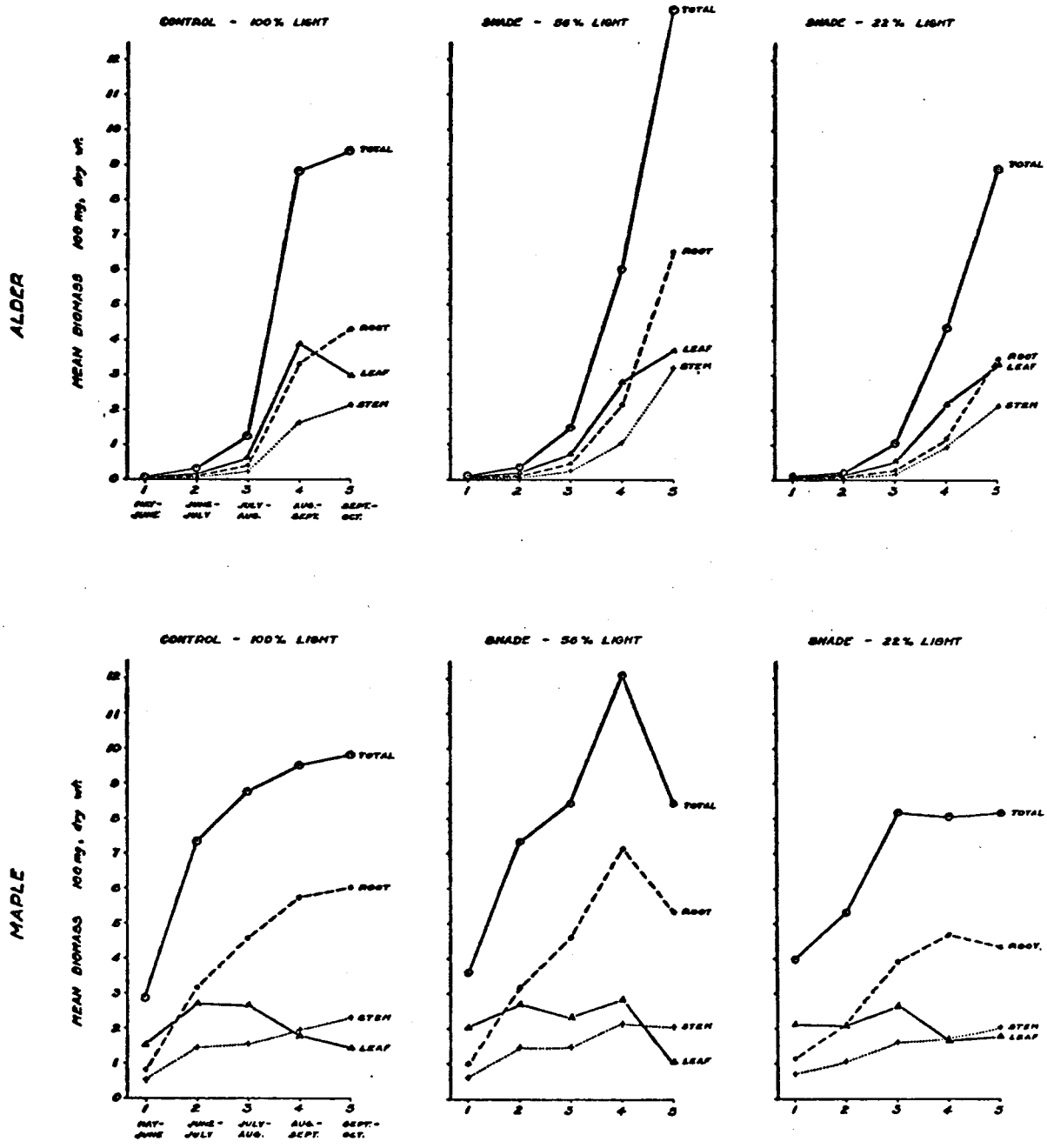


Figure 11. Mean total biomass of plant components for the alder and maple seedlings by treatment and harvest.

Table 2. Mean total biomass of the alder and maple seedlings by treatment and harvest (dry weight, mg).

Species	Treatment	Harvest 1	2	3	4	5
Alder	Control (100% light)	7	32	125	884	941
	Partial shade (56% light)	11	36	150	603	1345
	Full shade (22% light)	11	21	105	436	892
Maple	Control (100% light)	288*	733	876	948	979+
	Partial shade (56% light)	359	733	841	1212	843+
	Full shade (22% light)	399	532	818	807	818+

Values are averages of 3 plants; except *, 4 plants and +, 2 plants

Table 3. ANOVA for between species comparison of total biomass produced by treatment and harvest

Source	Degrees of freedom	Mean square	F-ratio	Probability
A) Species	1	2951906.00	46.51**	0.0000
B) Treatment	2	129355.38	2.04 ns	0.1379
C) Season (Harvest)	4	1794064.00	28.27**	0.0000
AB (Species/Treatment)	2	390.62	0.01 ns	0.9964
AC (Species/Harvest)	4	521917.50	8.22**	0.0001
BC (Treatment/Harvest)	8	33971.88	0.54 ns	0.8257
ABC (Species/Treatment/Harvest)	8	59885.25	0.94 ns	0.5104
E(ABC) Within, error term	56	63471.21		
Total	85	197418.31		

Table 4. Separate ANOVA's for within species comparison of total biomass produced by treatment and harvest.

Source	Degrees of freedom	Mean square	F-ratio	Probability
ALDER SEEDLINGS				
A) Treatment	2	76275.00	0.97 ns	0.6068
B) Season (Harvest)	4	1920532.00	24.39**	0.0000
AB (Treatment/Harvest)	8	66233.62	0.84 ns	0.5752
E(AB) Within, error term	30	78735.31		
Total	44	243786.56		
MAPLE SEEDLINGS				
A) Treatment	2	54812.66	1.20 ns	0.3190
B) Season (Harvest)	4	485159.75	10.58**	0.0001
AB (Treatment/Harvest)	8	29894.75	0.65 ns	0.7288
E(AB) Within, error term	26	45858.80		
Total	40	87043.75		

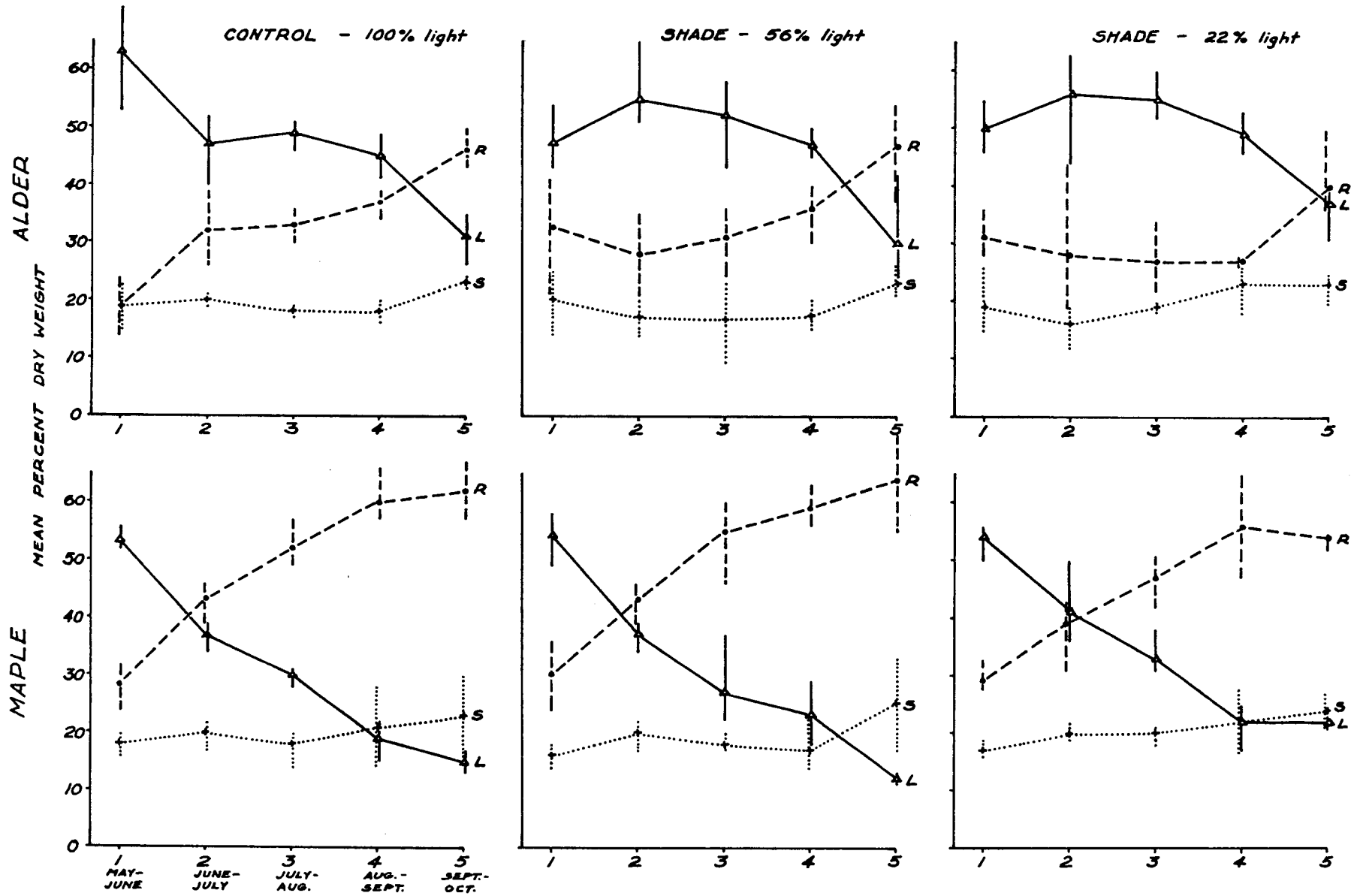


Figure 12. Mean percent dry weight of alder and maple leaf (L), stem (S) and root (R) components by treatment and harvest. Vertical lines represent absolute range in values.

the last harvest. For both species, final mean percent leaf dry weight was highest in the 22 percent light treatment.

Species differences in proportion of dry matter devoted to above ground (shoot) and below ground components are established clearly by root/shoot ratio data, although as Blackman (1968) found as well there is considerable variation among species. In all light treatments, alder consistently devoted more biomass to photosynthetic organs and their above ground support than to roots throughout the harvest period (Table 5). Mean root/shoot ratios did not reach 1.00 in any light treatment and were lowest in the 22 percent light (full shade) treatment near the end of the season. For alder treatments, the marked increase in mean root-shoot ratio from harvest 4 (August - early September) to harvest 5 (late September - early October) coincides with the mean biomass shift where root biomass equals or exceeds leaf biomass for the first time throughout the season (see Fig. 11). In at least the control alder treatment, the shift may be accounted for in part by leaf fall in late season.

In contrast, maple seedlings in all harvests generally showed a progressive increase in root/shoot ratios and approached or exceeded a mean ratio of 1.00 during July or early August (harvest 2 to 3). At harvest 3, however, maple seedlings were becoming root-bound in the plant pots and they were repotted before harvest 4. Root 'release' may account for the increased root/shoot ratios at the last two harvests (Table 5). Nevertheless, maple seedlings consistently devote more biomass to root components than to those above ground from early season despite the apparent large leaf size of this species.

Differences in root/shoot ratios between treatments by species do not appear to be significant due to variation between individual plants and was not tested.

Table 5. Mean root/shoot ratios of the alder and maple seedlings by treatment and harvest

Species	Treatment	Harvest 1	2	3	4	5
Alder	Control (100% light)	0.27	0.47	0.50	0.58	0.85
	Partial shade (56% light)	0.50	0.40	0.45	0.56	0.91
	Full shade (22% light)	0.46	0.43	0.37	0.38	0.69
Maple	Control (100% light)	0.38	0.76	1.10	1.54	1.70
	Partial shade (56% light)	0.43	0.76	1.26	1.49	1.88
	Full shade (22% light)	0.41	0.64	0.90	1.39	1.16

Further evaluation of possible differences among treatments and between species at each harvest included calculation of relative growth rates (RGR) based on Blackman's formula (1968) as follows:

$$RGR = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where: W_2 is total plant biomass at time t_2 (a subsequent harvest), and W_1 is total plant biomass at time t_1 (the base harvest or harvest preceding t_2).

Thus, relative growth rates may be calculated in two ways. The first method used a common base plant for W_1 and individual plants (W_2) from subsequent harvests in order that time differences ($t_2 - t_1$) between the base harvest date (1 June) and exact date of harvest for an individual plant within harvest period could be accounted for. The second method compared mean total plant biomass between successive harvests based on mean time intervals between harvests.

As base plants were not harvested for each species at t_0 , mean base plants were calculated from harvest 1 following tests for significant differences between root, stem and leaf components and total biomass between treatments for that harvest. The analyses of variance revealed no significant differences between treatments for either the alder or maple seedlings at harvest 1. Mean base plants used were, therefore:

Alder: total biomass 9.96 ± 1.67 mg

Maple: total biomass 371.0 ± 6.0 mg

The results, as might be expected, emphasize the different growth patterns between species and seasonal differences within species (Fig. 13). For all light treatments, alder seedlings increase rapidly from initially high values in early season with little or no decline at the final harvest when based on the base plant analysis. Based on the successive harvest analysis, the alder seedlings showed a slight to sharp decline in relative growth rate in late season. Maple seedlings have lower initial RGR's and on the basis of the base plant analysis show a generally consistent decline from early season until the end of the harvest schedule. Relative growth rate analysis based on successive harvests had an erratic pattern for the shade-treated maple seedlings.

Separate analyses of variance for each species indicated that seasonal patterns of RGR were

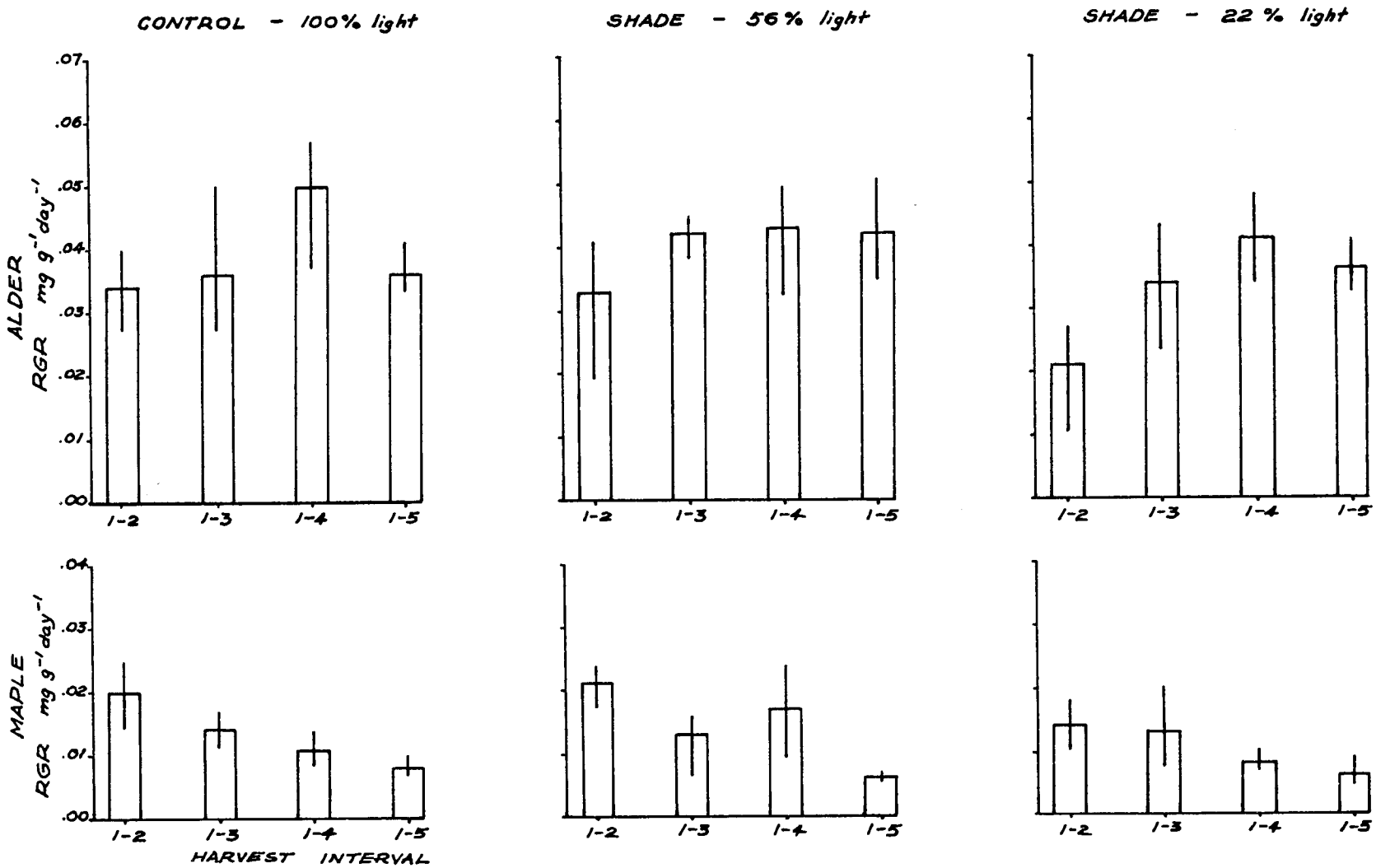


Figure 13. Mean relative growth rates (RGR) of the alder and maple seedlings by light treatment and harvest interval. Means and absolute range (vertical line) were determined using the base plants (see text for further explanation).

significantly different and that light treatment had no significant effect on relative growth rates (Table 6). These analyses were calculated using the base plant data.

Table 6. ANOVA for within species comparison of relative growth rates (RGR) by treatment and harvest period.

Source	Degrees of freedom	Mean square	F-ratio	Probability
ALDER SEEDLINGS				
A) Treatment	2	1.982	2.55 ns	0.0978
B) Harvest	3	3.676	4.72 •	0.0100
AB	6	0.606	0.78 ns	0.5960
Within, error	24	0.778		
Total	35	1.066		
MAPLE SEEDLINGS				
A) Treatment	2	0.389	1.65 ns	0.2176
B) Harvest	3	1.596	6.77 •	0.0030
AB	6	0.170	0.72 ns	0.6380
Within, error	19	0.236		
Total	30	0.369		

Leaf Characteristics of the Seedlings

Differences in number of leaves and leaf area between the alder and maple seedlings emphasize the different growth patterns of the species. After Harvest 2 (June - July), there is no increase in mean number of leaves for the maple seedlings, and with the exception of the control (100 percent light) plants, the mean number of leaves remains largely constant (Fig. 14). Mean number of leaves for the alder seedlings increases until Harvest 4 (August - September) and then declines.

Differences in leaf area increment are more pronounced between species. At Harvest 1 (May - June), mean total leaf area of the maple seedlings was approximately 30 - 40 times that of the alder seedlings (Table 7). Maple seedlings reached their maximum leaf area in early- to mid-summer, whereas alder seedlings reached maxima in late summer or early fall. At the end of the growing season following an almost continual increase in leaf area, mean total leaf area of the alder seedlings exceeded that of maple. This pattern is illustrated as well by differences in mean area per leaf of the seedlings by harvest period (Fig. 14). For both species, highest mean total leaf area and mean area per leaf

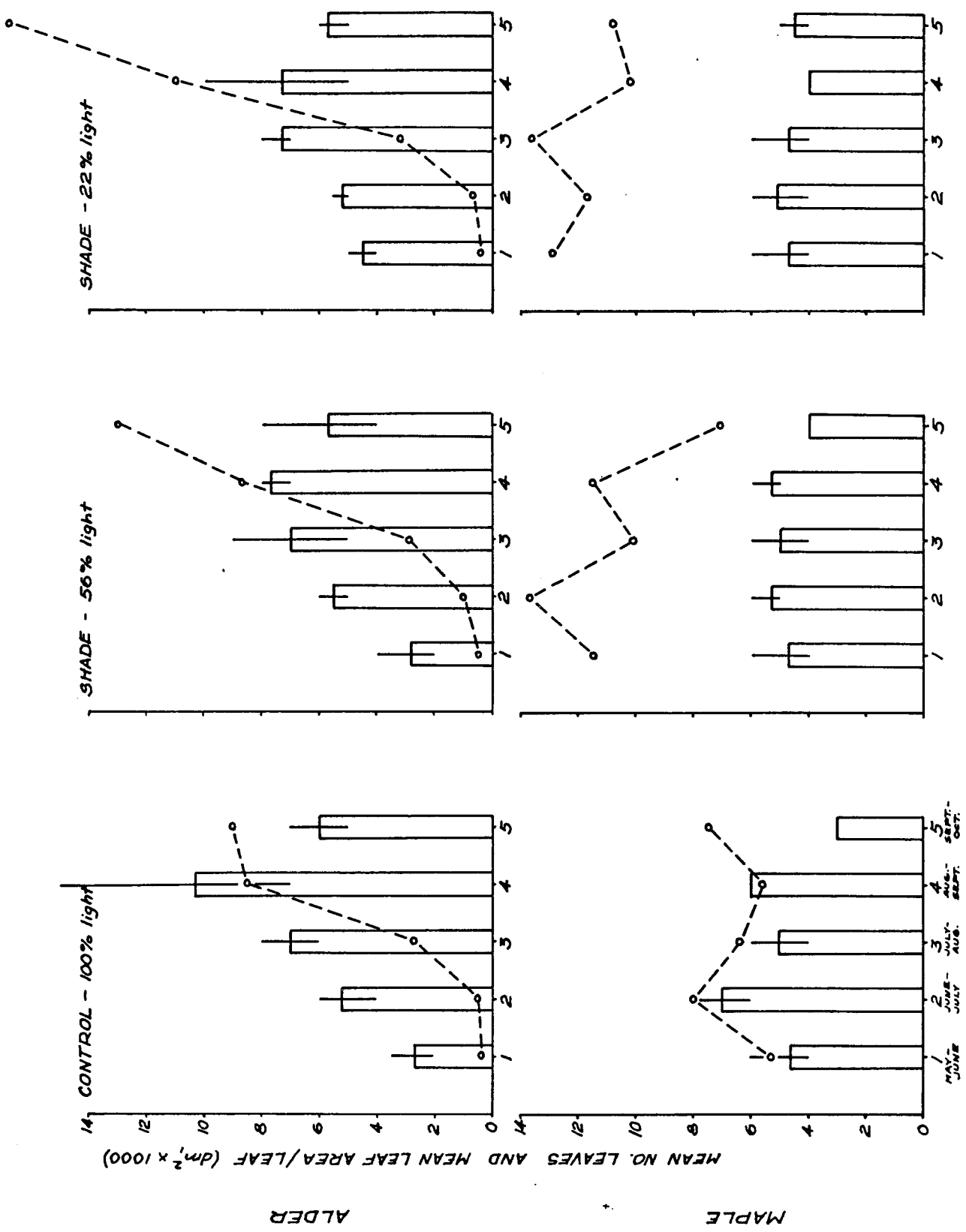


Figure 14. Mean number of leaves and absolute range (histogram) and mean area per leaf o- - - - -o of alder and maple seedlings.

Table 7. Mean total leaf area and mean necrotic leaf area (dm^2) of the alder and maple seedlings by light treatment and harvest period.

Species	Treatment	Harvest 1	2	3	4	5
Mean total leaf area						
Alder	Control (100% light)	0.0089	0.0283	0.1914	0.8714	0.5415
	Partial shade (56% light)	0.0144	0.0578	0.2021	0.6691	0.7405
	Full shade (22% light)	0.0183	0.0380	0.2333	0.8030	0.9628
Maple	Control (100% light)	0.2433	0.5573	0.3711	0.3330	0.2242
	Partial shade (56% light)	0.5401	0.7237	0.5068	0.6105	0.2854
	Full shade (22% light)	0.6073	0.5967	0.6404	0.4080	0.4837
Mean necrotic leaf area						
Alder	Control (100% light)	0	0.0005	0.0008	0.0013	0.0017
	Partial shade (56% light)	0.0004	0.0010	0	0.0009	0.0055
	Full shade (22% light)	0.0002	0	0	0.0058	0.0073
Maple	Control (100% light)	0	0.0047	0.0179	0.0320	0.0175
	Partial shade (56% light)	0.0343	0.0017	0.0302	0.0875	0.0178
	Full shade (22% light)	0.0031	0.0020	0.0476	0.0033	0.0202

occurred in the full shade (22 percent light) treatment. Necrotic leaf area was also lower in the alder seedlings (Table 7). Consequently, the effective leaf surface for photosynthesis is substantially higher for the alder seedlings than for the maple seedlings toward the end of the growing season.

To measure leaf density, specific leaf area was calculated for each species by harvest period and treatment. Specific leaf area expresses a single-surface area per unit dry weight of leaf tissue. Thus, the higher the ratio, the thinner and/or less dense the leaf. Highest mean specific leaf area occurred in the shade treatments for both species. For the alder seedlings, consistently high ratios occurred only in the full-shade (22 percent light) treatment, whereas consistently higher ratios occurred for the maple seedlings in both shade treatments (Fig. 15). As considerable variability occurs between individual plants for both leaf area and leaf dry weight (see Appendix II, Table 1), the specific leaf area data was not tested for significant differences.

Chlorophyll

Chlorophyll content (mg/g f. wt.) differs between species in magnitude and pattern (Fig. 15).

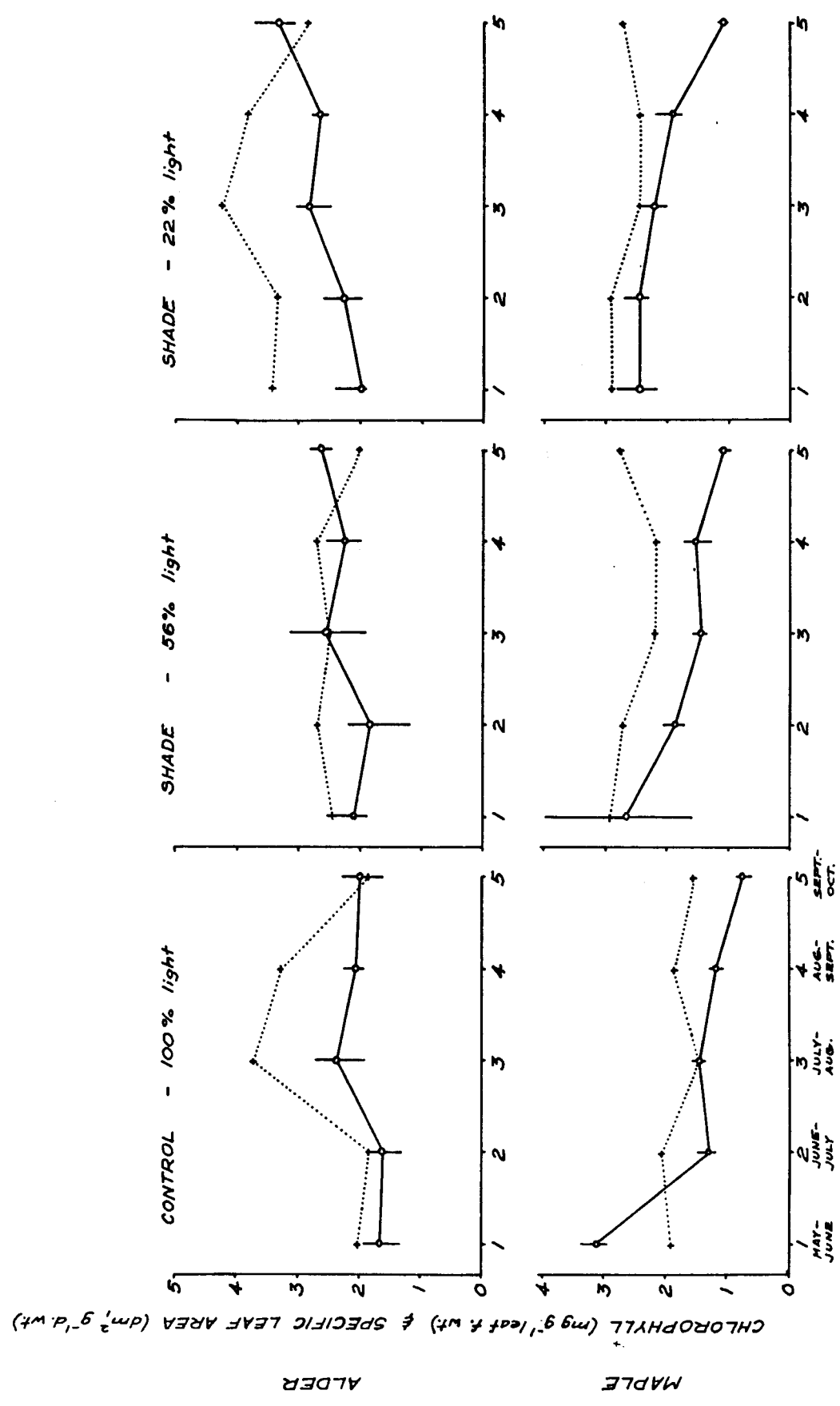


Figure 15. Mean specific leaf area +.....+ and mean chlorophyll content o——o of alder and maple seedlings by light treatment and harvest period. Vertical lines represent absolute range in chlorophyll content.

Initial chlorophyll content of the maple seedlings (Harvest 1) was generally higher than that of the alder seedlings (Fig. 15; Appendix II, Table 2), and showed almost continual decline over the growing season. Alder seedlings, on the other hand, increased in chlorophyll content at mid-season (100 percent and 56 percent light treatments) and then remained comparatively constant for the remainder of the season or had a progressive increase throughout the season (22 percent light treatment). A between species analysis of variance of the chlorophyll data showed significant differences between species, between treatments, and between harvest periods (Table 9).

The marked difference in seasonal pattern of chlorophyll content is especially evident by calculating total leaf chlorophyll content of the plants by treatment and harvest (Table 8). Mean total leaf chlorophyll content of the maple seedlings is approximately 30 to 50 times that of alder at Harvest 1. At the end of the season (Harvest 5), however, mean total leaf chlorophyll content of alder seedlings is about 8 to 16 times that of maple seedlings when compared by light treatment. Thus, total leaf chlorophyll content of the alder seedlings increases about 60 to 100 times over the season whereas maple seedlings decrease about 4 to 8 times in total leaf chlorophyll (Table 8).

For both species, highest chlorophyll content (mg/ g leaf f. wt.) occurred in the full shade (22 percent light) treatment (Fig. 15); shade treatments for both species had higher chlorophyll contents in the leaves than for the control (100 percent light) treatment. Separate analyses of variance by species revealed significant differences by treatment and harvest for the alder seedlings, and significant difference in chlorophyll content by harvest for the maple seedlings (Table 10). The rather large variability in chlorophyll content of the maple seedlings in the 56 percent light treatment at Harvest 1 (Fig. 15) may account for lack of significant differences between light treatments.

Separate analyses of variance were performed on various treatment combinations by species to further evaluate treatment effects. These analyses were based only on data from Harvests 2 to 5 inclusive. For the alder seedlings, chlorophyll content of the 56 percent light (partial shade) plants was not significantly higher than for the control (100 percent light) plants, but chlorophyll content of the full shade grown (22 percent light) alder seedlings was significantly higher than that for either the control or partial shade grown plants (Table 11). For the maple seedlings, full shade grown plants had

Table 8. Mean total chlorophyll content of the leaves of alder and maple seedlings by treatment and harvest period (mg / plant).

Species	Treatment	Harvest 1	2	3	4	5
Alder	Control (100% light)	0.16	0.81	6.08	27.7	16.7
	Partial shade (56% light)	0.46	0.79	5.37	24.1	28.7
	Full shade (22% light)	0.33	0.82	5.58	21.8	34.8
Maple	Control (100% light)	10.3	10.1	8.31	4.94	1.46*
	Partial shade (56% light)	14.2	14.1	7.93	9.54	1.80*
	Full shade (22% light)	16.1	13.8	13.9	13.0	4.10*

Values are averages of 3 plants; except *, 2 plants.

Table 9. ANOVA for between species comparison of chlorophyll content by treatment and harvest. [ANOVA based on chlorophyll data expressed as mg / g leaf fresh wt.]

Source	Degrees of freedom	Mean square	F-ratio	Probability
A) Species	1	5.811	40.91**	0.0000
B) Treatment	2	2.554	17.98**	0.0000
C) Harvest (season)	4	0.856	6.02**	0.0006
AB (Species/Treatment)	2	0.126	0.89 ns	0.5811
AC (Species/Harvest)	4	3.779	26.61**	0.0000
BC (Treatment/Harvest)	8	0.273	1.92 ns	0.0735
ABC (Species/Treatment/Harvest)	8	0.223	1.57 ns	0.1533
E(ABC) Within, error term	57	0.142		
Total	86	0.486		

Table 10. Separate ANOVA's for within species comparison of chlorophyll content by treatment and harvest. [Based on chlorophyll data expressed as mg / g leaf fresh wt.]

Source	Degrees of freedom	Mean square	F-ratio	Probability
ALDER SEEDLINGS				
A) Treatment	2	1.956	14.41**	0.0001
B) Harvest (season)	4	1.118	8.23**	0.0003
AB (Treatment/Harvest)	8	0.116	0.85 ns	0.5636
E(AB) Within, error term	30	0.136		
Total	44	0.304		
MAPLE SEEDLINGS				
A) Treatment	2	0.781	5.24 ns	0.0118
B) Harvest (season)	4	3.408	22.87**	0.0000
AB (Treatment/Harvest)	8	0.368	2.47 ns	0.0371
E(AB) Within, error term	27	0.149		
Total	41	0.541		

Table 11. Separate ANOVA's of treatment combinations for within species comparison of chlorophyll content. [Based on chlorophyll data expressed as mg / g leaf fresh weight, Harvests 2 to 5 inclusive].

Source	Degrees of freedom	Mean square	F-ratio	Probability
ALDER SEEDLINGS				
100% vs. 56% light treatment				
A) Treatment	1	0.637	3.93 ns	0.0623
B) Harvest	3	0.698	4.30 ns	0.0207
AB (Treatment/Harvest)	3	0.063	0.39 ns	0.7669
E(AB) Within, error term	16	0.162		
Total	23	0.240		
100% vs. 22% light treatment				
A) Treatment	1	3.776	37.55**	0.0001
B) Harvest	3	0.717	7.13*	0.0033
AB (Treatment/Harvest)	3	0.216	2.15 ns	0.1337
E(AB) Within, error term	16	0.101		
Total	23	0.356		
56% vs. 22% light treatment				
A) Treatment	1	1.312	8.63*	0.0094
B) Harvest	3	0.925	6.09*	0.0060
AB (Treatment/Harvest)	3	0.048	0.32 ns	0.8155
E(AB) Within, error term	16	0.152		
Total	23	0.290		
MAPLE SEEDLINGS				
100% vs. 56% light treatment				
A) Treatment	1	0.514	25.53**	0.0003
B) Harvest	3	0.459	22.78**	0.0001
AB (Treatment/Harvest)	3	0.077	3.80 ns	0.0343
E(AB) Within, error term	14	0.020		
Total	21	0.114		
100% vs. 22% light treatment				
A) Treatment	1	2.993	100.58**	0.0000
B) Harvest	3	1.092	36.68**	0.0000
AB (Treatment/Harvest)	3	0.153	5.14 ns	0.0133
E(AB) Within, error term	14	0.030		
Total	21	0.340		
56% vs. 22% light treatment				
A) Treatment	1	1.027	26.30**	0.0003
B) Harvest	3	1.103	28.26**	0.0000
AB (Treatment/Harvest)	3	0.156	3.99 ns	0.0297
E(AB) Within, error term	14	0.039		
Total	21	0.255		

significantly higher chlorophyll content of leaves than the partial shade and control plants, and the partial shade plants had significantly higher leaf chlorophyll content than the control plants.

The data suggest, therefore, that the shade treatments had a stronger and more consistent effect on leaf chlorophyll content of maple seedlings than on the alder seedlings. This effect together with the marked difference between species in seasonal leaf chlorophyll pattern is evaluated further in relation to apparent photosynthesis and growth pattern differences of the seedlings later in this thesis.

Apparent Photosynthesis and Dark Respiration Rates

Measurements of apparent photosynthesis and dark respiration were made on individual alder and maple seedlings from each light treatment at each harvest period. For each seedling , the measurements consisted of a number of runs (replicates) at each light intensity used for the CO_2 exchange study. As might be expected, individual seedlings within a light treatment and particular harvest period differed in absolute apparent photosynthesis and dark respiration rates (mg CO_2 dm^{-2}_1 h^{-1}). This variation is apparent in the mean apparent photosynthesis and dark respiration rates given by seedling in Appendix II, Table 2. Measurements made at Harvest 1 were not used in statistical analyses of the data; the light intensities employed were generally different from subsequent harvests, and temperature control within the plant chamber was neither as reliable or consistent as the control achieved for the remaining harvest periods.

Apparent photosynthesis rates (APS)

Alder seedlings have clearly higher rates of apparent photosynthesis than maple seedlings at all harvest periods, light treatments, and corresponding light intensities used in the CO_2 exchange measurements (Figs. 16 and 17). In no harvest did the values overlap; values for alder seedlings were consistently about 3 to 10 times greater than for the maple seedlings.

Despite these differences, however, there are similarities in response of both species to growth light treatment. By eliminating differences in absolute rates (mg CO_2 dm^{-2}_1 h^{-1}) when the rate for each species by treatment and harvest is expressed as a percent of the maximum rate (usually at 5000 ft-c), the shape of the APS curve vs. light intensity is similar by light treatment (Fig. 18).

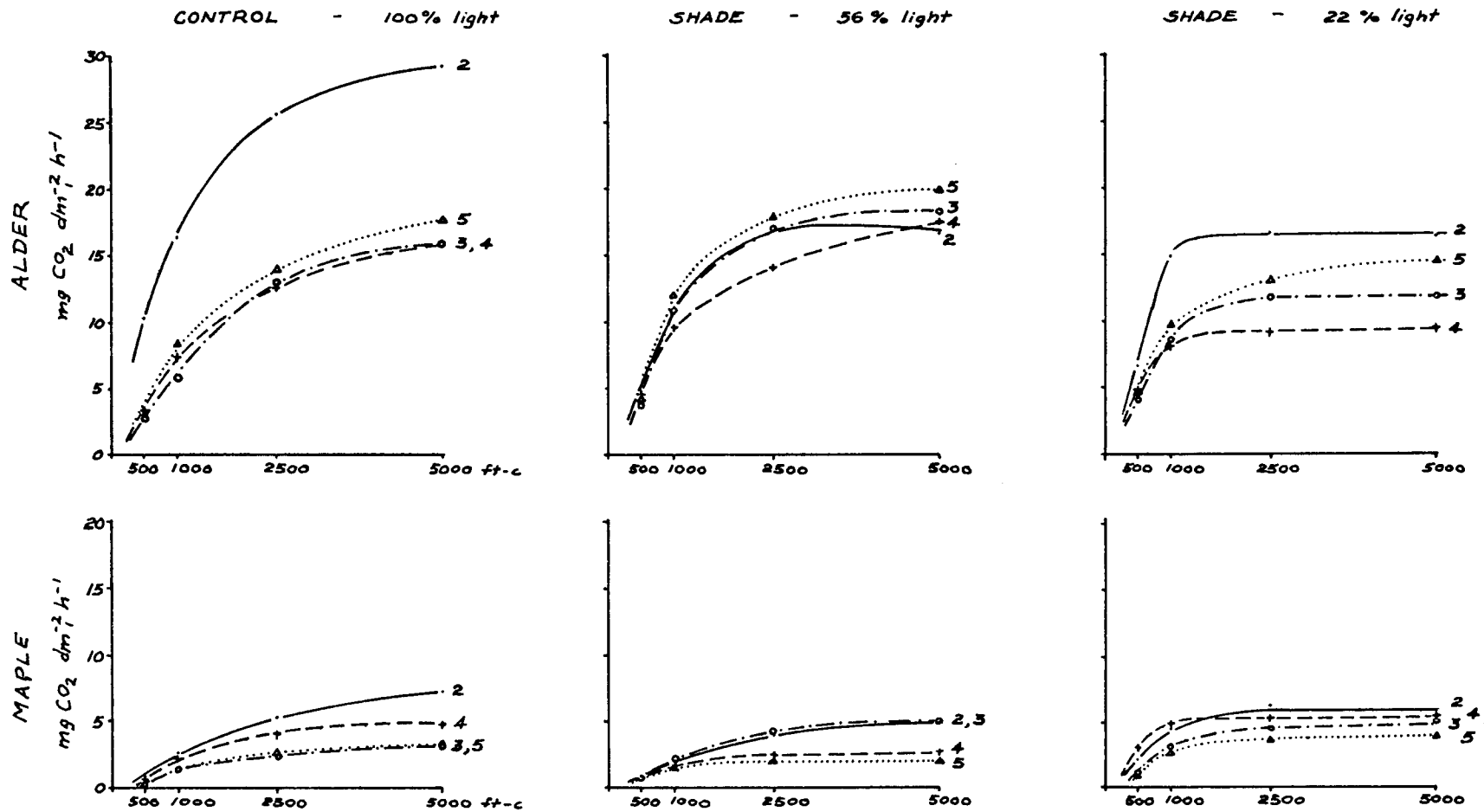


Figure 16. Mean apparent photosynthesis rates (mg CO_2 $dm^{-2}h^{-1}$) by light treatment and harvest period at different measurement light intensities (horizontal axis).

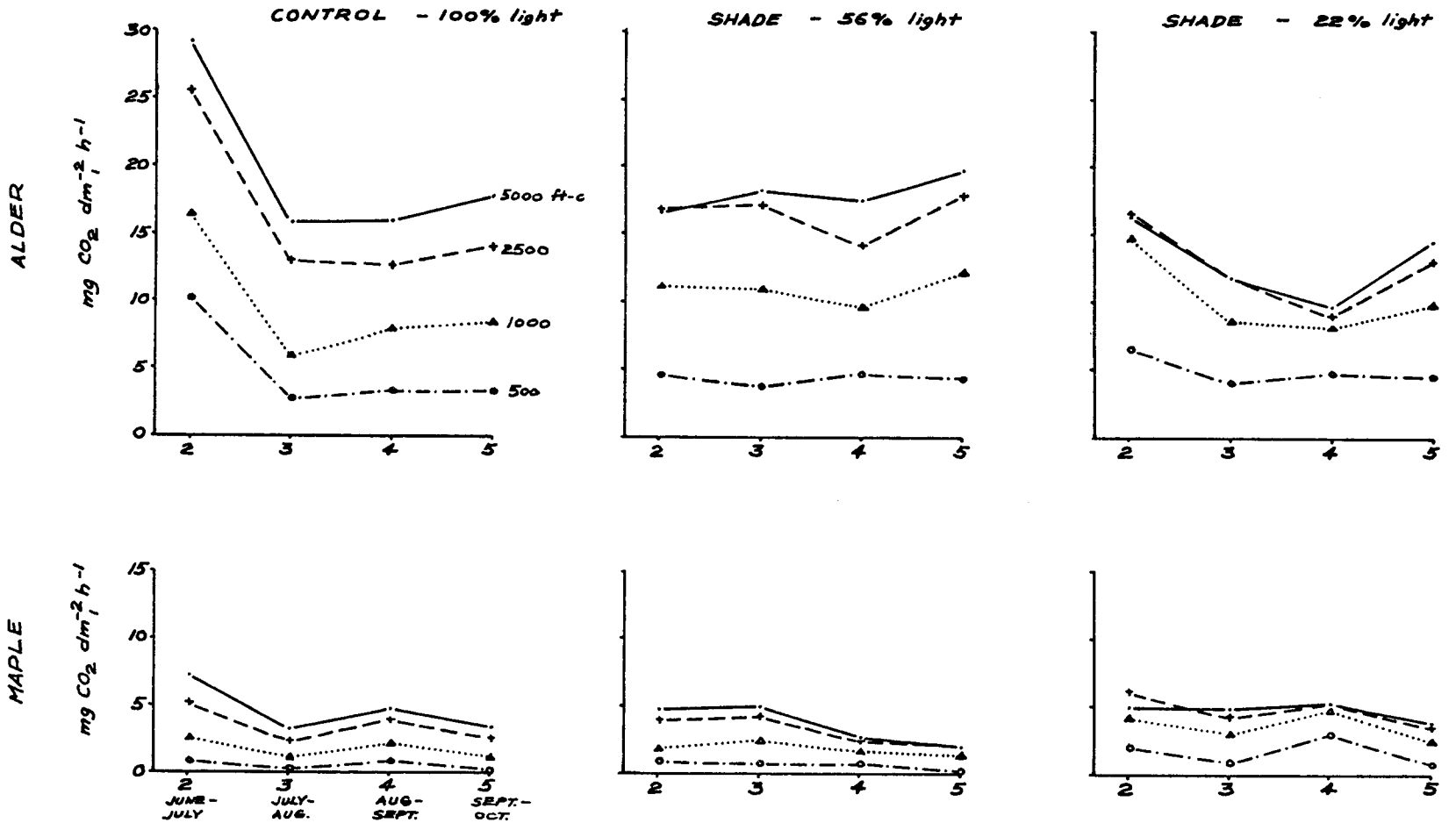


Figure 17. Seasonal pattern of apparent photosynthesis rates (mg CO_2 dm^{-2} h^{-1}) for the alder and maple seedlings by light treatment and harvest period at the measurement light intensities. Values are mean rates.

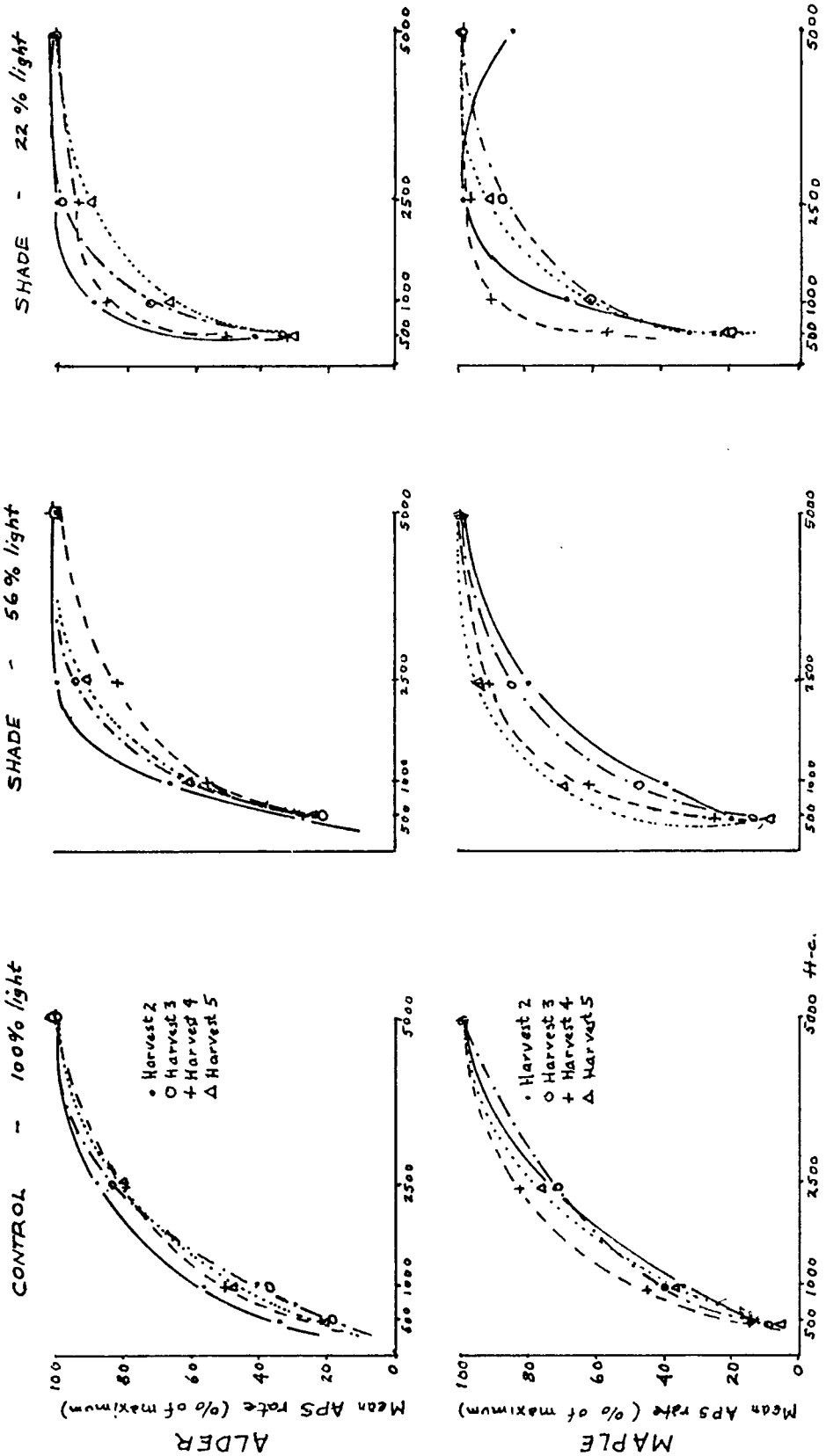


Figure 18. Mean apparent photosynthesis rates (percent of maximum) by light treatment and harvest period at different measurement light intensities (horizontal axis).

Thus for both species, the curves for the full shade (22 percent light) plants are more sharply inflected around 1000 ft-c than the curves for the control (100 percent light) plants (Fig. 18). The partial shade grown plants (56 percent light) appear intermediate in response.

Photosynthesis of the alder seedlings grown in full light (100 percent) is not light saturated at 5000 ft-c throughout the season (Fig. 16). Partial shade grown (56 percent light) alder seedlings, however, approach light saturation around 2500 ft-c during part of the growing season (Harvests 2 and 3), and full shade (22 percent light) plants approach light saturation between 1000 and 2500 ft-c at Harvests 2 and 3 and at slightly higher light intensities (around 2500 ft-c) later in the season. Maple seedlings grown under the different light treatments appear to respond similarly but the data suggest that for comparable treatments, light saturation is approached at slightly lower light intensities for the maple seedlings than for the alder seedlings. At least in the control (full light) maple seedlings during the first three harvest periods, however, photosynthesis was not light saturated at 5000 ft-c (Fig. 16).

For each species, statistical analyses revealed significant differences between mean apparent photosynthesis rates at CO_2 exchange measurement light intensities, light treatment, and harvest period (Table 12 and 13).

Table 12. ANOVA for comparison of mean apparent photosynthesis rates of alder seedlings by measurement light intensity, light treatment and harvest period (based on model given in Fig. 7, p. 19). Data input: mg CO_2 dm^{-2}_1 h^{-1}.

Source	Degrees of freedom	Mean square	F-ratio	Probability
A) Measurement light intensity (5000, 2500, 1000, 500 ft-c)	3	949.567	129.54**	0.0000
B) Light treatment (100, 56, 22 percent light)	2	74.281	10.13**	0.0003
C) Harvest period	3	206.894	28.22**	0.0000
AB) (APS light/Treatment)	6	35.857	4.89**	0.0004
AC) (APS light/Harvest)	9	6.705	0.91 ns	0.5172
BC) (Treatment/Harvest)	6	74.546	10.17**	0.0000
ABC) (APS light/Treatment/Harvest)	18	3.123	0.43 ns	0.9782
Within, error term	83	7.330		
Total	130	38.502		

Table 13. ANOVA for comparison of mean apparent photosynthesis rates (mg CO_2 $dm^{-2}h^{-1}$) of maple seedlings by measurement light intensity, light treatment and harvest period.

Source	Degrees of freedom	Mean square	F-ratio	Probability
A) Measurement light intensity	3	67.978	72.00**	0.0000
B) Light treatment	2	20.992	22.23**	0.0000
C) Harvest period	3	16.224	17.18**	0.0000
AB) (APS light/Treatment)	6	1.382	1.46 ns	0.2016
AC) (APS light/Treatment)	9	1.302	1.38 ns	0.2129
BC) (Treatment/Harvest)	6	4.073	4.31*	0.0011
ABC) (APS light/Treatment/Harvest)	18	0.730	0.77 ns	0.7247
Within, error term	74	0.944		
Total	121	3.488		

Seasonal pattern of apparent photosynthesis is different for the two species (Fig. 17). For the alder seedlings, control plants had highest APS rates early in the season, the rates dropped sharply in July-August (Harvest 3) and then remained comparatively uniform or increased slightly toward the end of the growing season. Control maple seedlings, on the other hand, did not increase in APS rate at Harvest 5 and had lower rates at Harvests 3 and 5 than at Harvests 2 and 4 (Fig. 17). At 5000 and 2500 ft-c, partial shade grown maple plants had higher APS rates during Harvest 2 and 3 (early to mid-summer) than later in the season. At lower light intensities, the seasonal pattern did not show a marked change for the maple seedlings. Alder seedlings grown in partial shade had highest APS rates late in the season at 5000, 2500 and 1000 ft-c and with the exception of Harvest 2 measurements, had higher APS rates throughout the season than the control (full light) plants. For the full shade grown plants (22 percent light), APS rates of alder and maple seedlings at 500 ft-c was higher than that for the control or partial shade grown seedlings at Harvests 3, 4 and 5. The seasonal pattern for the full shade grown maple seedlings was essentially the same as for the ccntrol maple plants with the exception of measurements made at 5000 ft-c which remained largely constant throughout the season. Alder seedlings grown in full shade (22 percent light) showed a decrease in APS rate from Harvest 2 to 4 at 5000, 2500 and 1000 ft-c, and then an increase at Harvest 5 (Fig. 17).

Treatment and seasonal differences in apparent photosynthesis rates were analyzed statistically

by comparing within species rates at each CO_2 exchange measurement light intensity for all treatment combinations. A summary of the ANOVA'S by species is given in Table 14, and the detailed results of treatment combinations is given in Appendix II, Table 3.

For the alder seedlings, APS rates of the full light (control) plants was significantly higher than rates for the full shade (22 percent light) plants at all times during the season when

Table 14. ANOVA summary for within species comparison of mean apparent photosynthesis rates for all treatment combinations.

APS light intensity	Treatment	Mean APS rate" by harvest 2	3	4	5	Treatment test combination	Significance Treatment (A)	Harvest (B)	(AB)
ALDER SEEDLINGS									
5000 ft-c	100%	29.2	15.8	15.9	17.7	100 vs. 22%	**	**	ns
	56%	16.6	18.2	17.5	19.7	100 vs. 56%	ns	ns	ns
	22%	16.4	11.8	9.6	14.5	56 vs. 22%	*	ns	ns
2500 ft-c	100%	25.6	13.0	12.6	14.0	100 vs. 22%	ns	**	ns
	56%	16.9	17.1	14.1	17.9	100 vs. 56%	ns	ns	ns
	22%	16.6	11.7	9.0	13.0	56 vs. 22%	ns	ns	ns
1000 ft-c	100%	16.4	5.8	7.9	8.3	100 vs. 22%	ns	**	ns
	56%	11.1	10.9	9.6	12.1	100 vs. 56%	ns	*	*
	22%	14.8	8.6	8.1	9.7	56 vs. 22%	ns	ns	ns
500 ft-c	100%	10.2	2.8	3.3	3.3	100 vs. 22%	ns	**	*
	56%	4.6	3.7	4.6	4.2	100 vs. 56%	ns	**	*
	22%	6.6	4.0	4.8	4.4	56 vs. 22%	ns	ns	ns
MAPLE SEEDLINGS									
5000 ft-c	100%	7.2	3.2	4.8	3.4	100 vs. 22%	ns	ns	ns
	56%	4.8	5.0	2.7	2.0	100 vs. 56%	ns	*	ns
	22%	5.0	4.9	5.2	3.8	56 vs. 22%	ns	ns	ns
2500 ft-c	100%	5.2	2.3	4.0	2.6	100 vs. 22%	ns	ns	ns
	56%	4.0	4.3	2.5	1.9	100 vs. 56%	ns	ns	ns
	22%	6.2	4.3	5.1	3.5	56 vs. 22%	ns	ns	ns
1000 ft-c	100%	2.6	1.3	2.2	1.3	100 vs. 22%	**	ns	ns
	56%	1.9	2.4	1.7	1.4	100 vs. 56%	ns	ns	ns
	22%	4.3	3.0	4.8	2.4	56 vs. 22%	**	ns	ns
500 ft-c	100%	0.9	0.3	0.7	0.2	100 vs. 22%	**	**	ns
	56%	1.0	0.7	0.7	0.2	100 vs. 56%	ns	ns	ns
	22%	2.0	1.0	3.0	0.8	56 vs. 22%	**	*	ns

"Rates are given as mg CO_2 dm^{-2}_{1} h^{-1}. ANOVA'S are based on the mean APS rate of individual plants at each harvest period and for each treatment.

measured at 5000 and 2500 ft-c (Table 14). At these light intensities, APS rates were also significantly lower in full shade (22 percent light) plants when compared with those grown under partial shade. Only at 1000 ft-c light intensities were differences significant between the control (full light) plants and partial shade (56 percent light) plants. Differences in APS rates of the alder seedlings between harvest periods were significant for all treatment combinations with the exception of the partial vs. full shade grown plants measured at 5000 ft-c.

Differences in apparent photosynthesis rates for the maple seedlings followed a somewhat different pattern. Control (100 percent light) maple seedlings had significantly lower APS rates than full shade (22 percent light) grown maple seedlings throughout the season when measured at 2500, 1000 and 500 ft-c. With the exception of Harvest 2 measurements, APS rates measured at 5000 ft-c for full light vs. full shade grown maples were also lower in the control treatment but not significantly so. Similarly, APS rates of full shade grown maple seedlings were significantly higher throughout the season when compared with the partial shade grown plants. Differences in this combination were significant at all light intensities used in the CO_2 exchange measurements. Control (100 percent light) maples were not significantly different from the partial shade grown plants in APS rates except at the 5000 ft-c light intensity. At this intensity, APS rates were significantly lower in general for the partial shade vs. control plants (Table 14).

Thus, highest APS rates for the maple seedlings occur in seedlings preconditioned in considerable shade; the APS rate of maple seedlings is depressed in seedlings preconditioned in increased levels of light. Alder seedlings show an almost opposite pattern except at the low light intensity measurements. Highest APS rates of alder seedlings occur when preconditioned in increasing levels of light at 5000 and 2500 ft-c, but are higher when preconditioned in increasing shade at 500 and to a lesser extent at 1000 ft-c.

Dark respiration rates

Dark respiration rates (mg CO_2 dm^{-2} h^{-1}) of the alder seedlings were higher than those of the maple seedlings for all light treatments and harvest periods with the exception of full shade grown plants at Harvest 4 (Fig. 19). Highest dark respiration rates were measured for the alder seedlings in

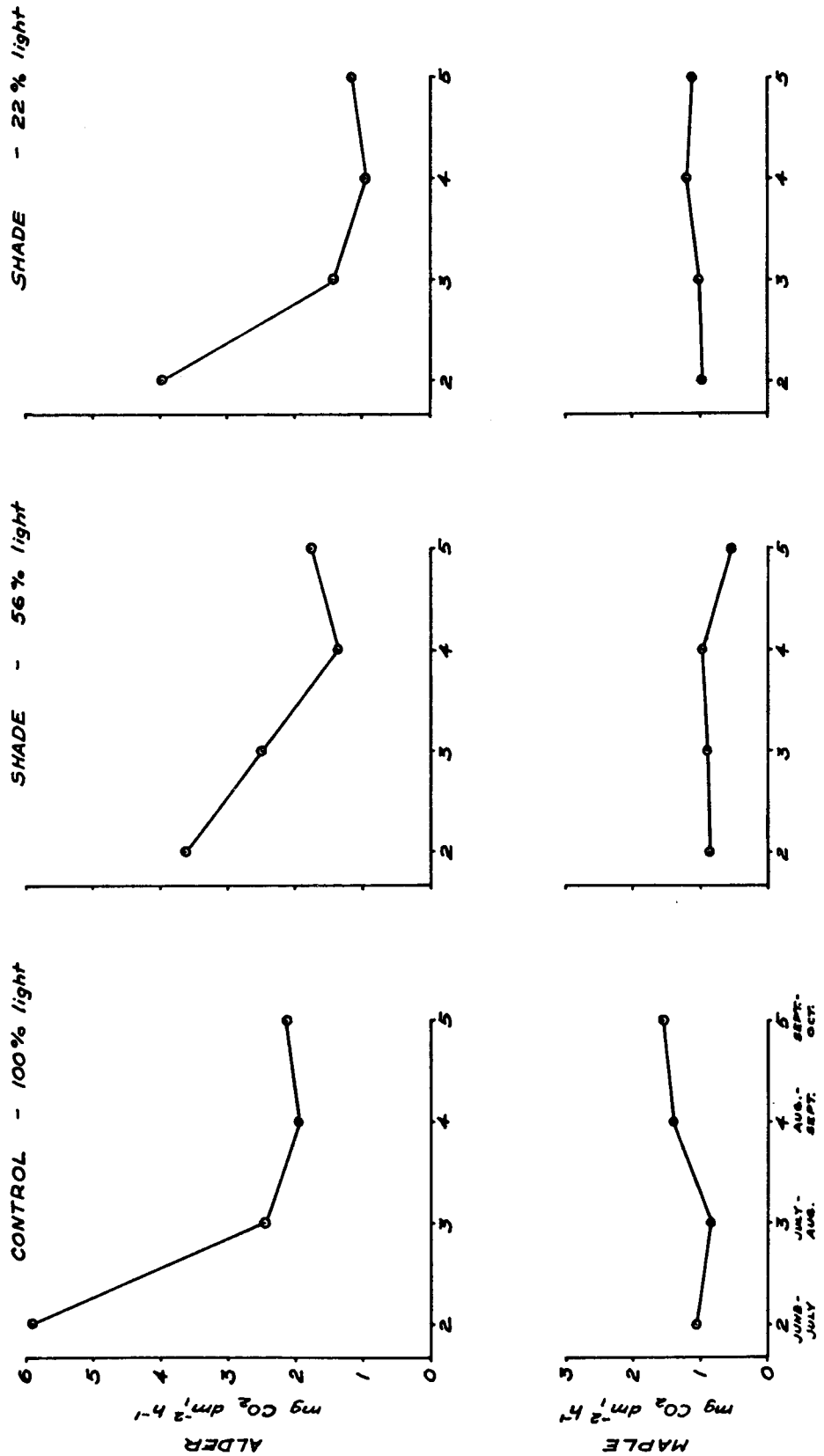


Figure 19. Mean dark respiration rates (mg CO_2 dm^{-2} h^{-1}) of the alder and maple seedlings by light treatment and harvest period.

June-July (Harvest 2), the respiration rates then decreased in all light treatments to August-September (Harvest 4) and then increased slightly at the end of the season. For the alder seedlings, highest respiration rates occurred in the control (100 percent light) plants. Dark respiration rates of the maple seedlings in all light treatments generally showed a pattern characterized by less change in rate throughout the season (Fig. 19). Highest respiration rates, however, occurred near the end of the growing season in the full light (control) and full shade grown maple seedlings. Partial shade grown maple seedlings had lowest dark respiration rates at the end of the growing season.

Statistical analyses of the dark respiration rates indicated that the alder seedlings had significantly higher rates than the maple seedlings (Table 15). Within species treatment and seasonal differences in respiration rate of alder seedlings were significant, but none of the differences were significant for the maple seedlings (Table 15). Further analyses were performed for all treatment

Table 15. ANOVA'S for between and within species comparison of mean dark respiration rates of the alder and maple seedlings (Harvests 2 to 5 inclusive).

Source	Degrees of freedom	Mean square	F-ratio	Probability
A) Species	1	30.027	121.37**	0.0000
B) Treatment	2	2.593	10.48**	0.0004
C) Harvest	3	6.673	26.97**	0.0000
AB) (Species/Treatment)	2	1.750	7.07*	0.0027
AC) (Species/Harvest)	3	8.046	32.52**	0.0000
BC) (Treatment/Harvest)	6	0.384	1.55 ns	0.1872
ABC) (Species/Treatment/Harvest)	6	0.490	1.98 ns	0.0917
Within, error term	39	0.247		
Total	62	1.577		
ALDER SEEDLINGS ONLY				
A) Treatment	2	4.298	12.54**	0.0004
B) Harvest	3	15.915	46.42**	0.0000
AB) (Treatment/Harvest)	6	0.803	2.34 ns	0.0683
Within, error term	21	0.343		
Total	32	2.136		
MAPLE SEEDLINGS ONLY				
A) Treatment	2	0.377	2.78 ns	0.0876
B) Harvest	3	0.141	1.04 ns	0.4012
AB) (Treatment/Harvest)	6	0.127	0.94 ns	0.5052
Within, error term	18	0.136		
Total	29	0.151		

combinations (Table 16). Full light (control) alder seedlings have significantly higher dark respiration rates than both the partial and full shade grown alder seedlings throughout the season. Conversely, the partial shade grown alder seedlings have not significantly different dark respiration rates from those grown in full shade despite the slightly higher respiration rate of the full shade vs. partial shade grown alders at Harvest 2 (Fig. 19). For all light treatments, dark respiration rates of the maple seedlings do not differ significantly throughout the season; this confirms the analysis of the within-species variance of the maple seedlings (see Table 15).

Table 16. ANOVA for within species comparison of mean dark respiration rates by all treatment combinations for the alder and maple seedlings.

Source		Degrees of freedom	Mean square	F-ratio	Probability
ALDER SEEDLINGS					
100 vs. 22%	A) Treatment	1	8.334	33.59**	0.0001
	B) Harvest	3	14.734	59.39**	0.0000
	AB) (Treatment/Harvest)	3	0.340	1.37 ns	0.2921
	Within, error term	14	0.248		
	Total	21	2.716		
100 vs. 56%	A) Treatment	1	3.558	9.38*	0.0083
	B) Harvest	3	10.633	28.05**	0.0000
	AB) (Treatment/Harvest)	3	1.566	4.13 ns	0.0268
	Within, error term	14	0.379		
	Total	21	2.165		
56 vs. 22%	A) Treatment	1	1.002	2.50 ns	0.1335
	B) Harvest	3	7.266	18.10**	0.0001
	AB)(Treatment/Harvest)	3	0.505	1.26 ns	0.3270
	Within, error term	14	0.401		
	Total	21	1.425		
MAPLE SEEDLINGS					
100 vs. 22%	A) Treatment	1	0.019	0.12 ns	0.7349
	B) Harvest	3	0.193	1.24 ns	0.3426
	AB) (Treatment/Harvest)	3	0.060	0.38 ns	0.7688
	Within, error term	11	0.155		
	Total	18	0.138		
100 vs. 56%	A) Treatment	1	0.641	7.93 ns	0.0150
	B) Harvest	3	0.086	1.06 ns	0.4020
	AB) (Treatment/Harvest)	3	0.236	2.92 ns	0.0767
	Within, error term	12	0.081		
	Total	19	0.136		
56 vs. 22%	A) Treatment	1	0.507	2.97 ns	0.1055
	B) Harvest	3	0.127	0.74 ns	0.5470
	AB) (Treatment/Harvest)	3	0.083	0.48 ns	0.7021
	Within, error term	13	0.171		
	Total	20	0.168		

DISCUSSION

From the results of this study, it is possible to propose certain definite findings about the behavior of alder and maple seedlings vis-a-vis each other and also concerning individual species responses to different light treatments during first-year of growth:

1) First-year alder seedlings add significantly more biomass than first-year maple seedlings,
2) Alder seedlings start as very small seedlings, grow at a rate which allows them to surpass the maple seedlings in a few months, and continue to grow late in the season, and
3) Both species respond to different light treatments during growth in ways that allow them to achieve similar final biomasses that are not significantly different between the shade treatments and the controls.

Thus, if one considers that the productivity of a tree is measured by the increase in biomass over a given time, then the alder seedlings are clearly and significantly superior to maple seedlings in the first growing season. Although the maple seedlings begin with a higher biomass (post-cotyledon stage) and continue to add a substantial increment up to the last harvest, the alder seedlings add increasingly larger increments until near the end of the growing season. The result is significantly large differences in biomass between species, but not among treatments within species.

The significantly higher relative growth rate (RGR) of alder seedlings in comparison to the maple reflect the biomass differences. Initial RGR's of the maple seedlings were 0.20 and 0.14 for the control (full light) and full shade plants respectively; initial RGR's of the alders were 0.34 and 0.21 for the same treatments (see Fig. 13, Tables 3 and 4). The relative growth rate of maple declines almost steadily throughout the season in all treatments, but the rates for alder increase until September-October (Harvest 5) when a slight decline appears for all treatments. Species differences of this nature are not uncommon; Pollard and Wareing (1968) report rates of 0.12 and 0.075 for birch and sycamore, respectively (both rates are higher than those of several conifers). A pattern

of seasonal change similar to that of the red alder seedlings was reported by Loach (1970) for Acer rubrum, Quercus rubra, Fagus grandifolia, and Liriodendron tulipifera in his study of shade tolerance in eastern deciduous species. His values range from about 0.05 at the beginning of the season to a maximum rate of 0.21 except for Acer rubrum which had RGR values comparable to those for red alder. Jarvis (1964) reported RGR's for 9-week old Quercus petraea of 0.09, 0.12, and 0.04 for plants grown in 100, 56 and 10 percent light respectively, however in none of the literature reviewed has a seasonal pattern like that of the broadleaf maple seedlings appeared. Rutter (1957) described a declining seasonal RGR for Pinus sylvestris, but the plants were four-year olds.

In contrast to the insignificant differences between light treatments reported here for the alder and maple seedlings, Blackman and Black (1959) and Blackman (1968) have reported significant increase in RGR of plants grown at high light levels or 100 percent light intensities. Their plants, however, were herbaceous with comparatively very high growth rates anyway.

Caution on the indiscriminate acceptance of RGR's at face value has been given by Radford (1967) who pointed out that use of a mean RGR rate is justified if the assumption can be made that the growth form is continuous throughout the period between harvests. Data reported in this study appear to fit these assumptions.

As the RGR's of the maple and alder seedlings are so different in magnitude and pattern, the question remains: what are the 'strategies' of the seedlings that lead to these results?

Apparent photosynthesis and dark respiration patterns are clearly different between the two species. As shown in Figures 16 and 17, the APS rates of alder seedlings (leaf area basis) from all treatments are significantly higher than those of the maple seedlings from comparable treatments. Not only do the alders start at a rate 5 to 10-fold greater, but they generally maintain higher rates than the maples at subsequent harvests. Indeed, at the last harvest, the alders from all light treatments show an increase in APS rate at all but the lowest light intensity; maple seedlings drop to the lowest rates of the season, regardless of treatment. On the other hand, dark respiration rates of maple seedlings are consistently lower than those of alder (Fig. 19). The differences may be in accord with

Loach's (1970) report of variability between shade-tolerant and intolerant species.

Apparent photosynthesis rates of the alder seedlings are approximately twice those reported by Logan (1970) for shade- and sun-grown yellow birch. They also exceed those given by Böhning and Burnside (1956) for fast-growing herbaceous full light grown species such as tobacco, soybean and tomato. Broadleaf maple seedlings, on the other hand, have APS rates comparable to those reported by Böhning and Burnside for Philodendron, Oxalis and Saintpaulia. Apparent photosynthesis values for both shade- and sun-grown Quercus petraea reported by Jarvis (1964), are intermediate between those of the broadleaf maple and red alder seedlings.

According to Worthington (1965) and Ruth and Muerle (1965), alder is considered less shade tolerant than broadleaf maple. This suggests that the alder should have lower APS rates regardless of light treatment than the maple when measured at low light intensities. However, that is not the case --- at 500 ft-c, alder seedlings have higher APS rates than broadleaf maple seedlings. The answer may lie in the observation of Krueger and Ruth (1969) that alder seedlings grown in both light and heavy shade had significantly higher APS rates at both high and low light intensities than other species in their study[1]. Furthermore, they found that alder's respiration rate is comparatively low when measured relative to organic nitrogen, which represents the proportion of active cellular material present. Therefore, they state, alder would appear to have either a higher proportion of functional tissue or a higher concentration of active consituents in the same weight of functional cells. Either possibility would predispose alder for high metabolic activity. Ruth (1968) also found that alder seedlings established under a forest canopy outgrew Sitka spruce and western hemlock in the first season at locations where radiation was about 10 percent of that in the open. Effectively, the alder seedlings are shade-tolerant, and this tolerance extended into the second season with seedlings surviving and growing at incident radiation levels averaging less than 20 percent.

This relationship is borne out by the APS data of alder plants in this study. As Figure 16

[1] Absolute values of APS rates of the partial and full-shade plants in this study almost exactly coincide with those of Krueger and Ruth (1969) for their plants grown in 79 and 31 percent light.

shows, the alder seedlings had consistent significantly higher APS rates at low light intensities (500 ft-c) than the maple seedlings. The rate did not fall below 2.5 mg $CO_2 dm^{-2} h^{-1}$, whereas for the maple seedlings the rate was below 1.0 mg .

To compare the effect of light treatment on the photosynthetic performance of each species, one approach is to examine the APS rate of the plant at the test light intensity proportionally nearest the growth regimen (Krueger and Ruth, 1969). At Harvest 2 (Fig. 16), full light grown alder and maple seedlings have higher APS rates at 5000 and 2500 ft-c than the partial shade grown plants. A similar pattern is maintained for the alder seedlings at 1000 and 500 ft-c. At later harvests, the control and partial shade grown alder plants have higher apparent photosynthesis rates than the full shade grown plants at 5000 and 2500 ft-c, but the shade treated alders have higher APS rates than the control plants at 1000 and 500 ft-c. For the maple seedlings, the full shade grown plants have significantly higher APS rates at 500, 1000 and 2500 ft-c than either the partial shade or full light plants.

This pattern resembles that exhibited by the shade- and sun-grown Solidago plants of Björkman and Holmgren (1963), when the APS vs. light intensity curves are compared for the full light (control) plants and the full shade grown plants (Figs. 16 and 18). The control plants of alder and maple show the characteristic less steeply inclined rate-intensity curve at low light intensities of the Solidago sun-grown plants, and the curve continues to rise without reaching light saturation at 5000 ft-c at all harvest periods for the alder seedlings and for all but the last harvest period for the maple seedlings. Full shade grown plants, on the other hand, have the typical steeply inclined rate-intensity curve at low light intensities followed by a pronounced inflection and flattening of the curve when light saturation is reached between 1000 and 2500 ft-c for almost all harvest periods.

Differences between APS rate of the alder seedlings by light treatment, however, do not follow a completely clear pattern. At Harvest 2 (Table 14) for example, highest rates of APS occurred consistently in the full light grown plants, but at Harvests 3, 4 and 5 higher rates of apparent photosynthesis occurred in the partial shade grown plants except at 500 ft-c where the

rate was highest in the full shade grown plants. Ruth (1967) reported that alder in forest stands showed better growth at 60 to 80 percent incident radiation levels than at higher levels. He found that different amounts of light preconditioning did not significantly affect biomass measurements, indicating, as found here, that there are plants grown in shade and full light which reach the same biomass endpoint regardless of treatment. Ruth found, however, that growth patterns were different with shoot heights remaining similar but root lengths increased with increasing incident radiation. He found that partial shade for first season growth was beneficial for alder seedlings.

In contrast to alder, the full shade maple seedlings have higher apparent photosynthesis rates than partial shade grown plants at all light intensities. This result conforms to Worthington's (1965) statement that maple is highly shade tolerant compared with other species. Further, except at 5000 ft-c, full shade grown maple seedlings have significantly higher APS rates than the control (full light) seedlings --- a more consistent pattern than that for red alder.

Despite these differences, biomass added (dry matter production) is not significantly affected by light treatment for either species, although between harvest 2 to 5, the alder adds about 30 times more biomass than the maple seedlings. Certain factors or patterns, however, are common to both species including similarities in the APS rate vs. intensity curves already discussed. Perhaps some of these enable the shade grown plants to reach the same endpoint as the full light controls through enhancement of their APS rates particularly at low light intensities. Chlorophyll content (a + b) may be a major factor.

Alder seedlings for all light treatments have significantly higher chlorophyll content (mg / g leaf fresh weight) than the maple seedlings. This may account in part for the lower photosynthesis and biomass production rates of the maple. Seasonal pattern of chlorophyll content for all light treatments (mg / plant basis), however, follows completely different patterns between species (Table 8). On this basis, chlorophyll content progressively decreases throughout the season for the maple seedlings and has the reverse pattern (progressive increase) for the alder seedlings. Between light treatments, there are similarities for both species (Fig. 15 and Table 11). Highest chlorophyll contents are found for both species in the full shade grown plants. For harvest periods

2 to 5, the chlorophyll content (mg / g leaf fresh weight) of full shade grown alder and maple seedlings is significantly greater than that for partial shade grown seedlings which in turn is significantly greater than for the control (full light) plants (see Table 11) for the maple seedlings but not for the alder. Thus maple seedlings and alder seedlings in part meet the challenge of lower light levels by increasing the amount of chlorophyll available in the partial and full-shade leaves. For both species, the chlorophyll content data of the full shade vs. control (full light) plants agrees with the general finding of Björkman and Holmgren (1963) that the chlorophyll content of plants grown in high light is lower than that of plants grown in low light. Similar results were reported by Jarvis (1964) for Quercus petraea in which seedlings grown in 20 percent light had almost twice as much chlorophyll as those grown in full light. He attributed the difference to light- or temperature-induced breakdown of chlorophyll.

Another factor may be inhibition of photosynthesis in the control (full light) seedlings at very high light intensities (8000 to 10000 ft-c or higher are not uncommon in July and August) and high intensities as described by Jarvis and Jarvis (1964). Several workers have pointed out the advantage of being able to screen out the destructive effect of continued high light intensities on chlorophyll content (see Loach, 1967; Jarvis, 1964; and Wassink, Richardson and Pieters, 1956). A possible relationship to performance may lie then in the bronzing appearance of the control plants resulting from the presence of carotenoids. Although this relationship was especially pronounced for the maple seedlings (Figs 9 and 10) in the light treatments and not as clearly established for the alder seedlings, the reason for the relationship is not clear although it may act to preserve the integrity of the photosynthetic process against the high intensities of full sunlight on Burnaby Mountain. Gaffron (1960) noted that the formation of carotenoids can prevent photo-oxidation of important enzymes and the bleaching of chlorophyll. Thomas (1955) reported that the presence of carotenoids favored the formation of proteins over that of carbohydrates, an effect that could result in the coarser, stiffer texture of the leaves of the full light grown plants.

The screening effect of red carotenes may also act on the photosynthetic metabolism of the leaf. Voskresenskaya and Nechaeva (1967) showed that replacing red and green light components by

blue increases the protein and RNA content up to the level characteristic for blue light for that species. Red-reflecting carotenoids would have that effect. The rate of photosynthesis at light saturation is also higher under blue than under red-blue light in shade-adapted plants (Gol'd, 1969).

Coupled with the high chlorophyll content of leaves in the full shade treatment, the leaf area of the alder seedlings provides it with a seasonal advantage over the maple seedlings. The alder starts with very small leaves, but the total leaf area per plant increases steadily and ends with the full shade grown plants having both the largest and most numerous leaves. Full light grown alders, on the other hand, reach a maximum in mean total leaf area before the shade grown plants (Table 7). Maple seedlings have an increase in mean total leaf area and number of leaves early in the season for all light treatments and do not show the regular leaf area increase with increased shading as Jarvis (1964) reported for oak. Leaf areas of the shade grown alder seedlings were comparable to those reported by Krueger and Ruth (1969). Their alder seedlings grown under 79 and 31 percent light had leaf areas of 0.8 and 1.2 dm^2 respectively compared to areas of 0.71 dm^2 for the 56 percent light grown plants and 0.9 dm^2 for the 22 percent light grown plants in this study (means of Harvests 4 and 5).

Specific leaf area ($dm^2\ g^{-1}$ dry weight) also gives a measure of leaf geometry that affects the photosynthetic response of the seedlings. The higher the index, the thinner the leaf, and one can suggest that this promotes increased light penetration and hence more efficient use of available chlorophyll. Alder seedlings grown in full shade had higher specific leaf areas than seedlings grown in partial shade or full light; Krueger and Ruth (1969) reported that alder seedlings grown under heavy shade had a specific leaf area 57 percent higher than those grown under less shade. This pattern together with the higher chlorophyll concentration may account for the steeper initial photosynthesis rate vs intensity curve in the full shade grown plants and thereby offset the effect of lower growth light intensities throughout the season. For the maple seedlings, specific leaf areas were higher in both shade treatments than the control (full light) plants (Fig. 15). Clear differences for both species occur in mean area per leaf between light treatments (Fig. 14). Shade grown alder and maple seedlings have highest mean area per leaf at the end of the season for alder and at most times throughout the season for maple.

The disposition of leaves from the stem for both species is so arranged that plants grown in full light reduce the angle of incidence to the leaves at high solar altitudes: the alder leaves tend to be stiffly inclined upward whereas those of maple droop in an almost vertical position. Both positions suggest disposition for best orientation to incident light in the early morning and again later in the day with less favorable disposition at high solar altitudes when the air temperatures would be highest during the day and the plant leaves most subject to temperature stress. For both species, leaves of the full shade grown plants are more horizontally disposed (see Figs. 9 and 10) which exposes the largest surface to receive light at highest angles of incidence during mid-day. Partial shade grown leaves of both species were intermediate in disposition from the stem.

Generally, root/shoot ratios tend to decline as level of shading increases although the degree of decline varies widely among species (Shirley, 1929; Loach, 1970). According to Logan (1966), shade tolerant species tend to have a higher root/shoot ratio, although he reported that the root/shoot ratio decreased only slightly in the shade tolerant sugar maple (Logan, 1965). But the relatively high ratio of the maples in this study, compared with alder, may have important implication for seedling survival. There are no reports on the second-year survival rates of the maple, but Ruth (1968) reports that alder has a very high seedling mortality rate in the first year (survival rate of 1:31 germinations). Thus the lower growth rate and germination rate of the maple may be offset by the germination of seedlings that grow slowly but develop sturdy, complex root systems. Thus the survival mechanism is durability, rather than proliferate germination.

Further differences in the plants that lead to similar relative growth rates can be detected in the allocation of plant material to different components. The consistently higher leaf dry weight percentage permits the alder to put more tissue into photosynthetic activity. It has the disadvantage that this tissue is almost all deciduous. The maple has a high root dry weight percentage but a concomitantly low leaf weight percentage: 15, 12 and 22 for the control and two treatments, respectively. The comparable alder percentages are 31, 30 and 37.

This is carried through to the root/shoot ratios, which are consistently higher at all harvests for the maples.

CONCLUSIONS

It is possible to draw some general conclusions from this series of experiments. First, regardless of the treatment given, the plants of moderately tolerant species such as red alder and broadleaf maple will adapt their physiological mechanisms to reach approximately the same point in growth as the other members of the species at the end of the growing season. As Donald Kennedy said, "Organisms have a way of coming up with an embarrassing number of solutions to a problem in evolutionary engineering." [1]

The most noticeable solution is the modification of the photosynthetic mechanism to adapt to the available light: the shade-grown plants can respond efficiently to low levels of illumination. Conversely, the full-light grown plants erect a protective mechanism to prevent damage to the chlorophyll structure at high light intensities.

The respiration rates also vary significantly between control and treatment plants (as well as between treatments in the alders). The full-light controls show a steady APS/dark respiration ratio throughout the season (5:1 during early season harvests and 6:1 later in the growing season). But the shade grown plants show the marked increase from 4:1 early in the season to 10:1 at the end of the season. Thus the balance between production and consumption is maintained regardless of the growth light.

The mechanisms underlying the APS adaptation appear to lie in the relative chlorophyll content: the shade-grown plants of both species was significantly higher (less so for maple) than that of the full - light grown plants. It also varied significantly with harvest. In addition, the growth pattern, the presentation of the leaves in both species, permits the full- and partial-shade grown plants to use the maximum incoming radiation. Conversely, the full-light grown plants turn their leaves away from the horizontal to minimize direct impact of energy on the photosynthetic apparatus.

The second conclusion is that in indirect competition (i.e. preferential establishment sensu

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[1] Personal communication, 1963.

Billings, 1957), the alder will win out over maple, when filling space made available by logging, fire, or other disturbance. This is primarily due to the relatively higher APS rates, the extended growing season, and the many-fold increase in biomass exhibited by alder under any light treatment. In addition, the alder has a larger proportion of its biomass in leaf production, and hence utilizes available light to grow and establish itself rapidly. Although the establishment rate for alder is low compared with that of maple (Ruth, 1968), its high seed production and germination (McVean, 1955) combined with high growth rate ensures that more alders will find a home on disturbed soil than maples.

In further studies, it would probably be fruitful to try additional experimentation to elucidate the plant / light relationships at very low test light intensities. It would also be helpful to have more condensed sampling periods (assuming the logistics could be worked out), and more replicates to reduce measures of plant-to-plant variability. These refinements would serve to reinforce the findings reported here.

But how applicable are the results of such a controlled-growth laboratory experiment to the behavior of the plants in the field? Admittedly one is isolating certain kinds of behavior, performing functional tests under unnatural conditions. But although it may not be justifiable to draw fine conclusions from this kind of experimental study, the major results given above may be verified empirically be taking a stroll on the south side of Burnaby Mountain, British Columbia.

LITERATURE CITED

Billings, W. D. 1957. Physiological ecology. Ann. Rev. Plant Physiol. 8: 375-392.

Björkman, O. and P. Holmgren. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol. Plant. 16: 889-914.

Blackman, G. E. 1968. The application of the concepts of growth analysis to the assessment of productivity. Proc. 1965 Symposium on Ecophysiology, Paris. UNESCO. pp. 243-259.

Blackman, G. E. and J. N. Black. 1959. Physiological and ecological studies in the analysis of plant environment. XI. A further assessment of the influence of shading on the growth of different species in the vegetative phase. Ann. Bot. N. S., 23: 51-63.

Böhning, R. H. and C. A. Burnside. 1956. The effect of light intensity on rate of apparent photosynthesis in leaves of sun and shade plants. Am. J. Bot. 43: 557-561.

Bulley, T. Ross. 1969. Effects of light quality and intensity on photosynthesis and photorespiration in attached leaves. Ph.D thesis, Dept. Biological Sciences, Simon Fraser University, Burnaby, Canada. 137 p.

Canada, Dept. of Transport, Meteorological Branch. 1969. Climatological station report, Simon Fraser University, Burnaby, B. C.

Crocker, R. L. and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecology 43: 427-448.

Gaffron, H. 1960. Energy storage. In: F. C. Steward [ed.]. Plant physiology. Vol. 1b, Part 3. Academic Press Inc., New York.

Gol'd, V. M. 1969. Some ecological-physiological features of the action spectrum of photosynthesis at light saturation. Fiziol. Rastenii (Sov. Pl. Physiol.) 16: 495-501.

Holden, M. 1965. Chlorophylls. In: T. W. Goodwin [ed.]. Chemistry and biochemistry of plant pigments. Academic Press Inc., N. Y. Ch. 17, pp. 461-487.

Jarvis, P. G. 1964. The adaptability to light intensity of seedlings of Quercus petraea (Matt.) Liebl. J. Ecology 52: 545-571.

Jarvis, P. G. and M. S. Jarvis. 1964. Growth rates of woody plants. Physiol. Plant. 17: 654-656.

Krueger, K. W. and R. H. Ruth. 1969. Comparative photosynthesis of red alder, Douglas-fir, Sitka spruce, and western hemlock seedlings. Can. J. Bot. 47: 519-527.

Loach, K. 1967. Shade tolerance in tree seedlings. 1. Leaf photosynthesis and respiration in plants raised under artificial shade. New Phytol. 66: 607-621.

_____. 1970. Shade tolerance in tree seedlings. 2. Growth analysis of plants raised under artificial shade. New Phytol. 69: 273-286.

Logan, K. T. 1965. Growth of tree seedlings as affected by light intensity. I. White birch, yellow birch, sugar maple, and silver maple. Canada, Dept. Forestry. Publ. No. 1121.

_____. 1966a. Growth of tree seedlings as affected by light intensity. II. Red pine, white pine, jack pine, and eastern larch. Canada, Dept. Forestry. Publ. No. 1160.

_____. 1966b. Growth of tree seedlings as affected by light intensity. III. Basswood and white elm. Canada, Dept. Forestry. Publ. No. 1176.

_____. 1970. Adaptation of the photosynthetic apparatus of sun and shade grown yellow birch (Betula alleghanensis Britt.). Can. J. Bot. 48: 1681-1688.

Logan, K. T. and G. Krotkov. 1969. Adaptations of the photosynthetic mechanism of sugar maple (Acer saccharum Marsh.) seedlings grown in various light intensities. Physiol. Plant. 22: 104-116.

Machlachlan, S. and S. Zalik. 1963. Determination of chlorophyll content on the basis of leaf fresh weight. Can. J. Bot. 41: 1053.

McVean, D. N. 1955. Ecology of Alnus glutinosa (L.) Gaertn. I. Fruit formation. J. Ecol. 43: 46-81.

Moses, L. and R. V. Oakford. 1963. Tables of random numbers. Stanford Univ. Press, Stanford, Calif.

Newhouse, M. E. and H. A. I. Madgwick. 1968. Comparative seedling growth of four hardwood species. For. Sci. 14: 27-37.

Pollard, D. F. W. and P. F. Wareing. 1968. Rates of dry matter production in forest tree seedlings. Ann. Bot. 32: 573-591.

Radford, P. J. 1967. Growth analysis formulae -- their use and abuse. Crop Sci. 7: 171-175.

Rohlf, F. J. and R. R. Sokal. 1969. Biometrical Tables. Freeman, San Francisco, Calif.

Ruth, R. H. 1968. Differential effect of solar radiation on seedling establishment under a forest stand. In: Trappe et al. [eds.]. Biology of alder. Pacific Northwest Forest and Range Expt. Station, U. S. Dept. Agric., Forest Service. Portland, Ore.

Ruth, R. H. and G. F. Muerle. 1965. Broadleaf maple. In: H. A. Fowells, [ed.]. Silvics of Forest Trees of the United States. U. S. Dept. Agric., Agriculture Handbook No. 271, Washington, D. C.

Rutter, A. J. 1957. Studies in the growth of young plants of Pinus sylvestris L. I. The annual cycle of assimilation and growth. Ann. Bot. N. S. 21: 399-426.

Sabhasri, S. and W. K. Ferrel. 1960. Invasion of brush species into small stand openings in the Douglas-fir forests of the Willamette foothills. Northwest Sci. 34: 77-88.

Salisbury, F. R. and G. G. Spooner. 1964. Leaf temperatures of alpine plants in the field. Planta 60: 497-505.

Shirley, H. L. 1929. The influence of light intensity and light quality upon the growth of plants. Am. J. Bot. 16: 354-390.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. Freeman, San Francisco, Calif.

Tarrant, R. F., K. C. Lu, W. R. Bollen and J. F. Franklin. 1969. Nitrogen enrichment of two forest ecosystems by red alder. Pacific Northwest Forest and Range Expt. Station, U. S. Dept. Agric., Forest Service. Research Paper PNW 76.

Thomas, M. 1955. Effect of ecological factors on photosynthesis. Ann. Rev. Plant Physiol. 6: 135-156.

Voskesenskaya, N. P. and E. P. Nechaeva. 1967. Effect of blue, red, and green light on the content of protein, nucleic acids and chlorophyll in young barley leaves. Fiziol. Rastenii (Sov. Plant Physiol.) 14: 299-308.

Wassink, E. C., S. D. Richardson and C. A. Pieters. 1956. Photosynthetic adaptation to light intensity in leaves of Acer pseudoplatanus. Acta Bot. Neerl. 5: 247-256.

Worthington, N. P. 1965. Red alder. In: H. A. Fowells, [ed.]. Silvics of forest trees of the United States. U. S. Dept. Agric., Agric. Handbook No. 271. Washington, D. C.

APPENDIX I

Table 1.

Light intensities (ft-c) used for the apparent photosynthesis runs at the different harvest periods.

Harvest	Long run	Short run
1	2500 2000 1500 1000 750 500	3000 1650 650 500
2	5000 2500 2000 1500 1000 750 500	5000 2500 1000 500
3 and 4	5000 3000 2500 2000 1500 1000 750 500	5000 2500 1000 500
5	No long runs	5000 2500 1000 500

APPENDIX II

Table I. Physical measurements of the alder and maple seedlings by treatment and harvest period.

Plant	Harvest period	Total leaf area (dm_1^2)	Dry weight (mg) Leaf	Stem	Root	Total	Specific leaf area (dm_1^2 g^{-1} dwt)
ALDER (Control, 100% light)							
A-12	1	0.0081	4.2	0.9	0.8	5.9	1.93
18		0.0108	4.7	2.0	2.1	8.8	2.30
24		0.0078	4.4	1.2	1.2	6.8	1.77
A- 5	2	0.0110	12.5	5.1	6.2	23.8	0.88
15		0.0464	17.4	9.2	17.1	43.7	2.67
22		0.0274	14.5	5.6	8.7	28.8	1.89
A-16	3	0.1243	21.4	7.9	16.7	46.0	5.81
20		0.3724	128.1	47.4	87.9	263.4	2.91
27		0.0776	33.5	12.5	19.5	65.5	2.32
A-19	4	0.3823	426.4	162.0	342.5	930.9	0.90
10		1.0720	155.9	51.9	108.7	316.5	6.88
31		1.1600	578.8	278.0	548.4	1405.2	2.00
A- 2	5	0.7356	394.7	247.2	483.4	1125.3	1.86
25A		0.4449	247.0	164.7	335.6	747.3	1.80
25B		0.4439	248.4	231.4	470.4	950.2	1.79
MAPLE (Control, 100% light)							
M-12	1	0.2432	265.0	96.8	132.2	494.0	0.92
18		0.1885	73.8	23.3	45.2	143.2	2.55
24		0.1950	156.8	52.2	95.2	304.2	1.24
30		0.3466	119.1	41.3	50.9	211.3	2.91
M- 5	2	0.6523	261.5	143.8	260.4	655.7	2.49
15		0.5687	298.8	183.0	387.2	869.0	1.90
22		0.4510	247.4	112.8	304.3	664.5	1.82
M-16	3	0.1720	288.9	178.0	454.2	921.1	0.60
20		0.4657	229.9	149.7	371.6	751.2	2.03
27		0.4757	272.1	135.7	547.8	955.6	1.75
M-25	4	0.3955	201.0	139.4	664.1	1004.5	1.97
21		0.2348	143.0	276.2	556.3	975.5	1.64
26		0.3687	191.1	177.6	494.6	863.3	1.93
M-29	5	0.2170	143.1	319.8	616.8	1079.7	1.52
8		0.2325	147.3	144.5	586.9	878.7	1.58

(continued ...)

APPENDIX II

Table I (continued)

Plant	Harvest	Total leaf area (dm_1^2)	Dry weight (mg) Leaf	Stem	Root	Total	Specific leaf area (dm_1^2 / g dwt)
ALDER (Partial shade, 56% light)							
A-12	1	0.0037	2.6	1.2	1.0	4.8	1.42
18		0.0311	8.2	3.9	6.9	19.0	3.79
24		0.0083	4.1	1.3	3.7	9.1	2.02
A- 5	2	0.0164	8.2	2.3	5.7	16.2	2.00
15		0.0684	24.2	8.2	8.0	40.4	2.83
22		0.0886	27.6	9.0	15.3	51.9	3.21
A-16	3	0.0613	50.9	8.3	33.1	92.3	1.20
20		0.2602	79.0	23.9	33.3	136.2	3.29
27		0.2849	96.2	50.3	76.1	222.6	2.96
A-29	4	0.8273	291.9	116.5	171.3	579.7	2.83
10		0.3101	92.3	30.0	76.8	199.1	3.36
21		0.8700	459.2	172.0	399.5	1030.7	1.89
A-19	5	0.5840	275.2	134.7	244.0	653.9	2.12
9		0.5619	295.3	269.7	666.5	1231.5	1.90
3		1.0757	541.1	558.9	1050.7	2150.7	1.99
MAPLE (Partial shade, 56% light)							
M-12	1	0.3637	112.7	35.8	82.4	230.9	3.23
18		0.3580	117.0	30.0	60.7	207.7	3.06
24		0.8985	372.2	113.2	153.8	639.2	2.41
M- 5	2	1.0611	261.5	143.8	260.4	665.7	4.06
15		0.6470	298.8	183.0	387.2	869.0	2.16
22		0.4630	247.4	112.8	304.3	664.5	1.87
M-16	3	0.6750	331.8	148.8	418.2	898.8	2.03
11		0.5824	239.2	174.8	622.9	1036.9	2.43
20		0.2630	126.3	117.5	343.5	587.3	2.08
M-25	4	0.3751	172.0	112.0	491.7	775.7	2.18
1		0.9427	448.3	236.4	878.9	1563.6	2.10
21		0.5136	228.6	296.7	771.2	1296.5	2.25
M- 3	5	0.3649	104.3	265.1	445.0	814.4	3.50
13		0.2060	101.2	144.3	625.4	870.9	2.04

(continued ...)

APPENDIX II

Table I (continued)

Plant	Harvest	Total leaf area (dm_1^2)	Dry weight (mg) Leaf	Stem	Root	Total	Specific leaf area (dm_1^2 / g dwt)
ALDER (Full shade, 22% light)							
A-12	1	0.0156	4.4	2.5	2.7	9.6	3.54
18		0.0170	5.4	1.8	4.1	11.3	3.15
24		0.0224	6.3	1.7	3.4	11.4	3.56
A- 5	2	0.0261	8.4	2.3	8.6	19.3	3.11
15		0.0508	17.3	5.5	5.5	28.3	2.94
2		0.0370	9.4	2.5	3.0	14.9	3.94
A-16	3	0.0848	20.8	6.4	7.7	34.9	4.08
20		0.3256	92.4	30.0	39.0	161.4	3.52
27		0.2895	56.3	22.7	40.9	119.9	5.14
A- 8	4	0.6488	139.2	77.4	75.0	291.6	4.66
28		0.6577	197.2	108.6	120.0	425.8	3.34
32		1.1024	315.8	106.9	168.8	591.5	3.49
A- 9	5	0.9557	342.9	212.8	289.0	844.7	2.79
14		0.5907	208.2	133.6	336.4	678.2	2.84
34		1.3420	449.0	291.7	412.5	1153.2	2.99
MAPLE (Full shade, 22% light)							
M-12	1	0.4631	130.5	37.1	65.5	233.1	3.55
18		0.4156	193.2	67.7	126.2	387.1	2.15
24		0.9431	314.8	108.3	153.4	576.5	3.00
M- 5	2	0.4279	138.0	51.4	85.1	274.5	3.10
15		0.5749	196.6	119.8	229.6	546.0	2.92
22		0.7872	289.6	151.0	334.7	775.3	2.72
M-16	3	0.5078	207.3	113.1	229.1	549.5	2.45
29		0.7441	320.2	212.7	510.9	1043.8	2.32
11		0.6693	265.2	158.6	437.4	861.2	2.52
M-28	4	0.3800	159.8	181.0	307.8	648.6	2.38
27		0.4360	173.8	161.6	630.6	966.0	2.51
M-26	5	0.5739	224.4	284.3	547.2	1055.9	2.56
31		0.3935	136.6	123.8	320.4	580.8	2.88

APPENDIX II

Table 2. Chlorophyll content (mg/g leaf f. wt.) and mean apparent photosynthesis (APS) and dark respiration rates (mg $CO_2/dm_1^2\ h^{-1}$) of alder and maple seedlings by treatment and harvest.

Plant	Harvest period	Chloro-phyll	Apparent photosynthesis at light intensity (ft -c) 5000	3000	2500	2000	1650	1500	1000	750	650	500	Dark resp.	No. runs
ALDER (Control, 100% light)														
A-12	1	1.86	.	.	.	.	.	16.6	9.2	6.4	.	4.0	5.0	2
18		1.26	.	23.8	.	.	17.4	.	.	.	7.8	.	4.6*	2
24		1.91	.	.	.	.	.	.	.	.	.	.	.	
A- 5	2	1.88	.	.	.	.	.	.	.	.	.	.	.	
15		1.41	34.3	.	31.3	.	.	.	18.3	.	.	10.6	5.7*	3
22			24.1	.	19.9	.	.	.	14.2*	.	.	9.7**	6.1**	3
sp.		1.28	.	.	.	.	.	.	.	.	.	.	.	
A-16	3	2.71	16.7*	16.6	13.2	11.7	.	8.9	4.9	4.3	.	1.9*	2.7*	3
20		1.88	12.1	.	10.2	.	.	.	5.8	.	.	2.2	1.8*	3
27		2.49	18.7*	.	15.6	.	.	.	6.7	.	.	4.3	3.0*	3
A-19	4	2.27	14.5	13.2	11.9	10.2	.	8.5	7.5	6.0*	.	4.1	1.8*	3
10		1.98	12.7	.	8.9	.	.	.	6.0	.	.	2.6	1.6*	3
31		1.95	20.5	.	16.9*	.	.	.	10.2	.	.	3.2	2.6*	3
A- 2	5	2.14	16.6	.	12.8	.	.	.	8.4	.	.	5.1	1.9*	3
25A		1.59	18.3	.	14.6	.	.	.	8.2*	.	.	2.4*	2.2*	3
25B		2.26	18.3	.	14.6	.	.	.	8.2*	.	.	2.4*	2.2*	3
MAPLE (Control, 100% light)														
M-12	1	3.37	.	17.8	.	.	14.8	.	.	.	.	4.4	2.4	2
18		2.97	.	8.0	.	.	6.1	.	.	2.4	.	.	1.9*	2
24		1.94"	.	12.8	.	.	9.9	.	.	.	.	3.5*	3.4	2
30		3.01	.	.	.	.	.	.	.	.	.	.	.	
M- 5	2	1.15	.	5.0	3.3	3.0	.	2.1	1.9	1.0	.	0.5	0.8+	2
15		1.26	7.2	.	6.5	.	.	.	3.5	.	.	1.1*	1.2*	3
22		1.47	7.1	.	5.8	.	.	.	2.4	.	.	1.0*	1.2*	3
M-16	3	1.52	3.4	2.4	2.5	2.0	.	1.6	1.3	0.7*	.	0.2*	1.0*	3
20		1.41	3.2	.	2.3	.	.	.	1.4	.	.	0.5	0.6*	3
27		1.40	3.1	.	2.2	.	.	.	1.1	.	.	0.3	0.8*	3
M-25	4	1.14	3.9	.	3.5	.	.	.	2.0	.	.	0.8*	.	2
21		1.27	5.6	.	4.6	.	.	.	2.5	.	.	0.6**	1.4**	3
26		1.17	.	.	.	.	.	.	.	.	.	.	.	
M-29	5	0.67	4.2	.	3.4	.	.	.	2.2	.	.	0.4	1.3**	3
8		0.77	2.5	.	1.8*	.	.	.	0.4**	.	.	0	1.6*	3

* Number of runs was one less than indicated in Table.
** Number of runs was two less than indicated in Table.
" Measurement not used in analyses of chlorophyll.
+ Number of measurements was 6.

(continued ....)

APPENDIX II

Table 2 (continued)

Plant	Harvest period	Chloro-phyll	Apparent photosynthesis at light intensity (ft-c) 5000	3000	2500	2000	1650	1500	1000	750	650	500	Dark resp.	No. runs
ALDER (Partial shade, 56% light)														
A-12	1	1.84	.	.	.	.	.	.	.	.	.	.		
18		1.87	.	.	.	.	19.0	.	.	.	.	13.3	3.4	2
24		2.60	.	20.9	.	.	.	.	.	.	.	8.2	4.5	2
A- 5	2	1.16	.	.	.	.	.	.	.	.	.	.	.	
15		2.19	13.4	.	14.0	.	.	.	10.0*	.	.	3.5	3.4*	3
22		2.11	19.7	.	19.8	.	.	.	12.2	.	.	5.8*	3.8*	3
A-16	3	2.62	25.1	24.6	24.5	22.6	.	20.1	15.9	10.7	.	6.2	3.8*	3
20		1.89	13.4	.	12.6	.	.	.	7.4	.	.	1.9	1.4*	3
27		3.16	16.1	.	14.3	.	.	.	9.4	.	.	2.9	2.3*	3
A-29	4	2.57	16.4	15.6	14.5	12.2*	.	11.0*	9.4	6.8*	.	5.4	1.5*	3
10		2.22	.	.	12.5	.	.	.	9.3	.	.	5.0	0.9*	3
21		1.97	18.6	.	15.4	.	.	.	10.1	.	.	3.3*	1.8*	3
A-19	5	2.80	18.4	.	16.7	.	.	.	11.8	.	.	4.4	1.4*	3
3		2.60	21.3	.	20.0*	.	.	.	12.9	.	.	4.7*	2.0**	3
9		2.46	19.5	.	16.9	.	.	.	11.7	.	.	3.6	2.1*	3
MAPLE (Partial shade, 56% light)														
M-12	1	3.98	.	6.2	6.1*	5.8	.	5.2	4.1	.	.	.	1.4	2
18		1.55	.	6.8	.	.	5.0	.	.	.	.	2.9	0.6	2
24		2.36	.	.	.	.	.	.	.	.	.	.	.	
M- 5	2	2.07	3.4	3.1	2.3	.	.	2.0	1.2	0.6*	.	0.4	0.4	2
15		1.70	4.5	.	4.4	.	.	.	2.0	.	.	0.7	0.8*	3
22		1.79	6.4	.	5.4	.	.	.	2.4*	.	.	1.5*	1.4*	3
M-16	3	1.52	5.1	4.4	3.9	3.5	.	2.9	2.4	1.6*	.	0.8	0.9*	3
11		1.42	3.2	.	2.7	.	.	.	1.5	.	.	0.3	0.8*	3
20		1.34	6.8	.	6.2	.	.	.	3.3	.	.	0.9	1.0*	3
M-25	4	1.27	1.8	.	2.1	.	.	.	1.6	.	.	0.8*	0.9*	3
1		1.67	3.8*	.	3.3	.	.	.	2.1	.	.	0.8*	0.8*	3
21		1.67	2.6*	.	2.2	.	.	.	1.5	.	.	0.1**	1.2*	3
M- 3	5	1.14	2.0	.	1.9*	.	.	.	1.5	.	.	0.4*	0.7*	3
13		1.01	1.9	.	1.9	.	.	.	1.3*	.	.	0.0*	0.2**	3

* Number of runs was one less than indicated in Table.

** Number of runs was two less than indicated in Table.

(continued ....)

APPENDIX II

Table 2 (continued)

Plant	Harvest period	Chloro-phyll	Apparent photosynthesis at light intensity (ft-c) 5000	3000	2500	2000	1650	1500	1000	750	650	500	Dark resp.	No. runs
ALDER (Full shade, 22% light)														
A-12	1	1.96	.	.	8.6	8.4	.	7.1*	7.2	6.0*	.	3.1	3.6	2
18		2.40	.	.	.	.	9.0	.	.	.	.	4.0	2.5	2
24		1.98	.	.	.	.	.	.	.	.	.	.	.	
A- 5	2	2.60	.	.	.	.	.	.	.	.	.	.	.	
15		1.96	16.1**	.	16.2	.	.	.	15.4	.	.	6.0*	4.4**	3
2		2.29	16.7**	.	17.1*	.	.	.	14.1	.	.	7.2*	3.6*	3
A-16	3	3.05	16.0	15.8*	16.0	15.6*	.	13.7	10.7	8.2	.	5.7	2.4*	3
20		3.04	9.8	.	9.9	.	.	.	7.8	.	.	3.2	1.0*	3
27		2.45	9.5	.	9.2	.	.	.	7.3	.	.	3.1	0.9*	3
A- 8	4	2.77	9.7	.	9.4	.	.	.	9.0	.	.	5.5	0.9*	3
28		2.52	9.0	.	8.4	.	.	.	7.4	.	.	5.1	1.1*	3
32		2.68	10.0	.	9.3	.	.	.	7.8	.	.	3.9	0.9*	3
A- 9	5	3.01	16.6	.	14.3	.	.	.	10.3	.	.	4.6	0.9*	3
14		3.28	13.0	.	11.8*	.	.	.	8.8	.	.	3.8*	1.4*	3
34		3.71	14.0	.	12.9	.	.	.	10.1	.	.	4.8	1.3+	3
MAPLE (Full shade, 22% light)														
M-12	1	2.14	.	8.3	.	6.6	.	5.8	5.3	3.6	.	2.2*	1.2	2
18		2.42	.	10.6	.	.	8.2	.	.	.	5.4	.	1.1	2
24		2.83	.	5.6	.	.	4.2	.	.	.	.	2.4	0.6	2
M- 5	2	2.31	.	9.0	9.0	.	.	6.7*	6.0	4.4*	.	2.0*	1.7"	3
15		2.71	5.1	.	4.7	.	.	.	3.4	.	.	2.2*	0.6*	3
22		2.39	4.9	.	5.0	.	.	.	3.6	.	.	1.7*	0.6*	3
M-16	3	2.47	3.2*	.	3.1	.	.	.	2.3	.	.	0.7	1.1	3
29		2.00	5.7	5.1	4.4	4.1	.	3.6	3.1	1.7*	.	0.9	0.8*	3
11		2.15	5.9	.	5.3	.	.	.	3.7	.	.	1.5	1.2*	3
M-28	4	2.20	5.9	.	5.5	.	.	.	4.8	.	.	3.5	0.9*	3
27		1.77	4.4**	.	4.7	.	.	.	4.7	.	.	2.4*	1.8**	3
M-26	5	1.07	3.5	.	3.3	.	.	.	2.6	.	.	1.1*	0.8*	3
31		1.07	4.1	.	3.7*	.	.	.	2.3	.	.	0.6*	1.4*	3

* Number of runs was one less than indicated in Table.
** Number of runs was two less than indicated in Table.
+ Number of runs was 4.
" Number of runs was 5.

APPENDIX II

Table 3. ANOVA'S for comparison of apparent photosynthesis rates for all treatment combinations

Light intensity	Source	Degrees of freedom	Mean square	F-ratio	Probability
ALDER SEEDLINGS (100 vs. 22 percent light)					
5000 ft-c	A) Treatment	1	232.320	22.47**	0.0005
	B) Harvest	3	108.855	10.53**	0.0010
	AB)	3	25.106	2.43 ns	0.1080
	Within, error	14	10.339		
	Total	21	37.093		
2500 ft-c	A) Treatment	1	72.846	6.96 ns	0.0186
	B) Harvest	3	112.339	10.73**	0.0009
	AB)	3	18.063	1.72 ns	0.2070
	Within, error	14	10.470		
	Total	21	29.078		
1000 ft-c	A) Treatment	1	2.675	1.31 ns	0.2713
	B) Harvest	3	77.674	38.01**	0.0000
	AB)	3	4.699	2.30 ns	0.1213
	Within, error	14	2.044		
	Total	21	13.257		
500 ft-c	A) Treatment	1	0.028	0.02 ns	0.8763
	B) Harvest	3	28.659	23.84**	0.0001
	AB)	3	7.815	6.50*	0.0058
	Within, error	14	1.202		
	Total	21	6.013		
MAPLE SEEDLINGS (100 vs. 22 percent light)					
5000 ft-c	A) Treatment	1	0.044	0.05 ns	0.8211
	B) Harvest	3	5.230	5.95 ns	0.0136
	AB)	3	2.849	3.24 ns	0.0685
	Within, error	10	0.879		
	Total	17	1.946		
2500 ft-c	A) Treatment	1	7.253	3.96 ns	0.0673
	B) Harvest	3	7.308	3.99 ns	0.0344
	AB)	3	0.270	0.15 ns	0.9288
	Within, error	12	1.830		
	Total	19	2.734		
1000 ft-c	A) Treatment	1	15.337	22.03**	0.0008
	B) Harvest	3	3.523	5.06 ns	0.0170
	AB)	3	0.367	0.53 ns	0.6752
	Within, error	12	0.696		
	Total	19	1.861		
500 ft-c	A) Treatment	1	6.627	51.08**	0.0001
	B) Harvest	3	1.807	13.93**	0.0005
	AB)	3	0.665	5.13 ns	0.0164
	Within, error	12	0.130		
	Total	19	0.821		

(continued ...)

APPENDIX II

Table 3 (continued)

Light intensity	Source	Degrees of freedom	Mean square	F-ratio	Probability
ALDER SEEDLINGS (100 vs. 56 percent light)					
5000 ft-c	A) Treatment	1	14.104	0.86 ns	0.6280
	B) Harvest	3	40.752	2.50 ns	0.1046
	AB)	3	67.796	4.16 ns	0.0282
	Within, error	13	16.294		
	Total	20	27.579		
2500 ft-c	A) Treatment	1	0.247	0.02 ns	0.8987
	B) Harvest	3	61.903	3.84 ns	0.0333
	AB)	3	48.887	3.04 ns	0.0637
	Within, error	14	16.098		
	Total	21	26.571		
1000 ft-c	A) Treatment	1	9.780	2.23 ns	0.1550
	B) Harvest	3	31.890	7.26*	0.0039
	AB)	3	28.480	6.48*	0.0059
	Within, error	14	4.393		
	Total	21	12.018		
500 ft-c	A) Treatment	1	1.974	1.07 ns	0.3187
	B) Harvest	3	19.281	10.49**	0.0010
	AB)	3	14.220	7.74*	0.0030
	Within, error	14	1.838		
	Total	21	6.105		
MAPLE SEEDLINGS (100 vs. 56 percent light)					
5000 ft-c	A) Treatment	1	4.800	3.58 ns	0.0799
	B) Harvest	3	9.094	6.79*	0.0065
	AB)	3	4.379	3.27 ns	0.0585
	Within, error	12	1.339		
	Total	19	3.226		
2500 ft-c	A) Treatment	1	0.664	0.44 ns	0.5267
	B) Harvest	3	4.749	3.12 ns	0.0625
	AB)	3	3.100	2.03 ns	0.1582
	Within, error	13	1.524		
	Total	20	2.201		
1000 ft-c	A) Treatment	1	0.000	0.00 ns	0.9865
	B) Harvest	3	0.703	1.60 ns	0.2377
	AB)	3	0.884	2.01 ns	0.1622
	Within, error	13	0.440		
	Total	20	0.524		
500 ft-c	A) Treatment	1	0.013	0.10 ns	0.7524
	B) Harvest	3	0.391	3.15 ns	0.0608
	AB)	3	0.050	0.40 ns	0.7556
	Within, error	13	0.124		
	Total	20	0.147		

(continued ....)

APPENDIX II

Table 3 (continued)

Light intensity	Source	Degrees of freedom	Mean square	F-ratio	Probability
ALDER SEEDLINGS (56 vs. 22 percent light)					
5000 ft-c	A) Treatment	1	122.760	11.72*	0.0047
	B) Harvest	3	13.051	1.25 ns	0.3333
	AB)	3	14.401	1.38 ns	0.2939
	Within, error	13	10.473		
	Total	20	17.063		
2500 ft-c	A) Treatment	1	81.641	7.99 ns	0.0130
	B) Harvest	3	25.866	2.53 ns	0.0985
	AB)	3	8.021	0.78 ns	0.5242
	Within, error	14	10.218		
	Total	21	15.541		
1000 ft-c	A) Treatment	1	2.225	0.58 ns	0.5361
	B) Harvest	3	16.640	4.36 ns	0.0227
	AB)	3	11.136	2.91 ns	0.0706
	Within, error	14	3.820		
	Total	21	6.621		
500 ft-c	A) Treatment	1	2.461	1.50 ns	0.2390
	B) Harvest	3	3.071	1.88 ns	0.1793
	AB)	3	0.963	0.59 ns	0.6358
	Within, error	14	1.637		
	Total	21	1.785		
MAPLE SEEDLINGS (56 vs. 22 percent light)					
5000 ft-c	A) Treatment	1	5.808	3.67 ns	0.0767
	B) Harvest	3	4.639	2.93 ns	0.0761
	AB)	3	1.795	1.13 ns	0.3749
	Within, error	12	1.581		
	Total	19	2.320		
2500 ft-c	A) Treatment	1	12.801	6.26 ns	0.0253
	B) Harvest	3	5.183	2.53 ns	0.1017
	AB)	3	1.623	0.79 ns	0.5213
	Within, error	13	2.046		
	Total	20	2.991		
1000 ft-c	A) Treatment	1	16.219	26.97**	0.0003
	B) Harvest	3	1.762	2.93 ns	0.0728
	AB)	3	1.620	2.69 ns	0.0886
	Within, error	13	0.601		
	Total	20	1.709		
500 ft-c	A) Treatment	1	6.395	33.75**	0.0002
	B) Harvest	3	1.551	8.19*	0.0029
	AB)	3	1.004	5.30 ns	0.0132
	Within, error	13	0.189		
	Total	20	0.826		