

AN ABSTRACT OF THE THESIS OF

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Title: THE EFFECT OF PRECONDITIONING LIGHT INTENSITY ON
PHOTOSYNTHESIS OF SEEDLINGS OF TWO ECOTYPES OF
DOUGLAS-FIR

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Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) seedlings of a high elevation Rocky Mountain source and a low elevation coastal source were pretreated under both high and low intensity artificial light in a growth chamber and outside in a cold frame. Net photosynthesis was then measured at three ages, 6, 10, and 18 weeks, by determining net carbon dioxide exchange with an infrared gas analyzer. The light intensity-photosynthesis relationships of the seedlings were determined at a number of light intensities, and the data were fitted by least squares to a photosynthesis-light response curve with the formula

$$P = \frac{B_1 E}{1+B_2 E} - B_3,$$

in which P is equal to the net photosynthesis, E is equal to the incident light energy, and B_1 , B_2 , and B_3 are empirical constants.

Seedlings from the coastal source were significantly more efficient photochemically regardless of age or light pretreatment as indicated by the steeper initial slope of the light response curve of photosynthesis. The coastal seedlings also had higher average light-saturated rates of photosynthesis, except at 6 weeks of age.

The seedlings' response to light preconditioning was similar for both sources but varied with the age and development of the seedlings. The cotyledons of the six-week-old seedlings had a lower maximum photochemical efficiency and were less susceptible to photoinhibition of the light reactions of photosynthesis by high preconditioning light than were the young juvenile needles of the ten-week-old seedlings. The older juvenile needles of the 18-week-old seedlings were less susceptible to photoinhibition of the dark reactions of photosynthesis than were the immature needles of the ten-week-old seedlings. For seedlings of both sources, at any given age, increased preconditioning light intensity resulted in decreased photosynthetic efficiency.

The Effect of Preconditioning Light Intensity on
Photosynthesis of Seedlings of Two
Ecotypes of Douglas-fir

by

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THE EFFECT OF PRECONDITIONING LIGHT INTENSITY
ON PHOTOSYNTHESIS OF SEEDLINGS OF TWO
ECOTYPES OF DOUGLAS-FIR

INTRODUCTION

In any environment, the most successful organisms are, by definition, those which have best adapted to that particular habitat morphologically and physiologically and can reproduce. If a species such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is widespread and is successful in a variety of habitats, then it has adapted to each of these habitats resulting in genetically differentiated races or ecotypes.

Ecotypic variation has been repeatedly demonstrated for Douglas-fir. For example, such differences have been shown in drought resistance (Ferrell and Woodard, 1966; Pharis and Ferrell, 1966) and in photosynthesis (Sorensen, 1964; Krueger and Ferrell, 1965; Zavitkovski and Ferrell, 1968, 1970; Pope, 1973).

In these studies, however, possible light preconditioning effects were not considered. Light preconditioning has a significant effect on photosynthesis of some conifers (Bourdeau and Laverick, 1958; Clark, 1961), and it is possible that this may also be true for Douglas-fir.

The purpose of this investigation was to determine how some of

the photosynthetic mechanisms of Douglas-fir respond to various light preconditioning and how these responses vary between low elevation coastal and high elevation interior Rocky Mountain sources of Douglas-fir.

LITERATURE REVIEW

The Effect of High Light Intensity on Photosynthesis

Visible light (400-700 nm) of high intensities has an inhibitory effect on the photosynthetic mechanisms. There are at least three forms of photoinhibition of photosynthesis due to visible light. One form of photoinhibition affects the biochemical or dark reactions of photosynthesis and causes a depression of the light-saturated rate of photosynthesis (Steeman-Nielson, 1952; Kok, 1956; Kozlowski, 1957; Ronco, 1970). The remaining two photoinhibitory mechanisms affect the photochemical reactions of photosynthesis and result in a reduction of the photosynthetic efficiency at low light intensities (Jones and Kok, 1966a, b). One of these two photoinhibitory reactions is oxygen dependent and acts on photosystem I, the other is oxygen independent and affects photosystem II (Satoh, 1970a, b, c).

The Effect of Light Preconditioning on Photosynthesis

Because high light intensity affects the photosynthetic apparatus, it is of interest to know if light preconditioning can alter these effects. The response of photosynthesis to light preconditioning varies greatly. In general, the response depends on the light regime under which a

plant species is normally found. Those species which are normally considered sun plants such as Alianthus (Bourdeau and Laverick, 1958) and yellow birch (Logan, 1970) have higher light saturated rates of photosynthesis when grown in full sunlight than when grown under shade. Full-sunlight-preconditioned yellow birch seedlings also were more efficient photosynthetically at low light intensities than were the shade-grown seedlings (Logan, 1970). In contrast, shade species such as sugar maple (Logan and Krotkov, 1969) and balsam fir (Clark, 1961) have lower photosynthetic rates at all light intensities.

Not all sun and shade plants respond to light preconditioning like the previous examples. Red and white pine (Bourdeau and Laverick, 1958) and white spruce (Clark, 1961), none of which are considered shade plants, respond to light preconditioning like the shade plants sugar maple and balsam fir. Photosynthesis of seedlings of eastern hemlock, which has been traditionally considered a shade species, performed the same whether grown in sun or shade (Bourdeau and Laverick, 1958).

Ecotypic Variation in Photosynthesis

If any species of plant is to be successful in a variety of habitats, it is necessary for it to adapt to the environmental conditions in each habitat often resulting in genetically differentiated races or ecotypes. Photosynthetic mechanisms, like other physiological

processes, are frequently modified to better suit the environmental conditions of the immediate habitat.

A large portion of the work dealing with ecotypic variation in photosynthesis has been done with ecotypes of herbaceous plants native to exposed and shaded habitats. Sun and shade ecotypes have been demonstrated for Solidago virgaurea L. (Björkman and Holmgren, 1963), Rumex acetosa L. and Geum rivale L. (Björkman and Holmgren, 1966), and Solanum dulcamara L. (Gauhl, 1969). With all the above species, except Geum rivale L., the ecotypic response of photosynthesis to preconditioning light was the same. The plants of the exposed habitat ecotypes had higher light-saturated rates of photosynthesis when preconditioned under high light than when preconditioned under low light. Light preconditioning had no significant effect on the efficiency of the exposed habitat ecotype plants at low light intensities. Plants of the shade ecotypes, on the other hand, were less efficient at low light intensities when preconditioned under high light. Light preconditioning had no significant effect on the light-saturated rates of photosynthesis of plants of the shade ecotypes. Geum differs from the other examples in that the light-saturated rate of photosynthesis is higher in both the sun and shade ecotype plants after high-light preconditioning.

Elevational differences also affect adaptation of the photosynthetic mechanisms. Milner and Hiesey (1963) demonstrated that the

light required for light-saturation of the photosynthetic apparatus of Mimulus cardinalis Dougl. plants was greater for plants of ecotypes adapted to higher altitudes.

Ecotypic differences in photosynthesis have also been found in some species of coniferous trees with large geographical distributions. Observations made during a study of eastern white pine from northern and southern sources indicated that seedlings from northern habitats tended to have higher light saturated rates of photosynthesis and higher light compensation points than seedlings from southern sources (Bourdeau, 1963). Krueger and Ferrell (1965) found similar responses in low elevation coastal and high elevation interior Rocky Mountain Douglas-fir seedlings. The coastal seedlings were more efficient at low light intensities and had lower rates at high light intensities than the interior seedlings. As part of the same study, seedlings of both ecotypes were exposed to continuous high light intensity for a period of 11 hours while photosynthesis was measured periodically. Photosynthesis of the coastal seedlings was reduced more rapidly by the high light exposure than that of the interior seedlings. This would indicate that the interior seedlings are more resistant to photoinhibition.

Zavitkovski and Ferrell (1968, 1970) found that under low moisture conditions the interior seedlings were capable of higher rates of photosynthesis than the coastal seedlings. Given adequate

moisture, the coastal seedlings had the highest photosynthetic rates. Variation in needle morphology and photosynthesis had also been demonstrated between seedlings of Rocky Mountain Douglas-fir from different origins (Pope, 1973).

METHODS AND MATERIALS

Seed Sources

Douglas-fir seed from two different sources was used for this experiment. The areas were selected to represent two extreme natural light regimes under which Douglas-fir may grow. Forks is a low elevation coastal area and Coconino is a high elevation interior area. The seed of both sources was obtained from commercial collections.

The Forks seed is from the west slope of the Olympic Peninsula, under 1,000 feet elevation, near Forks, Washington. The closest weather station to Forks with a complete record is Tatoosh Island. This station recorded an average of 87 cloudy days, 39 partly cloudy days, and only 27 clear days for the five-month period of May through September (U. S. Dept. of Commerce, 1965). The mean daily sky cover for the same period was 6.9 on a one to ten scale (see Fig. 1). Tatoosh Island is approximately 35 air miles from Forks and cloud cover between the two locations should not vary significantly with the exception of fog which is greater at Tatoosh Island. Tatoosh Island has an average yearly precipitation of 78 inches.

The Coconino seed was collected from the Coconino National Forest near Flagstaff, Arizona, at an elevation of 8,000 to 10,000 feet.

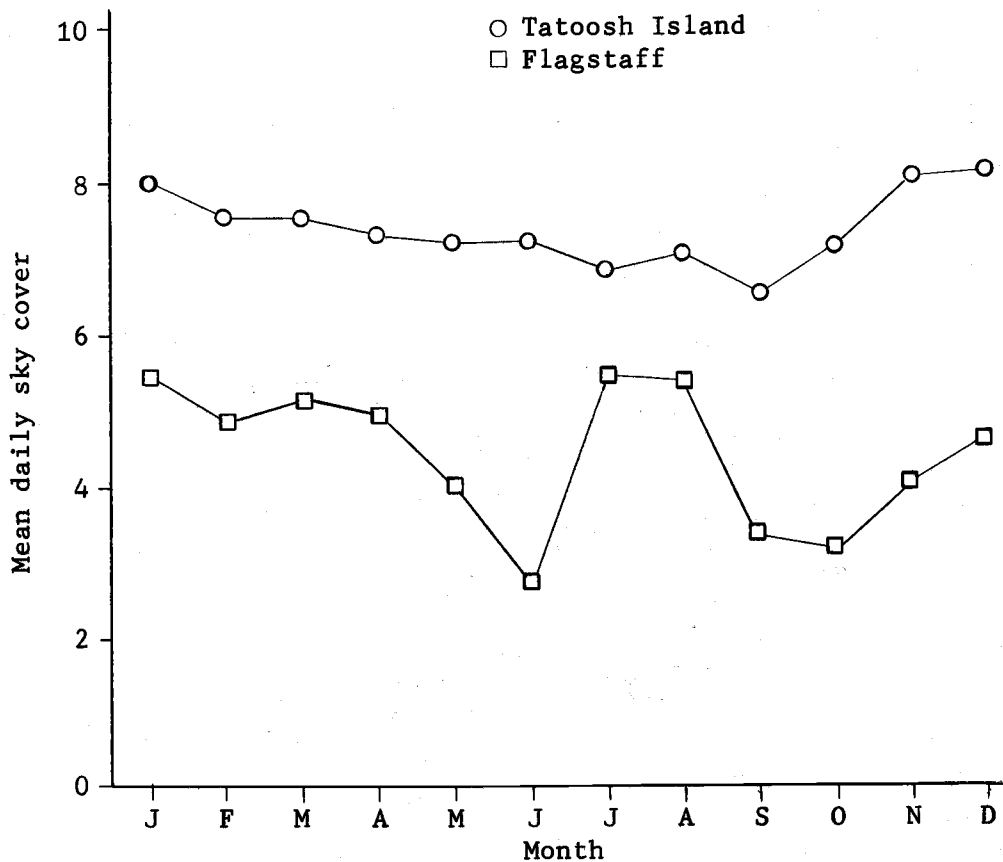


Figure 1. Monthly mean daily sky cover for Tatoosh Island, Washington and Flagstaff, Arizona on a one to ten scale (U. S. Dept. of Commerce, 1965 and U. S. Environmental Services Administration, 1966).

Flagstaff has an average of 17 cloudy days, 36 partly cloudy days and 100 clear days for the five-month period of May through September (U. S. Environmental Services Administration, 1966). The mean daily sky cover was 4.1 for the same period (see Fig. 1). The average yearly precipitation at Flagstaff is 18 inches.

Preparation of Plant Material

Seeds of both sources were stratified for two to three weeks and then germinated on moist filter paper in petri dishes. Three germinated seeds were planted in each one pint plastic pot containing forest soil that had been mixed for uniformity. The pots of seedlings were placed in a growth room and allowed to grow for two weeks. After two weeks the pots of seedlings were transferred to a growth chamber under a high or low intensity artificial light source or outside into a cold frame under natural light conditions. Six pots of seedlings of each ecotype were placed in each of the pretreatment light conditions for 4 weeks, 8 weeks, or 16 weeks. The seedlings were thinned to two seedlings per pot prior to measurement of photosynthesis.

Pretreatments

Growth Chamber Pretreatments

A Percival growth chamber equipped with a special light source was used for the high and low intensity artificial light pretreatments. A 16-hour photoperiod and thermoperiod with a 25°C day temperature and a 20°C night temperature were used. The light source was a

combination of five 400-watt G. E. Lucalux lamps, three 400-watt G. E. Multivapor lamps, and two 500-watt color corrected mercury vapor lamps with a filter of 10 cm of water to remove long wave radiation. This light system provided 0.28 ly/min (61.4% full sunlight) between 400 to 700 nm at the plant crown level and a daily total light energy of 271.2 ly (400-700 nm). This is 158% of the average daily energy received from sunlight in the summer, July through September, in the 400 to 700 nm band.¹ The spectrum of this light system is shown in Figure 2.

Low light intensity conditions in the growth chamber were obtained with the use of several layers of cheese cloth for a filter. Light energy under the filter was 0.029 ly/min (400-700 nm) and the daily total energy received at the plant crown level was 28.2 ly, 10.4% of the high light intensity level.

Natural Light Pretreatment

The seedlings pretreated outside under natural light conditions were placed in cold frames and were covered with a one-half inch mesh wire screen which allowed an average of 78% transmission of sunlight. The average daily energy received by the seedlings through July,

¹ All light energy values except daily total sunlight were determined with an ISCO spectrophotometer (model SR) calibrated with a National Bureau of Standards standard lamp. Total daily sunlight energy information was supplied by Mr. Earl Bates, Advisory Agricultural Meteorologist, National Weather Service. Total daily sunlight energy in the 400 to 700 nm band was calculated from the total radiation by a method suggested by Szeicz (1965).

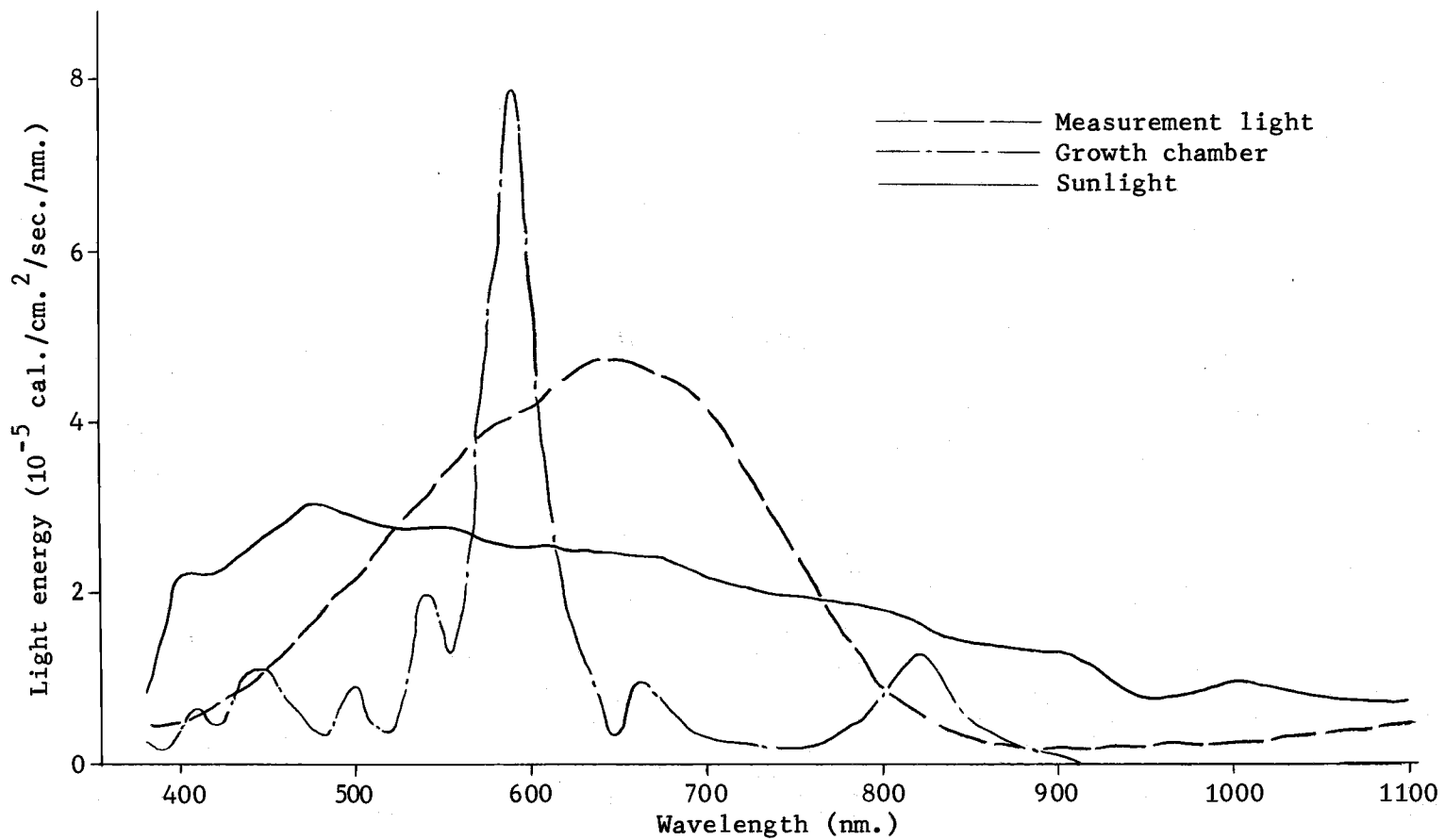


Figure 2. Spectral energy distribution of sunlight, the growth chamber light source, and the light source used for measurement of photosynthesis.

August, and September was 135.6 ly (400-700 nm). Photoperiod and day and night temperatures were uncontrolled and unrecorded. Seedlings in this and other pretreatments were watered daily.

Measurement of Photosynthesis

Net photosynthetic rates were determined by measuring the rate of carbon dioxide uptake by the seedlings in a closed gas tight system described by Cleary (1971). The total volume of the system was 3.06 liters. Measurement of changes in the carbon dioxide concentration was made with a Beckman 15A infrared gas analyzer calibrated with dry carbon dioxide of known concentrations. Rates of carbon dioxide uptake were determined by measuring the time required for the carbon dioxide concentration to drop 20 ppm at carbon dioxide concentrations within the range of 330 and 370 ppm. Following measurement the seedlings were removed from the cuvette and the tops were dried at 70°C for 24 hours. After drying, the needles were removed from the stem and weighed to determine the dry foliage weight of the seedlings. Net photosynthetic rates were calculated and expressed in terms of milligrams carbon dioxide assimilated per gram dry foliage weight per hour.

Temperature in the cuvette during measurement was maintained at $25 \pm 1^\circ\text{C}$ and relative humidity at approximately 50%. Air flow through the cuvette was 40 liters per minute, sufficient to break the boundary layer of the foliage (Unterschuetz, 1970).

Light for the photosynthesis measurements was supplied by a bank of four 500-watt G. E. Quartzline narrow spot lamps and was filtered through 8 cm of water and an infrared cut-off filter. The spectrum of this light system is shown in Figure 2. The total light energy available with this system was 0.87 ly/min of which 61.37% was in the 400 to 700 nm band. The light energy available with this system in the 400 to 700 nm band approximately is 116% the energy available from sunlight in the same wavelength band. Through the use of filters and by varying the number of lights used it was possible to obtain a variety of light levels from 0.013 to 0.87 ly/min. Photosynthesis measurements were made at light energy levels of 0.013, 0.032, 0.069, 0.14, 0.24, 0.47, and 0.87 ly/min. Measurements were taken at the lowest light intensity first with each next measurement at the next higher light intensity. The seedlings were allowed to acclimate in the cuvette for 20 minutes prior to the first measurement and for 10 minutes after each change in light intensity.

Analysis of Data

In order to determine accurately the light compensation point and the initial slope of the light curve of photosynthesis, it was necessary to describe the light curve in mathematical terms to allow these values to be calculated. Through the use of a computer and a curve fitting program the light response photosynthesis data for each

pot of seedlings were fitted to the formula

$$P = \frac{B_1 E}{1 + B_2 E} - B_3$$

in which P is equal to the net photosynthesis, E is equal to the incident light energy, and B_1 , B_2 , and B_3 are constants estimated by the computer program and are different for each pot of seedlings. The above equation is a modified form of the formula

$$P = \frac{B_1 E}{1 + B_2 E}$$

for absolute photosynthesis (Chartier, 1966). The term B_3 was added to allow the curve to "float" instead of forcing it through the coordinate origin as in absolute photosynthesis. The formula used provided a close fitting curve for the light dependent phase of the light curve for accurate calculation of the light compensation point and the slope of the light curve.

The light compensation point was determined by calculating the value of E at the point on the light curve where P is equal to zero. The initial slope of the light curve was determined by calculating the slope of a line tangent to the light curve at the light compensation point. The slope was calculated by taking the first derivative of the light curve equation

$$\frac{dy}{dx} = \frac{B_1}{(1 + B_2 E)^2}$$

where E is equal to the incident light energy required for light compensation.

The light curve formula used did not give a good fit for the light saturated phase of the light curve of photosynthesis. Therefore, actual measurements of the light saturated rate of photosynthesis were used in the analysis.

A three factor analysis of variance was used to test for significant pretreatment effects on the light compensation point, the slope of the light curve, and the light saturated rate of photosynthesis. The three main factors were seed source, light pretreatment, and age. The experimental design was $2 \times 3 \times 3$. There were two seed sources, three light pretreatments, and three ages. There were six replications in each pretreatment combination. An experimental unit was a pot of two seedlings which were measured together.

RESULTS

Light Compensation Point

The light pretreatment had a statistically significant effect on the light compensation point of the seedlings (Table I). The average light compensation point for the low-light pretreated seedlings was about one-third the average light required for light compensation in the high-light pretreated seedlings (Table II). The average light required for compensation of the cold frame pretreated seedlings was slightly higher than that for the high-light pretreated seedlings.

The effect of age on the light compensation point was different for seedlings of the two ecotypes, as was shown by the significant age x ecotype interaction term in the analysis of variance (Table I). The average light compensation point for the Forks seedlings was high at six weeks of age, dropped to a low at 10 weeks, and rose to an intermediate level at 18 weeks of age (Table III). The change with age of the light required for compensation by the Coconino seedlings was opposite to that of the Forks seedlings (Fig. 3). The average light compensation point for the Coconino seedlings started low at six weeks of age, rose at 10 weeks to 0.0086 ly/min, and dropped to an intermediate level at 18 weeks of age. The changes of the light compensation point with age were independent of the light pretreatment.

Table I. Analysis of variance table for the light compensation point.
 (*) 5% significance level. (**) 1% significance level.

Source	Degrees of Freedom	Sums of Squares	Mean Squares	F Ratio	Sign
Ecotype	1	0.000025	0.000025	0.703	
Age	2	0.000008	0.000004	0.112	
Light	2	0.000628	0.000315	8.858	**
E x A	2	0.000338	0.000169	4.753	*
E x L	2	0.000052	0.000026	0.731	
A x L	4	0.000080	0.000020	0.562	
E x A x L	4	0.000064	0.000016	0.450	
Error	87	0.003094	0.000036		

Table II. Light compensation point means (ly/min) for seedlings of three ages pretreated under three light regimes.

Light Pretreatment	Age			Light Pretreatment Means
	6 weeks	10 weeks	18 weeks	
Low light	0.00280	0.00083	0.00338	0.00234
Cold frame	0.00815	0.00796	0.00709	0.00773
High light	0.00731	0.00828	0.00579	0.00713
Age means	0.00609	0.00569	0.00542	

Table III. Light compensation point means (ly/min) for the seedlings of two ecotypes at three different ages. Least Significant Difference (L. S. D.) at the 5% significance level was 0.00281 ly/min.

Ecotype	Age			Ecotype Means
	6 weeks	10 weeks	18 weeks	
Forks	0.00734	0.00278	0.00565	0.00525
Coconino	0.00484	0.00860	0.00520	0.00621

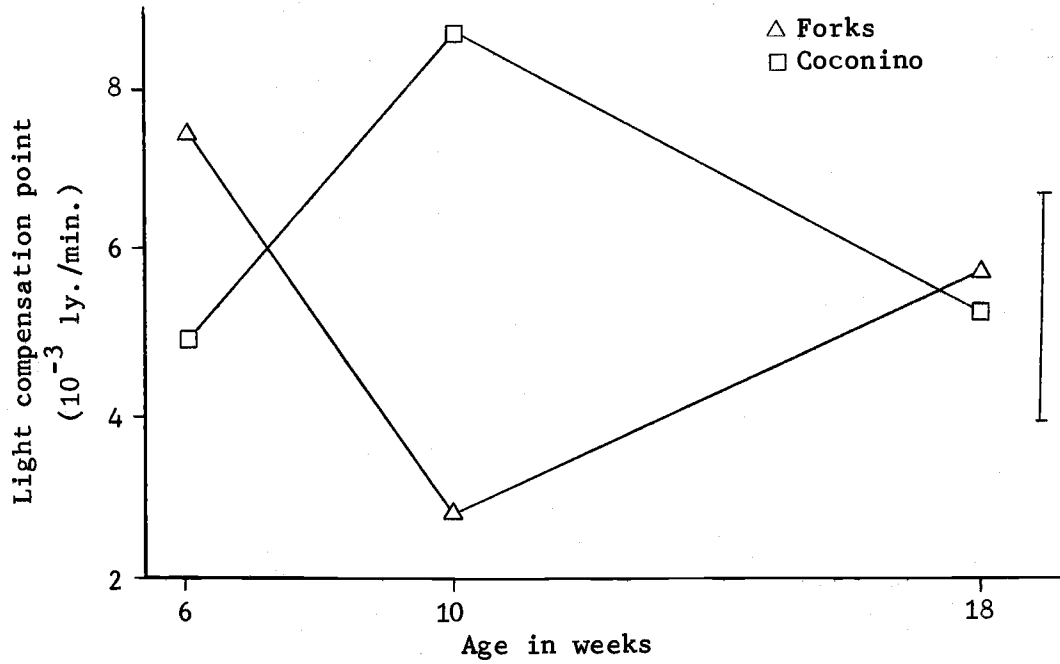


Figure 3. Change in light compensation point with age of seedlings of the Forks and Coconino ecotypes. Bar indicates 5% L.S.D.

Initial Slope of the Light Curve

Seedlings of the two ecotypes had significantly different average initial slopes of the light curve (Table IV). The Forks seedlings had steeper average slopes than the Coconino seedlings at all ages and with all light pretreatments. The average slope for the Forks seedlings was 425.34 mg CO₂/g dry wt/hr/ly/min. The average slope for the Coconino seedlings was 342.99 mg CO₂/g dry wt/hr/ly/min.

The light pretreatment also had a significant effect on the slope of the photosynthetic rate curve of the seedlings. The slope was inversely related to the average daily incident light received during pretreatment (Table V). The low-light pretreated seedlings had the steepest slopes and the high-light pretreated seedlings had the lowest slope values. The relative response of the slope to the light pretreatment was independent of ecotype and age.

Age had a statistically significant effect on the slope as well. In general, the younger seedlings had the steeper slopes (Table V). This relationship of slope to age did not hold true for all light pretreatments. There was a statistically significant age x light interaction term in the analysis of variance indicating that the response of the seedlings to age was different for the different light pretreatments. The high-light and cold frame pretreated seedlings behaved as described above. However, the low-light pretreated seedlings responded quite differently to age (Fig. 4). While there was no

Table IV. Analysis of variance table for the initial slope of the light curve.

(*) 5% significance level. (**) 1% significance level.

Source	Degrees of Freedom	Sums of Squares	Mean Squares	F Ratio	Sign
Ecotype	1	183131.58	183131.58	5.593	*
Age	2	503832.41	251911.20	7.693	**
Light	2	3538026.64	1769013.32	54.889	**
E x A	2	59490.96	29245.48	0.893	
E x L	2	1687.96	843.98	0.026	
A x L	4	431654.29	107913.57	3.296	*
E x A x L	4	26771.41	6692.85	0.204	
Error	87	2848689.95	32743.56		

Table V. Slope means (mg CO₂/g dry wt/hr/ly/min) for seedlings of three ages pretreated under three light regimes.

Light Pretreatment	Age			Light Pretreatment Means
	6 weeks	10 weeks	18 weeks	
Low light	590.75	741.20	550.37	627.44
Cold frame	444.77	289.56	260.11	331.48
High light	343.62	164.82	72.32	193.59
Age means	459.71	398.53	294.27	

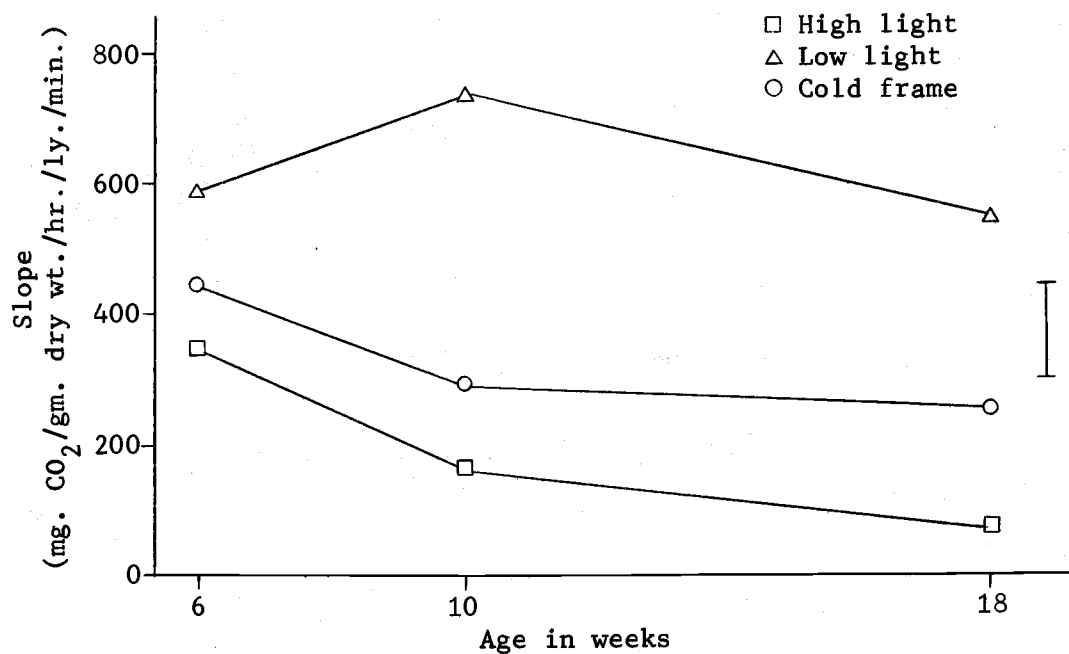


Figure 4. Change in slope of the light curve of photosynthesis with seedling age of high-light, low-light, and cold frame pretreated seedlings. Bar indicates 5% L.S.D. of 146.786 mg. CO₂/gm. dry wt./hr./ly./min.

significant difference between the average slopes of the 6-week-old and the 18-week-old low-light pretreated seedlings (Table V), the average slope of the 10-week-old low-light pretreated seedlings was considerably steeper than either the 6-week-old or the 18-week-old low-light pretreated seedlings. This relationship of slope to age in the low-light pretreated seedlings is the same for both ecotypes.

Light-Saturated Rate of Photosynthesis

Ecotype, age, and light pretreatment all had a statistically significant effect on the light-saturated rate of photosynthesis of the seedlings (Table VI). The rates for the Forks seedlings averaged higher than the rates for the Coconino seedlings (Table VII). The light-saturated rate decreased as age increased with the biggest drop in rate occurring in the period between 6 and 10 weeks of age (Table VIII). There was no significant difference between the average light-saturated rates of the low-light and cold frame pretreated seedlings and the high-light pretreated seedlings had a much lower average rate (Table VIII).

Three of the four possible interactions of factors had a statistically significant effect on the light-saturated rate of photosynthesis (Table VI). The significant age x ecotype interaction term indicates that each ecotype had a different change in rate with increasing age (Fig. 5). Although the average rates of both ecotypes decreased as

Table VI. Analysis of variance table for the light-saturated rate of photosynthesis.

(*) 5% significance level. (**) 1% significance level.

Source	Degrees of Freedom	Sums of Squares	Mean Squares	F Ratio	Sign
Ecotype	1	89.398	89.398	7.193	**
Age	2	2507.042	1253.521	100.860	**
Light	2	953.196	476.598	38.348	**
E x A	2	149.783	74.891	6.026	**
E x L	2	32.754	16.377	1.318	
A x L	4	176.280	44.070	3.546	*
E x A x L	4	148.882	37.221	2.995	*
Error	87	1081.269	12.428		

Table VII. Mean light-saturated rates of photosynthesis (mg CO₂/g dry wt/hr) for seedlings of two ecotypes at three ages pretreated under three light regimes.

Light Pretreatment	Age			Light-Ecotype Means
	6 weeks	10 weeks	18 weeks	
<u>Forks Ecotype</u>				
Low light	24.27	15.76	14.08	18.03
Cold frame	22.35	13.70	18.29	18.11
High light	17.92	12.13	8.76	12.93
Ecotype x age means	21.51	13.86	13.71	
Ecotype mean		16.36		
<u>Coconino Ecotype</u>				
Low light	26.44	15.13	8.91	16.82
Cold frame	26.44	12.21	13.04	17.23
High light	16.16	4.50	8.05	9.57
Ecotype x age means	23.01	10.61	10.00	
Ecotype mean		14.54		

Table VIII. Mean light-saturated rates of photosynthesis (mg CO₂/g dry wt/hr) for seedlings of three ages pretreated under three light regimes.

Light Pretreatment	Age			Light Pretreatment Means
	6 weeks	10 weeks	18 weeks	
Low light	25.35	15.44	11.49	17.43
Cold frame	24.40	12.96	15.66	17.67
High light	17.04	8.31	8.40	11.25
Age means	22.26	12.24	11.85	

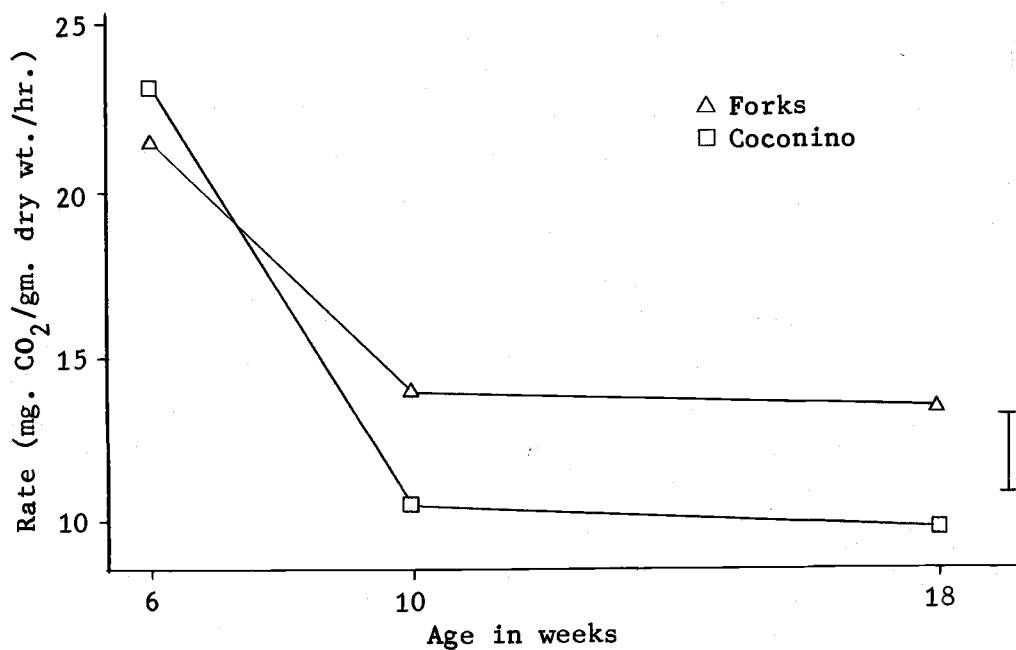


Figure 5. Change in the light-saturated rate of photosynthesis of Forks and Coconino seedlings with age. Bar indicates 5% L.S.D. of 2.33 mg. CO₂/gm. dry wt./hr.

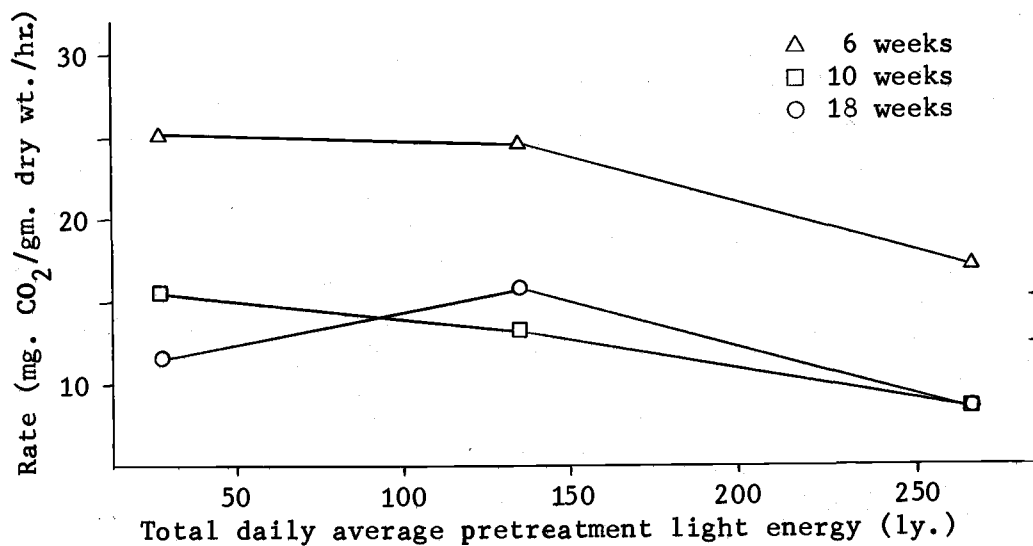


Figure 6. Response of the light-saturated rate of photosynthesis of 6-week, 10-week, and 18-week-old seedlings to pretreatment light conditions. Bar indicates 5% L.S.D. of 2.86 mg. CO₂/gm. dry wt./hr.

they grew older, the decrease was greater for the Coconino seedlings. This change with age occurred primarily in the period between 6 and 10 weeks of age (Table VII). The change in rate for the Forks seedlings from 6 weeks to 10 weeks of age was a drop of 35.6%. The reduction in rate for the Coconino seedlings was 53.9%. The reduction in rate from 10 weeks to 18 weeks of age was 1.1% for the Forks seedlings and 5.7% for the Coconino seedlings.

The statistically significant age x light pretreatment interaction in the analysis of variance (Table VI) indicated that the response of the light saturated rate to the light pretreatment changed as the seedlings grew older (Fig. 6). At six weeks of age, the average rates for the low-light and cold frame pretreated seedlings were not significantly different, but the average rate of the high-light pretreated seedlings was much lower (Table VIII). At 10 weeks of age, there was a greater difference between the low-light and cold frame pretreated seedlings and not as large a difference between the cold frame and high light pretreated seedlings as there was at six weeks of age. The 18-week-old cold frame seedlings had a significantly higher average rate than either the high-light or low-light pretreated seedlings of the same age. The high-light pretreated seedlings had the lowest rates.

The light-saturated rates of the seedlings of the two ecotypes responded differently to age and the light pretreatments. This is indicated by the significant ecotype x age x light pretreatment

interaction term in the analysis of variance (Table VI). The pattern of response of seedlings of both ecotypes was similar to that described in the previous paragraph. The primary difference was that at 6 and 10 weeks of age the Coconino seedlings were more inhibited by the high-light pretreatment than were the Forks seedlings of the same ages (Table VII). At 18 weeks of age, the pattern reversed and it was the Forks seedlings that were more inhibited by the high-light pretreatment (Fig. 7).

Light Required for Light Saturation

An analysis of variance was also made to determine if there was any significant pretreatment effect on the light required for saturation. Saturating light was the light energy level at which the highest measured rate of photosynthesis was obtained.

Age of the seedlings had a statistically significant effect on the light required for saturation (Table IX). The 18-week-old seedlings had the highest light required for saturation and the 10-week-old seedlings had the lowest (Table X). The light required for saturation by the 6-week-old seedlings was slightly higher than that for the 10-week-old seedlings.

The significant age x light pretreatment interaction in the analysis of variance (Table IX) indicated that light required for saturation by the seedlings is affected by an interaction of age and light

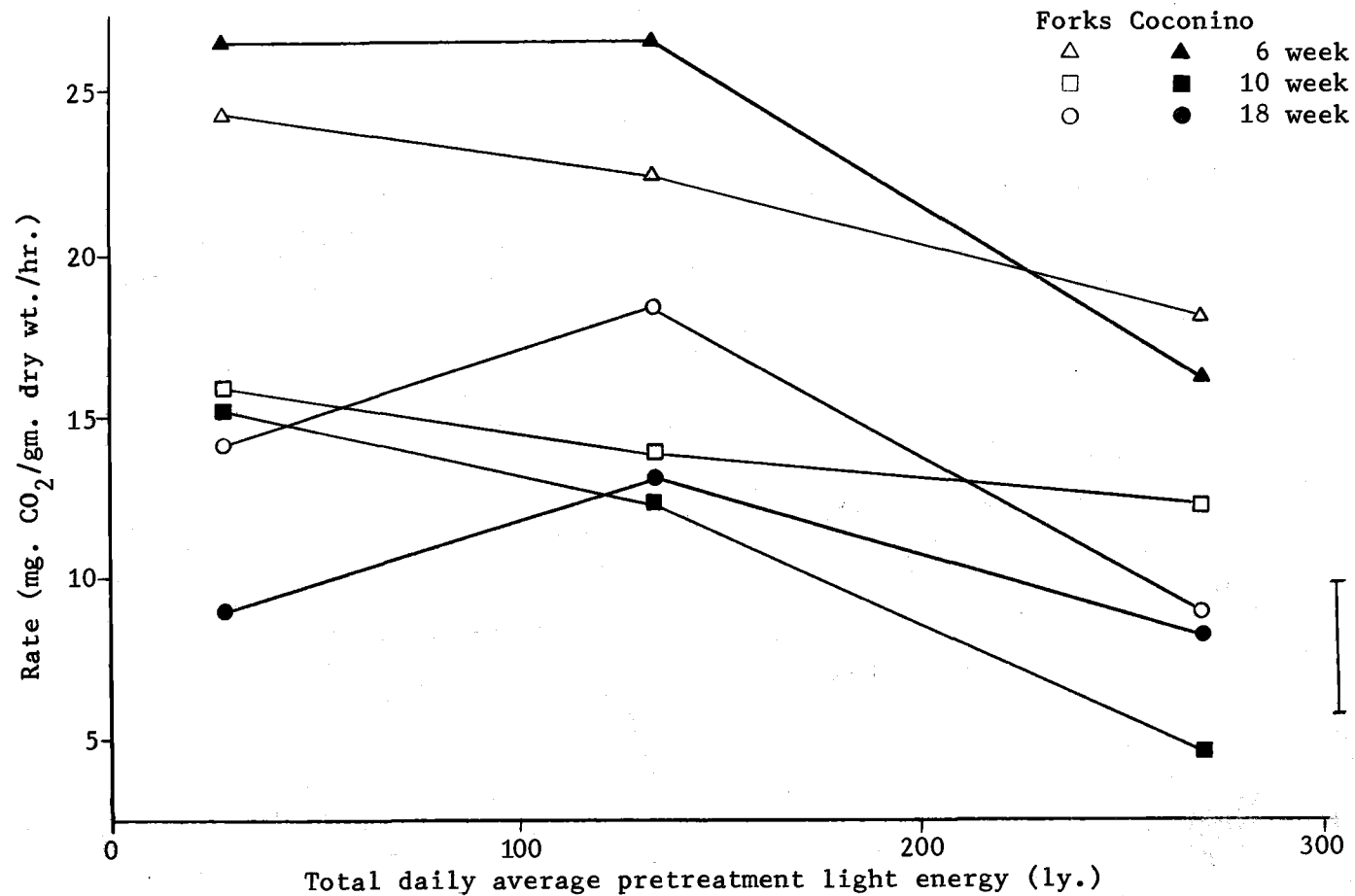


Figure 7. Response of the light-saturated rate of photosynthesis of 6-week, 10-week, and 18-week-old Forks and Coconino seedlings to pretreatment light conditions. Bar indicates 5% L.S.D. of 4.04 mg. CO₂/gm. dry wt./hr.

Table IX. Analysis of variance table for the light required for light saturation.

(*) 5% significance level. (**) 1% significance level.

Source	Degrees of Freedom	Sums of Squares	Mean Squares	F Ratio	Sign
Ecotype	1	0.0131	0.0131	0.290	
Age	2	2.4109	1.2054	26.727	**
Light	2	0.1967	0.0984	2.182	
E x A	2	0.0311	0.0155	0.344	
E x L	2	0.1439	0.0719	1.594	
A x L	4	0.5167	0.1292	2.865	*
E x A x L	4	0.1826	0.0457	1.013	
Error	87	3.9264	0.0451		

Table X. Mean saturating light intensity (ly/min) for seedlings of three ages pretreated under three light regimes.

Five percent L. S. D. is 0.1723 ly/min.

Light Pretreatment	Age			Light Pretreatment Means
	6 weeks	10 weeks	18 weeks	
Low light	0.3875	0.2642	0.5325	0.3614
Cold frame	0.4217	0.3417	0.5900	0.4511
High light	0.3692	0.2808	0.8367	0.4956
Age means	0.3928	0.2956	0.6497	

pretreatment (Fig. 8). At 6 and 10 weeks of age the cold frame grown seedlings required the most light for saturation. At 18 weeks of age it was the high light pretreated seedlings that required the greatest light energy for saturation (Table X).

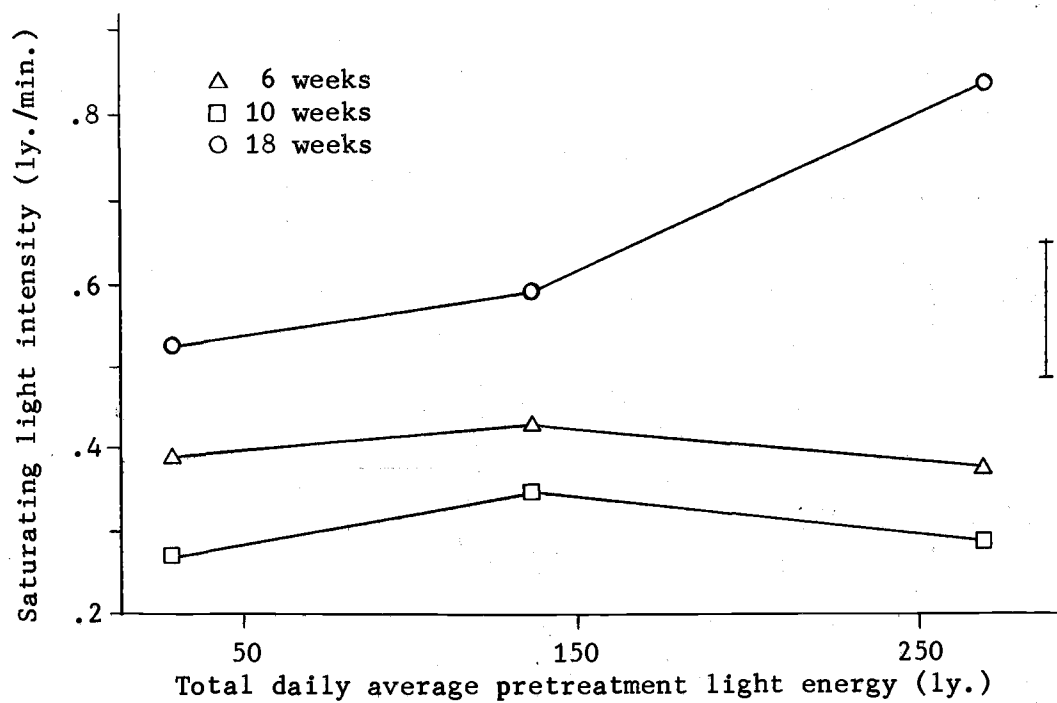


Figure 8. Response of the light required for saturation by 6-week, 10-week, and 18-week-old seedlings to pretreatment light conditions. Bar indicates 5% L.S.D. of 0.1723 ly./min.

DISCUSSION

The Initial Slope of the Light Curve

The photochemical efficiency of the seedlings, as indicated by the initial slope of the light curve, was inversely related to the average total daily light energy received during preconditioning (Table V). This effect was probably a result of the photoinhibition of the photochemical reactions by the preconditioning light treatments. Photoinhibition is directly proportional to the product of light intensity and time of exposure (Kok, 1956).

Self-shading was apparently variable in affecting the photochemical efficiency of the seedlings. Cold frame seedlings had the lowest average foliage weight and, therefore, were least likely to be affected by self-shading. Yet they had a significantly lower photochemical efficiency than the low-light preconditioned seedlings which had apparently higher average foliage weight. It is possible that self-shading may have adversely affected the high-light pretreated seedlings because they had the highest average foliage weight and the densest needle arrangement and a low photochemical efficiency.

The differences between the average photochemical efficiency of the 10- and 18-week-old seedlings were probably due to self-shading. The decrease in photochemical efficiency between 10 and 18 weeks of age was proportional to the increase in the dry foliage weight of the

seedlings in each of the pretreatments. The low light and high light preconditioned seedlings which had foliage weight increases of 188% and 320% respectively from 10 to 18 weeks of age also had decreases in the average slope values of 25% and 58% respectively, as well. The cold frame pretreated seedlings, which had the lowest increases in foliage weight (40%) from 10 to 18 weeks of age, had the smallest reduction of slope values, and so the smallest reduction in efficiency.

It is likely that the different responses of the photochemical reactions of seedlings of 6 and 10 weeks of age to light pretreatments were the result of physiological changes in the seedlings as they grew and the foliage matured. At six weeks of age, the cotyledons make up the majority of the photosynthetic tissue of the seedlings. The initial slopes of the light curves, which are an indication of photosynthetic efficiency, of those seedlings were significantly lower than those of the 10-week-old low light seedlings in which the juvenile needles make up the majority of the photosynthetic tissue. The cotyledons also seem to be less susceptible to photoinhibition by higher light intensities. Six-week-old seedlings preconditioned in the cold frame and under high light had significantly higher efficiency in the light-limiting portion of the photosynthesis-light relationship than the 10-week-old seedlings from the same pretreatments. It is possible that in Douglas-fir seedlings the factor which allows the juvenile needles to have a higher potential photochemical capacity is closely related to

the susceptibility of the photochemical reactions to inhibition by visible light. This corresponds to the conclusion by Jones and Kok (1966a) that photoinhibition of the photochemical capacity of photosynthesis by visible light is a secondary photoreaction of the photochemical mechanisms.

The significantly higher photochemical efficiency of the Forks seedlings over that of the Coconino seedlings is probably a result of the genetic adaptation to the different light environments of the seed sources. Since coastal Washington has considerably more cloud cover and probably more light competition from other vegetation than northern Arizona, it is likely that the seedlings of the Forks ecotype would be better adapted for more efficient utilization of low light.

The photochemical efficiency of seedlings of the two seed sources responded in the same way to changes in age and to pretreatment. The Forks seedlings were more efficient at low light intensities, and they maintained this advantage under all conditions of age and preconditioning.

The Light Compensation Point

The photochemical efficiency of the photosynthetic apparatus was affected by the light preconditioning and this should be reflected in part in differences in light compensation points. There were significant differences in photochemical efficiency between high-light and cold

frame preconditioned seedlings, but there were no corresponding differences between the light compensation points. This may have been the result of different respiration rates for seedlings of the two pretreatments. This is difficult to substantiate because respiration was not measured directly.

The effect of age on the average light compensation point for the seedlings of the two ecotypes was possibly due to different changes in respiration rates with age. In both ecotypes the change in the average light compensation point with age is parallel to that of respiration calculated from the light curve of photosynthesis (Fig. 9). Although changes in the respiration rate with age between the two ecotypes were not significant, the additional effect of differences in the photochemical efficiency between the two ecotypes modified the light compensation point so that there was a significant age x ecotype interaction on the light compensation point of the seedlings.

Light-Saturated Rate of Photosynthesis

The higher average light-saturated rate of photosynthesis of the 6-week-old seedlings compared to that of the 10-week-old seedlings of both ecotypes was also probably due to physiological differences between the cotyledons and the juvenile needles. The cotyledons of the Coconino seedlings also appear to respond differently to light preconditioning from those of the Forks seedlings. There were no

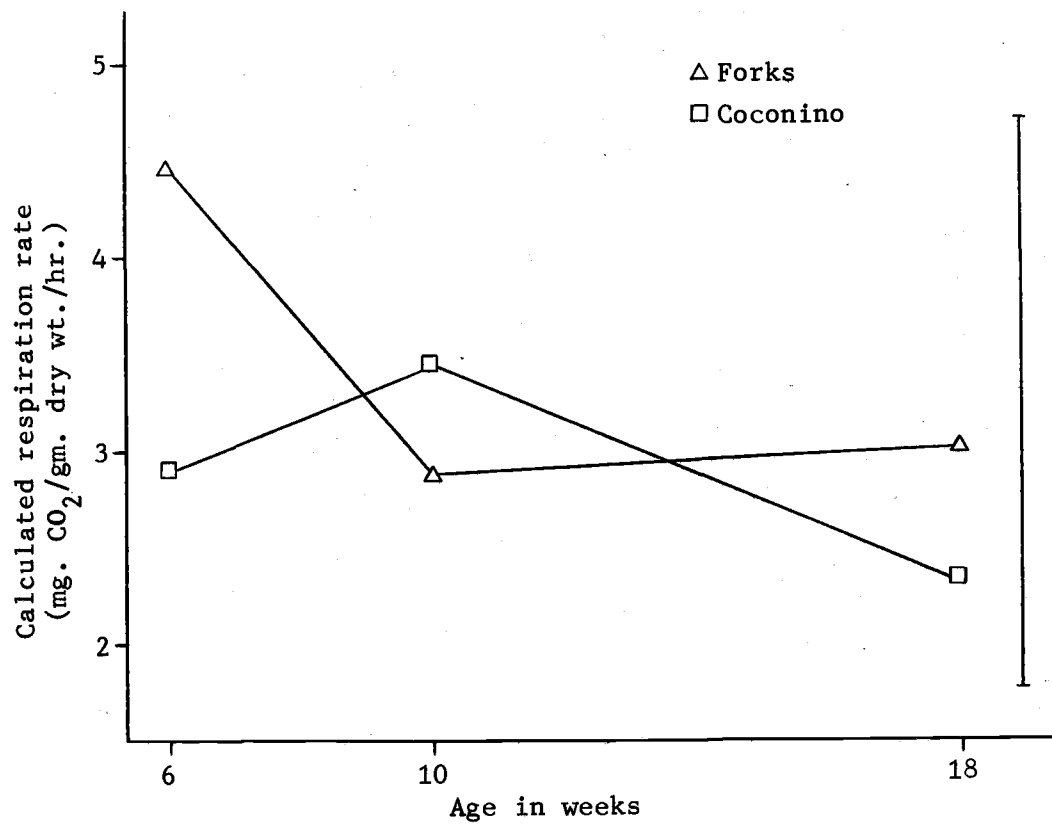


Figure 9. Change in average calculated respiration rate of seedlings of the two seed sources with age. The respiration rate is calculated from the light response curve of photosynthesis. Bar indicates the 5% L.S.D. of 2.93 mg. CO₂/gm. dry wt./hr.

differences in rate between the low-light and cold frame pretreated six-week-old Coconino seedlings. In contrast, high-light preconditioned Coconino seedlings of the same age had a much lower average light-saturated rate. Unlike the Coconino seedlings, the light-saturated rate of the six-week-old Forks seedlings had a gradual linear decrease in response to increasing preconditioning light energy (Fig. 7). It is possible that the photosynthetic mechanism of the cotyledons of the Coconino seedlings have a light threshold below which there is no apparent photoinhibition. Once this threshold is exceeded, photoinhibition is much more severe for the Coconino seedlings than for the Forks seedlings.

If the response of the seedlings to light preconditioning was not caused by some uncontrolled environmental factor in the cold frame pretreatment, then it may be a genetic adaptation of the Coconino seedlings to natural light conditions. Under natural environmental conditions the period in which the seedlings of the Coconino ecotypes would germinate and grow is the summer rainy season.² Cloud cover for this period generally consists of a number of partly cloudy days (13 per month) (U. S. Environmental Services Administration, 1966). This would result in the seedlings receiving periods of bright light interspersed with clouds. A protective or recovery system which

²Personal communication from Dr. Richard Berry, Northern Arizona State University, Flagstaff, Arizona.

might result in a light threshold of a type suggested by the data would protect the seedlings from photoinhibition during short periods of high light conditions or longer periods of more moderate light intensity.

The different response to light preconditioning of the 10-week-old from that of the 6-week-old seedlings was probably due to the increasing influence of the juvenile needles. The proposed threshold effect noted above for the cotyledons was not readily apparent at 10 weeks of age. It was probably masked by the increasing influence of the juvenile needles which do not seem to exhibit the same response to the light pretreatments as the cotyledons. However, as with the 6-week-old seedlings, the inhibition of the biochemical reactions of the 10-week-old Coconino seedlings by the high light pretreatment was much more severe than for the Forks seedlings of the same age.

At 18 weeks of age, the response of the light-saturated rate of photosynthesis of the seedlings of both ecotypes to light preconditioning was radically different from that of the younger seedlings. The 18-week-old cold frame preconditioned seedlings had a higher rate than either the low light or high light preconditioned seedlings of the same age (see Fig. 7). This change in behavior could have been the result of the combination of several factors. Since the high and low-light preconditioned 18-week-old seedlings had the highest average increase in folage weight, it is possible that self-shading was a factor in influencing the rates of seedlings from these pretreatments. Some

other factor is involved with the cold frame seedlings since the rate for the 18-week-old seedlings is higher than that of the 10-week-old seedlings.

The higher light-saturated rate of photosynthesis of the cold frame pretreated seedlings at 18 weeks of age compared to that of the low-light pretreated seedlings of the same age noted here is similar to the light preconditioning effects reported by Björkman and Holmgren (1963) for fully expanded leaves of sun-adapted ecotypes of Solidago virgaurea L. This effect seems to be restricted to the fully expanded juvenile needles of Douglas-fir seedlings since it is not apparent in the younger seedlings. The rates of the 18-week-old high-light pretreated seedlings may have been lower than the cold frame seedlings of the same age because of self-shading or increased photo-inhibition by the harsher light regime during preconditioning. Self-shading is likely since the high-light preconditioned seedlings had a dense needle arrangement and a high average foliage weight. If the effect of self-shading could be eliminated, it is possible that the differences of the light saturated rate between the 18-week-old high-light and cold frame preconditioned seedlings could be reduced or eliminated.

Light Required for Light Saturation

The significant age x light effect noted for the light required for

saturation of photosynthesis was probably due to the different response of the 18-week-old seedlings to light preconditioning (see Fig. 8). Unlike the 6- and 10-week-old seedlings, which did not respond significantly to light preconditioning, the light required for saturation of photosynthesis of the 18-week-old seedlings was proportional to the incident light energy during preconditioning. The 18-week-old seedlings preconditioned under the highest light required the most light for the light saturation of photosynthesis, while the low-light preconditioned seedlings required the least. The 18-week-old seedlings were more capable of responding to varying light conditions than were the younger seedlings.

The differences in the light required for saturation of photosynthesis between the 6- and 10-week-old seedlings (see Fig. 8) is probably also due to physiological differences between the cotyledons and the juvenile needles. The needles of the 10-week-old seedlings are in the process of expanding and physiologically maturing and are evidently saturated at much lower light intensities than either the cotyledons of the 6-week-old seedlings or the matured needles of the 18-week-old seedlings. This may be the results of increased short-term photoinhibition of the dark reactions of these immature needles.

SUMMARY

The results and statistical analysis of the photosynthesis measurements allow these summary statements: Physiological age of the seedlings of both ecotypes was an important factor in the response of photosynthesis to light preconditioning. The cotyledons are less susceptible to photoinhibition of the light reactions of photosynthesis and are less photochemically efficient than the juvenile needles. This indicates a possible link between high photochemical efficiency and a high susceptibility to photoinhibition of the light reactions of photosynthesis. At a given age, the changes in photochemical efficiency in response to changes in light preconditioning were similar for the seedlings of the two ecotypes. In general, the photochemical efficiency of the seedlings of both ecotypes was reduced in response to higher light during preconditioning.

The response of the dark reactions of photosynthesis of the juvenile needles changed as the needles matured. The dark reactions of the immature needles were inhibited by preconditioning under moderate light. Needles that matured under moderate light pretreatment were not inhibited but had a significantly higher light-saturated rate than those of the same age preconditioned under low light.

Some differences between the two ecotypes were apparent. Seedlings from the coastal source were able to utilize low light more

effectively than those from the Arizona source. Except for the six-week-old seedlings, the coastal seedlings also had higher light-saturated rates of photosynthesis. The cotyledons of the six-week-old Arizona seedlings apparently had a protective or recovery mechanism that prevents short-term inhibition of the dark reactions of photosynthesis during measurement allowing higher maximum rates of photosynthesis.

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APPENDIX

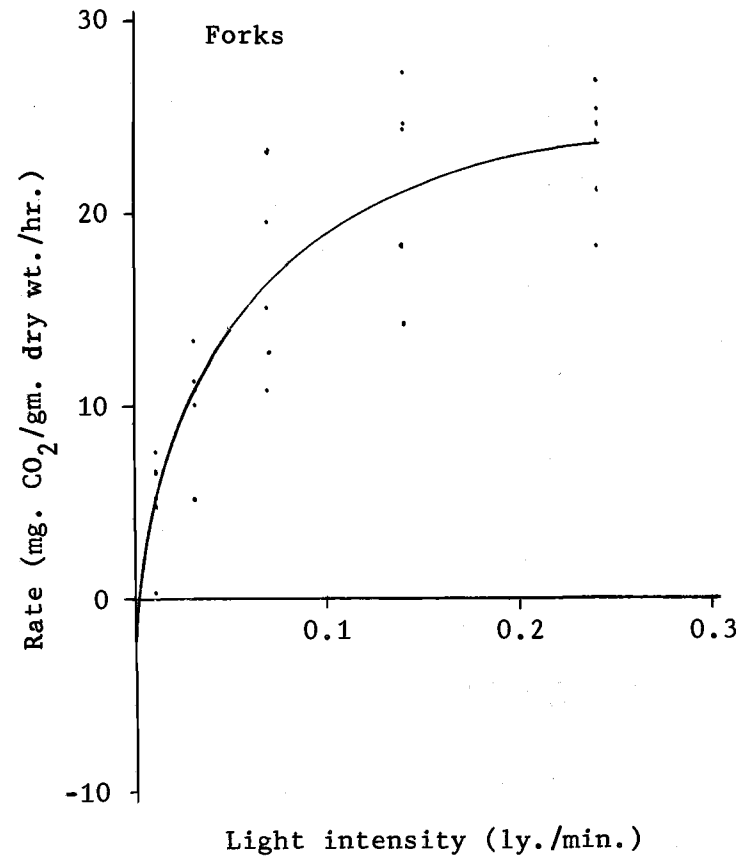
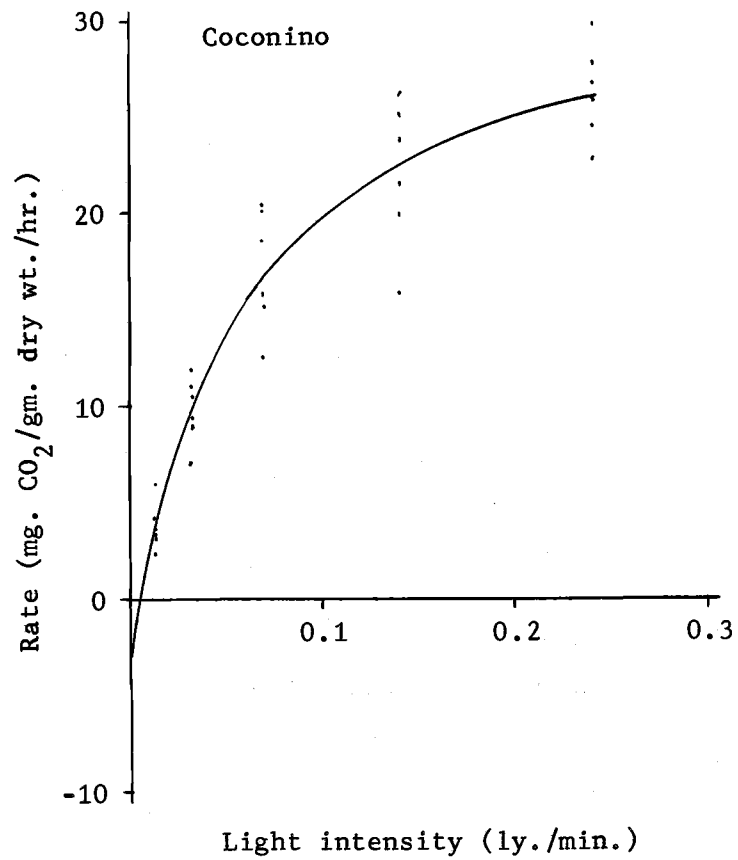


Figure 10. Light response curves of photosynthesis of the six-week-old low-light-preconditioned seedlings

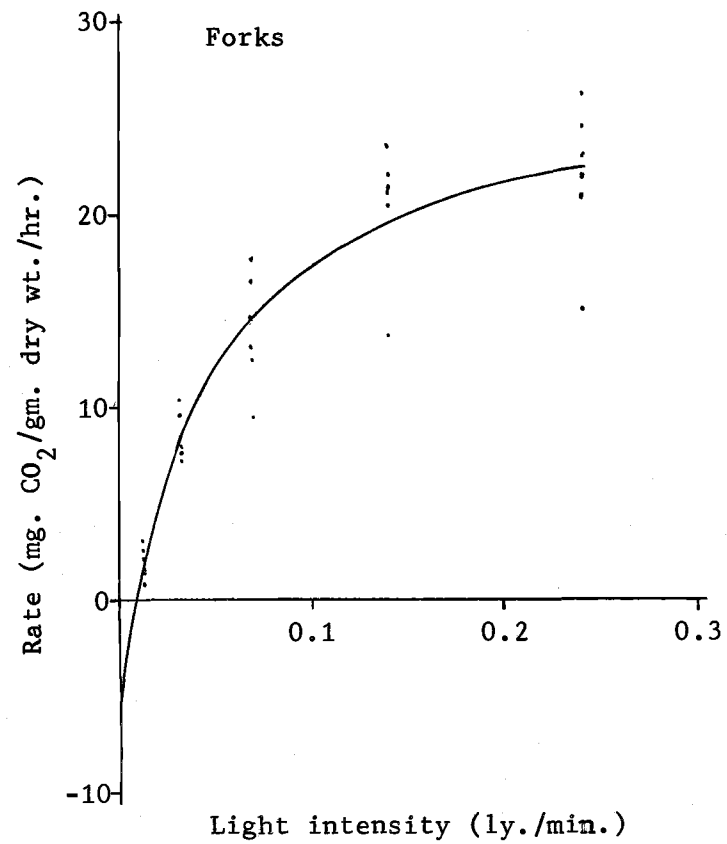
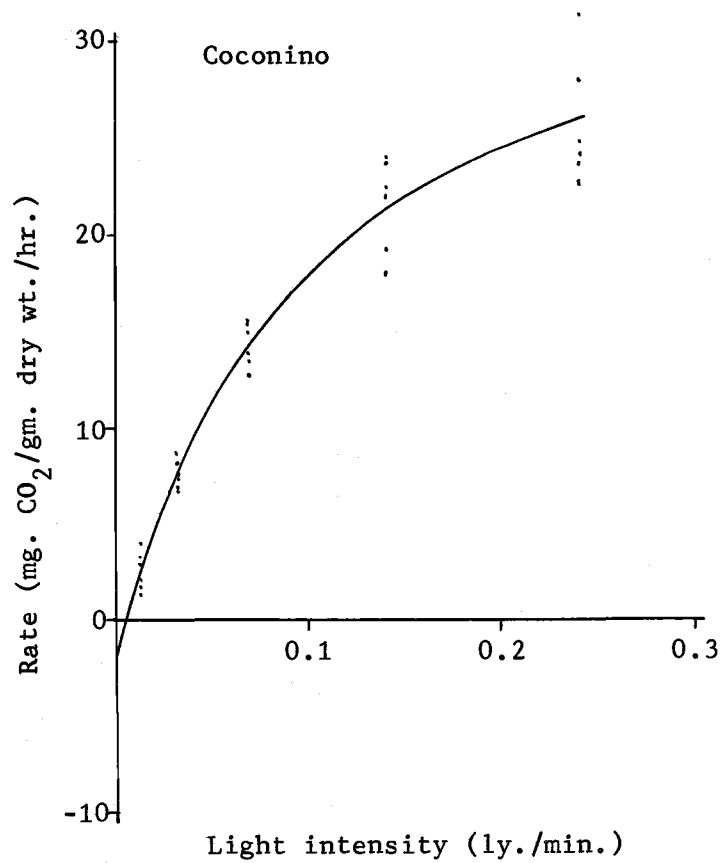


Figure 11. Light response curves of photosynthesis of the six-week-old cold frame preconditioned seedlings.

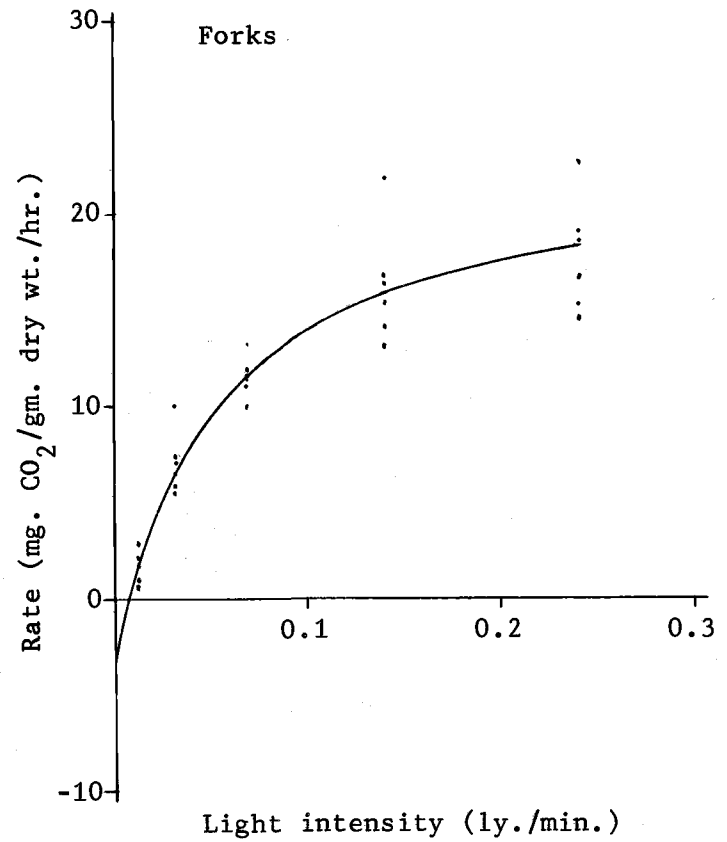
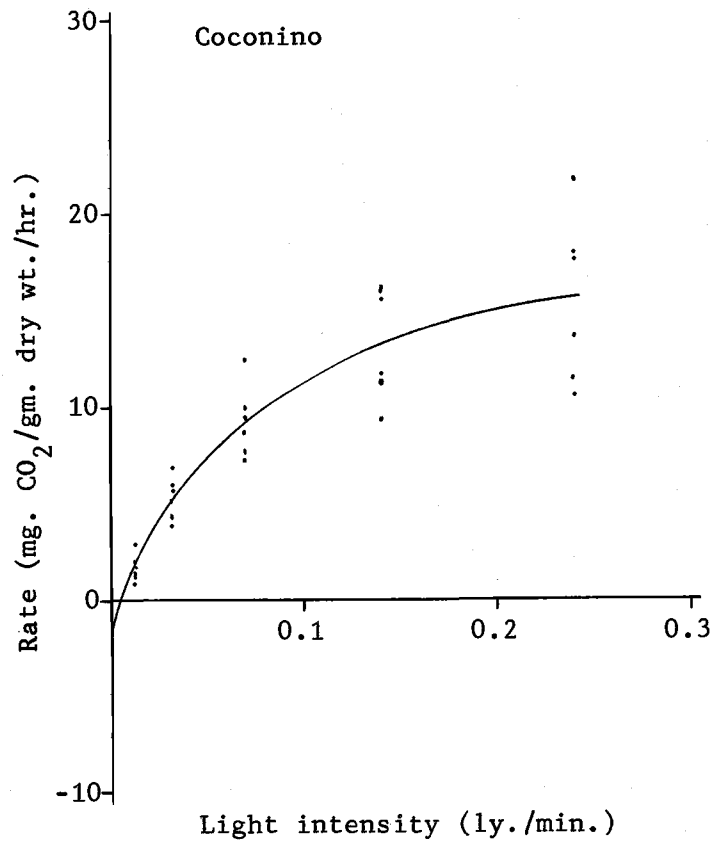


Figure 12. Light response curves of photosynthesis of the six-week-old high-light preconditioned seedlings.

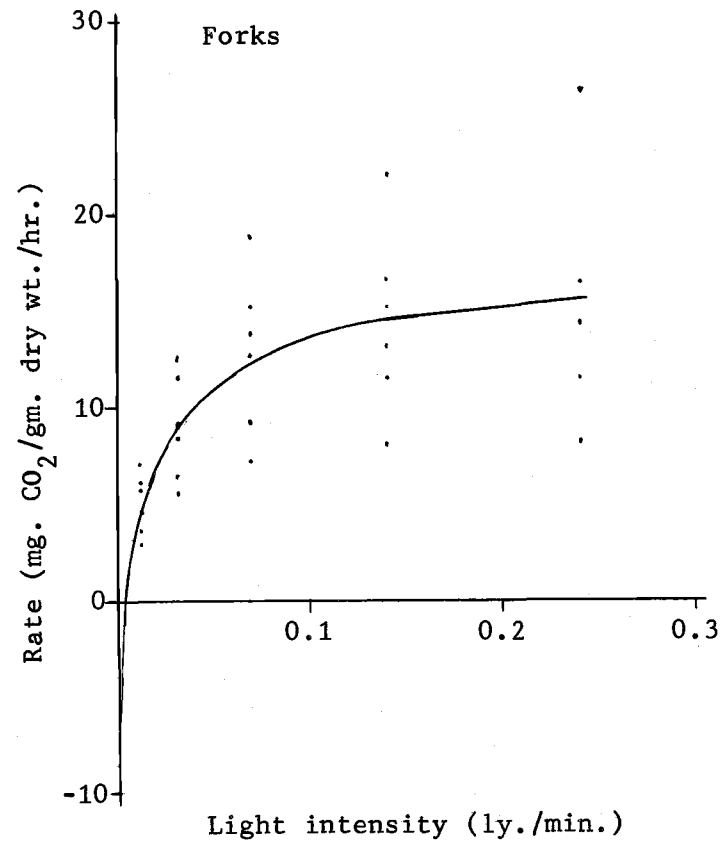
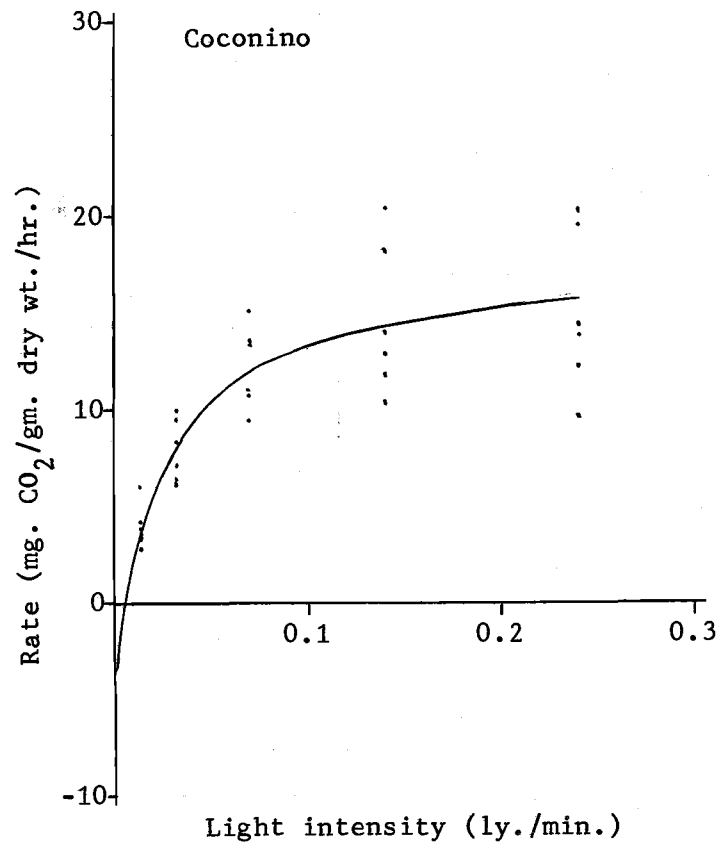


Figure 13. Light response curves of photosynthesis of the 10-week-old low-light preconditioned seedlings.

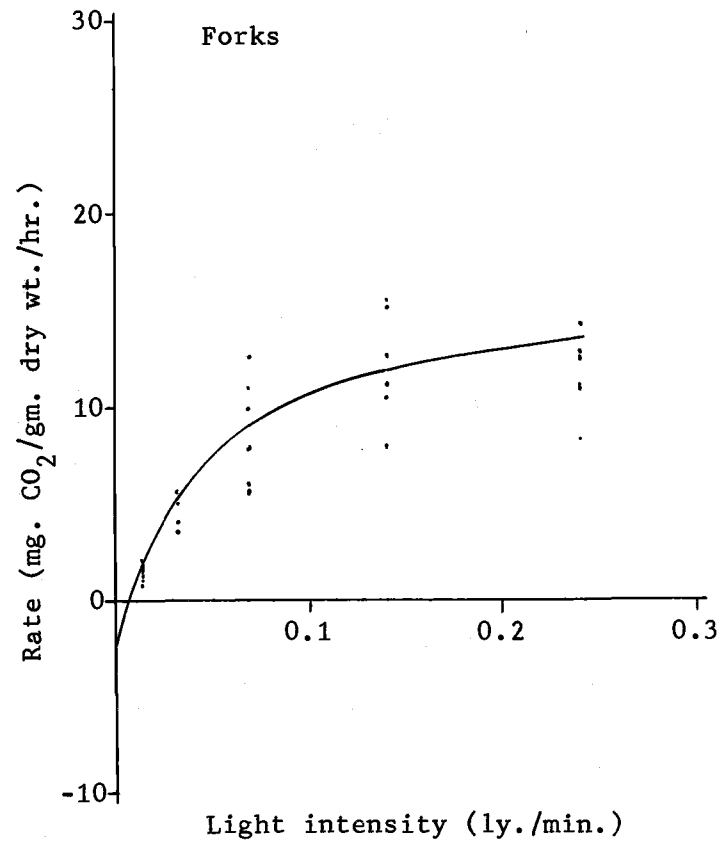
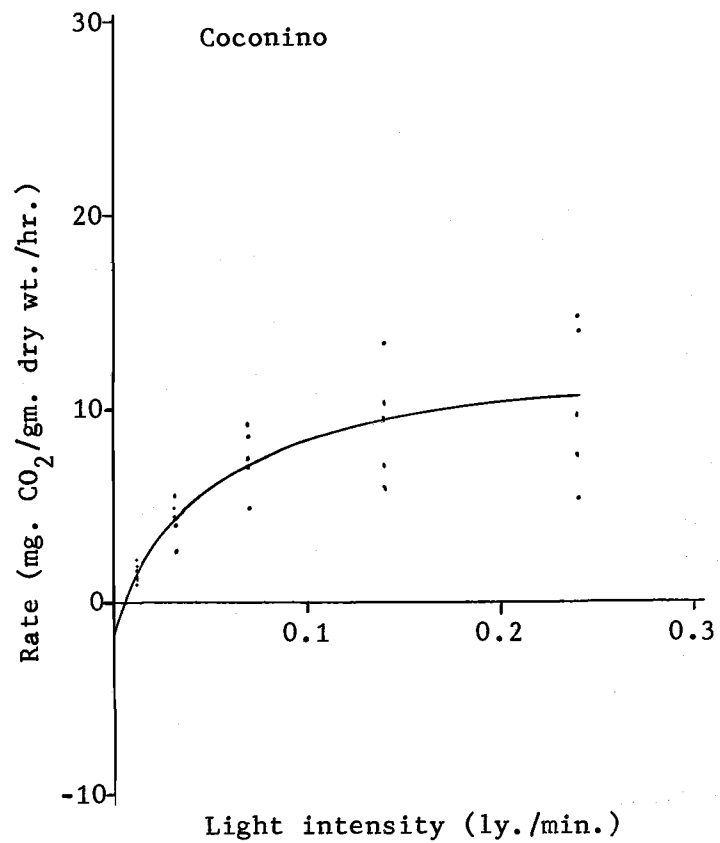


Figure 14. Light response curves of photosynthesis of the 10-week-old cold frame preconditioned seedlings.

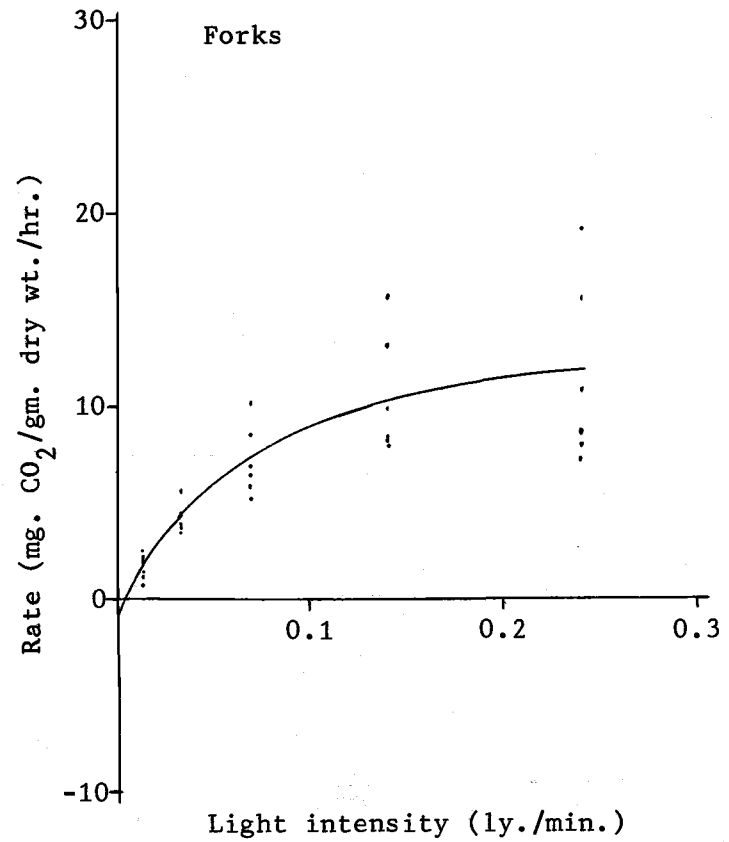
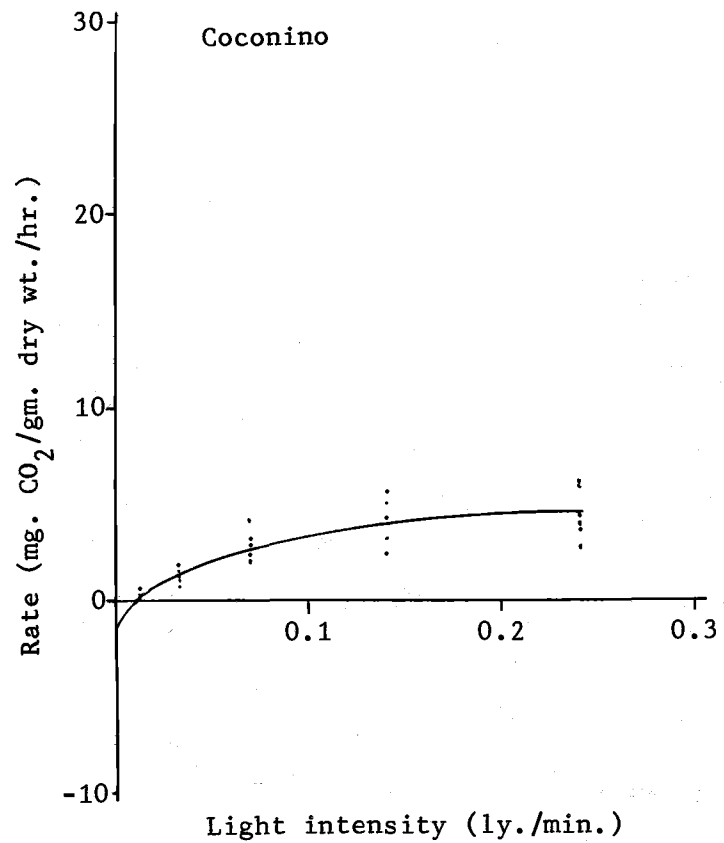


Figure 15. Light response curves of photosynthesis of the 10-week-old high-light preconditioned seedlings.

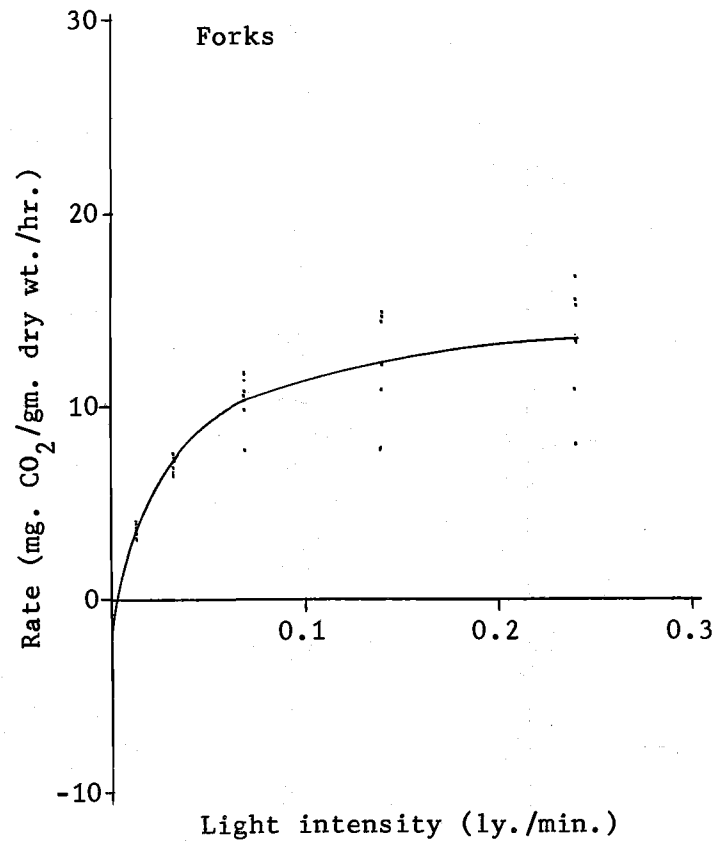
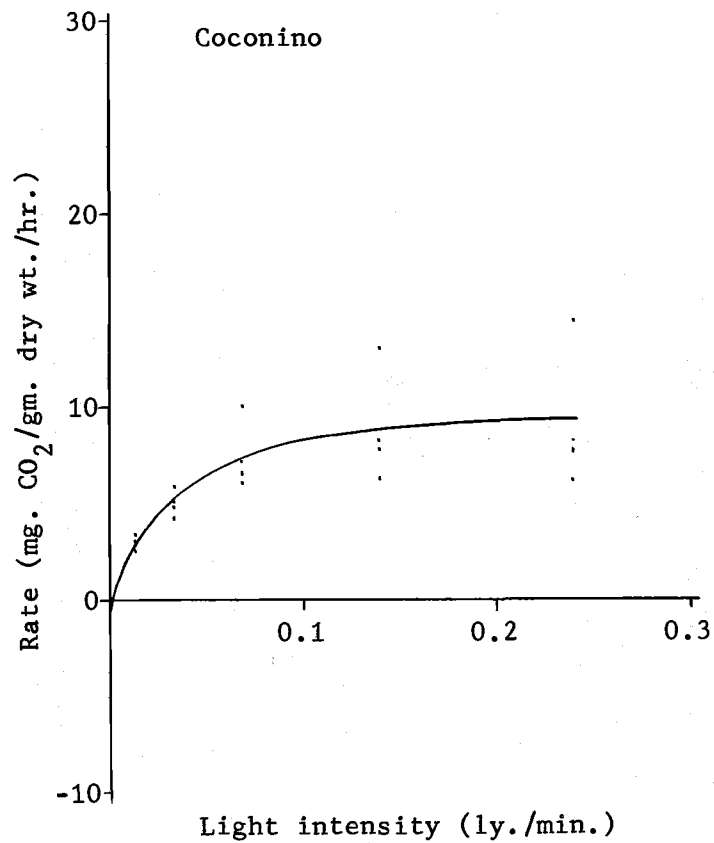


Figure 16. Light response curves of photosynthesis of the 18-week-old low-light preconditioned seedlings.

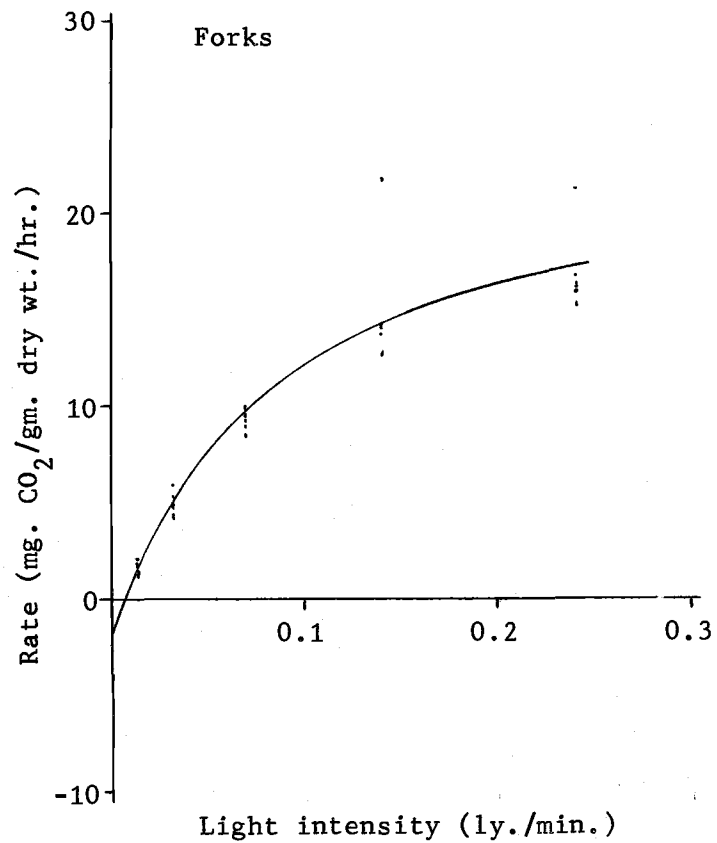
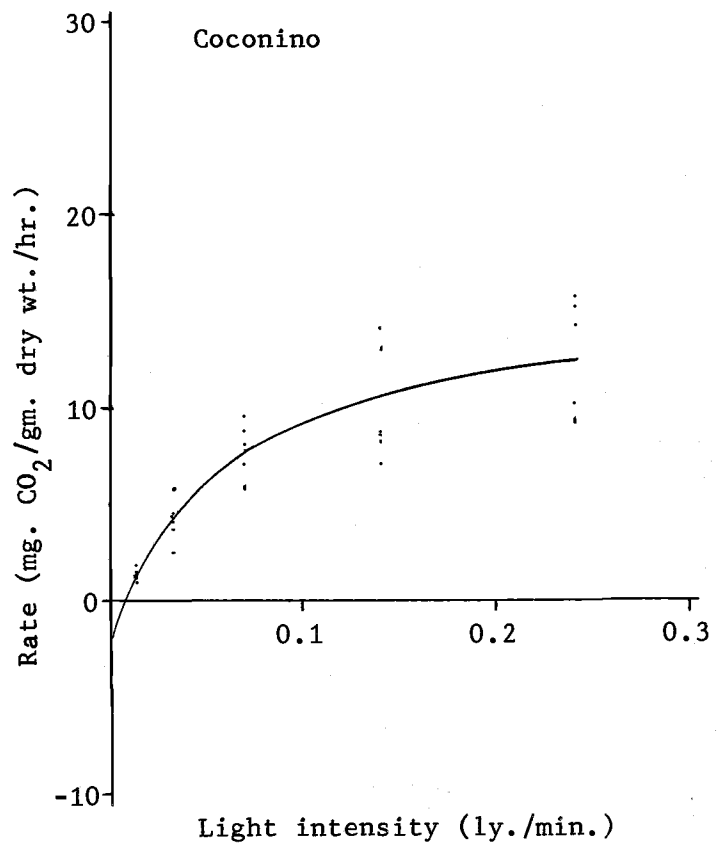


Figure 17. Light response curves of photosynthesis of the 18-week-old cold frame preconditioned seedlings.

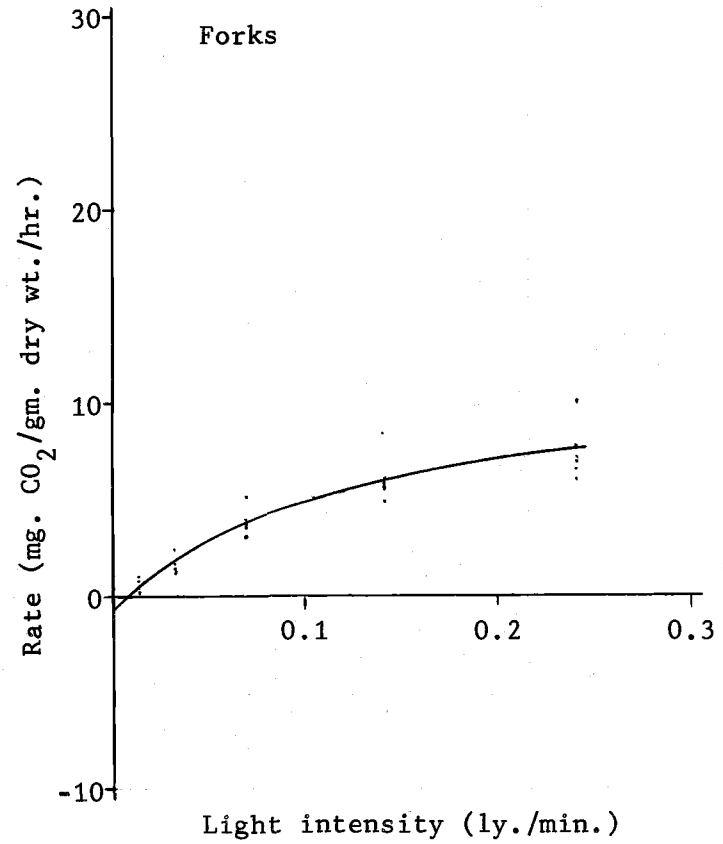
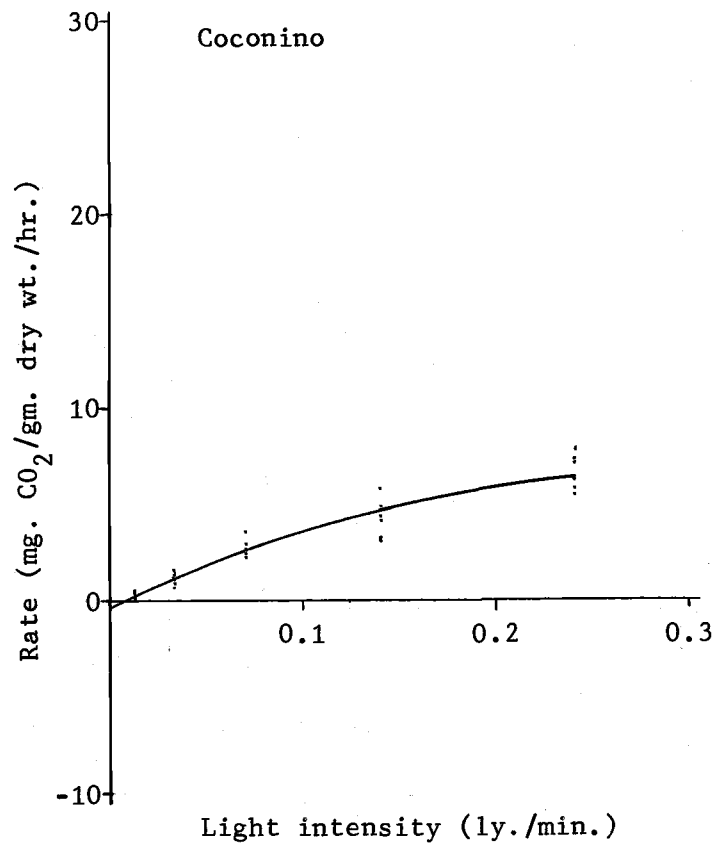


Figure 18. Light response curves of photosynthesis of the 18-week-old high-light preconditioned seedlings.