

**AN ABSTRACT OF THE THESIS OF**

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**Title: "Comparative Photosynthesis and Respiration Rates of  
Douglas-fir Seedlings from Vancouver Island and Montana  
under Various Conditions of Light and Temperature."**

**Abstract approved** . Signature redacted for privacy.

The photosynthetic and respiratory response of Douglas-fir seedlings from two seed sources, southern Vancouver Island, B. C. and western Montana, was investigated with respect to temperature, light intensity and seedling age. Seedlings were grown and measured under highly controlled conditions.

At saturating light intensity and 20° C, the photosynthetic rates of seedlings declined significantly for both sources as they aged from 15 to 35 days. Comparison at 15, 25, and 35 days of age found photosynthetic rates for seedlings of Vancouver Island significantly higher than for those of Montana. At ages from 50 to 100 days there was no significant difference in rates between seedlings of the two sources under these conditions. Respiration rate declined gradually as seedlings aged from 15 to 50 days. A significant difference in

respiration rate between the two sources was found only at 35 days of age when seedlings of Vancouver Island were higher.

Photosynthetic and respiration rates were measured over the range from 10° C to the temperature compensation point for photosynthesis. Maximum photosynthesis was found near temperatures of 20° C to 25° C for the seedlings at both 35 and 65 days of age. A shift with age from 25° C to 20° C for maximum photosynthesis was indicated for seedlings of Montana. Seedlings of Vancouver Island had significantly higher rates of photosynthesis than seedlings of Montana at 20° C and 25° C at 35 days of age and at 25° C at 65 days. Respiration rates of Vancouver Island as compared to Montana seedlings were significantly higher at the 35 day age over a wide range of temperatures, but at 65 days only at 15° C and 40° C.

Seedlings of Montana required more light to reach the compensation point at 20° C, and evidenced a lesser photosynthetic response at light intensities of 200 to 1000 foot-candles than did Vancouver Island seedlings. Saturation intensity for seedlings of both sources was about 3000 foot-candles.

Based on statistical evidence, seedlings from these two seed sources may be considered as "ecotypes" although significant differences often disappeared with age. Measurement of other Vancouver Island and Montana seedlings showed that differences

between seedlings of geographically associated seed sources may be greater than for sources more widely separated in location.

**COMPARATIVE PHOTOSYNTHESIS AND RESPIRATION  
RATES OF DOUGLAS-FIR SEEDLINGS FROM  
VANCOUVER ISLAND AND MONTANA UNDER  
VARIOUS CONDITIONS OF LIGHT AND TEMPERATURE**

by

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degree of

**DOCTOR OF PHILOSOPHY**

**June 1963**

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**Date thesis is presented** May 10, 1963

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**Comparative Photosynthesis and Respiration Rates  
of Douglas-fir Seedlings from Vancouver Island  
and Montana under Various Conditions  
of Light and Temperature**

**INTRODUCTION**

For plant species ranging over thousands of square miles, localized adaption to specific environments through long-term selection may be expected. Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, native to Mexico, Canada and every state west of the Rocky Mountains, has shown evidence of ecotypic differentiation with respect to photoperiodic sensitivity (23). Although most physiological processes will be influenced by the environment, the effectiveness of environmental pressure toward genotypic modification may vary among the various processes.

Douglas-fir in areas as different climatically as the Rocky Mountains of western Montana and southern Vancouver Island, British Columbia, might be expected to have developed some differential response of the photosynthetic and respiratory processes to temperature and light intensity. Accordingly, seedlings grown from seed collected in these two areas were investigated as to their comparative photosynthetic and respiratory behavior.



## REVIEW OF LITERATURE

Several studies of intraspecific variation of photosynthesis and respiration of higher plants have been made in recent years. Particularly noteworthy are studies of altitudinal races of Mimulus cardinalis (31). Clones of a mid-Sierran race of Mimulus were found to require higher light levels for saturation, to attain a maximum rate of apparent photosynthesis at a lower temperature, and to have a slightly lower temperature compensation point for apparent photosynthesis at high temperatures than clones from a coastal race. Respiration rates per unit leaf area of the mid-Sierran race were higher than those of the coastal race over the range 10° to 40° C (21).

Results similar to those for Mimulus were obtained in comparisons of an arctic race with a more southerly alpine race of Oxyria digyna with the exception that the arctic race required less rather than more light to reach saturation (32, p. 21).

The temperature response of photosynthesis of Solidago virgaurea has been investigated for plants from alpine, inland and coastal areas. Under experimental conditions of less than saturating light intensity, the alpine plants reached maximum photosynthetic rates at temperatures several degrees Celsius lower than those for the other two sources (4).

A few studies of intraspecific variation in photosynthetic or respiration rates have been made for conifers. It has been reported that northern populations of Eastern white pine, Pinus strobus, require more light to reach compensation than southern populations and at high temperatures respire less rapidly (8). Another study obtained preliminary indications that seedlings of Eastern hemlock, Tsuga canadensis, from Tennessee and New York sources may differ in photosynthetic response to changes in light and temperature (17). Two-year-old seedlings of an East Norwegian provenance assimilated more and a North Swedish provenance less than two German provenances of Norway spruce (Picea excelsa) when measured at 3000 lux and 10° C (40). Seedlings of climatic provenances of Pinus silvestris have been reported to differ in their respiration rate (41).

Reviews of the variables affecting photosynthesis and respiration and the measurement of these processes using infrared analysis of Carbon dioxide have been numerous in the last 10 years (38) (46) (47). Extensive repetition of these reviewers' remarks would serve no purpose here and reference will be made as appropriate.

## METHODS

The need for considerable numbers of seedlings for use in preliminary experiments necessitated the use of commercial seed collections. The two sources selected were southern Vancouver Island, a region producing seedlings with rapid early growth (12), and western Montana which is approximately the same latitude as Vancouver Island but of continental climate.

Following a period of naked stratification, seeds of the two lots were germinated and grown in a "controlled environment" chamber at  $19-9^{\circ}\text{C}$  day-night temperature for 10 and 8 hours respectively, interspaced by 3 hours of change at constant rate. Warm white and cool white fluorescent tubes and incandescent bulbs provided 1100 foot candles of illumination at plant level for 16 hours daily. Seedlings were grown in black polystyrene pots of pint or quart size in washed stream gravel of approximately 3 mm. diameter. Daily watering with nutrient solution was conducted except once weekly when tap water was used for flushing purposes.<sup>1/</sup>

Photosynthetic and respiration rates were measured as changes in  $\text{CO}_2$  concentration in a closed 2.95 liter system using a Beckman

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<sup>1/</sup>

Composition of the nutrient solution is given in the Appendix, Table 6.

L/B 15 infrared gas analyzer. The experimental apparatus is similar to others described in the literature (29) and is shown diagrammatically in the Appendix (Figure 14). To avoid loss of  $\text{CO}_2$  by diffusion, connecting tubing was made of glass with tygon joints. A peristaltic pump circulated air through the system at 1.7 liters per minute; two desiccation tubes in series--one containing calcium chloride, the second magnesium perchlorate--served to remove moisture from the air prior to entry into the  $\text{CO}_2$  analyzer. Preliminary tests showed a curvilinear effect of increasing water vapor concentration on apparent  $\text{CO}_2$  concentration response of the analyzer due to infrared absorption by the  $\text{H}_2\text{O}$  molecules (Appendix, Figure 15). Consequently, analyses were made with no  $\text{H}_2\text{O}$  present rather than attempting to hold constant water vapor pressure or applying a variable correction factor. Air moisture was restored to 50 per cent relative humidity or higher by blowing the air stream against a water surface which had been acidified with  $\text{H}_3\text{PO}_4$  to prevent  $\text{CO}_2$  absorption. Humidity within the system was monitored using an American Instrument Company Electric Hygrometer. Providing the calcium chloride desiccant was changed before excessive moisture accumulated, changes of  $\text{CO}_2$  concentration within an empty system were negligible over a period of an hour which was much more time than was usually

required for measurement. Dark respiration measurements were made in a smaller 1.7 l liter system.

Water of 4.5 cm. depth flowing across the glass top of the copper cuvette was used to reduce the heat input from the 1200 watt "Hi-Spot" reflector-back light source.<sup>2/</sup> A piece of frosted 1.5 mm. thick glass served to diffuse a uniform light flux over the illuminated field, while interposition of variable numbers of black screens accompanied by slight changes in the distance from lamp to cuvette was used to adjust the light intensity. Light intensity was measured with a Model 756 Weston Illumination meter with quartz filter photo-cell. With the apparatus arranged as if for photosynthetic measurement, the light intensity (foot-candles) was related to light energy (calories per square centimeter per minute) as shown in the Appendix, Figure 16.

By pumping water from a thermostated water bath through copper coils which surrounded the cuvette as well as passing the system air stream through a coil in the same bath, air temperature as measured with a double shielded thermocouple was held within  $\pm 1^{\circ}\text{C}$  during measurement periods.

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<sup>2/</sup>

Radiant Lamp Corp., Newark, New Jersey.

Analyzers were calibrated daily with dry air containing CO<sub>2</sub> in known concentration.<sup>3/</sup>

Prior to measurements a pot of well-watered seedlings was taken from the growth chamber, all seedlings but one or two were clipped off, and a seal was made at the base of the seedling stem with modeling clay. A second seal was formed between the bottom of the cuvette and the clay. The apparatus was then placed in the desired conditions of light and temperature for 20 minutes before measurement of the CO<sub>2</sub> uptake or evolution was made. The 20 minute period was adequate for stabilization of rates to occur as determined from an extensive number of trials. Following measurement of the CO<sub>2</sub> concentration change, the seedlings were clipped off at the surface of the clay and dried overnight in an oven at 100° C. The weight of the foliage, which is easily removed from the stem after drying, was then determined.

Carbon dioxide depletion by photosynthesis was measured in the range 329 to 371 ppm; this range was chosen for convenience, although there is evidence that it may be more similar to natural conditions for forest seedlings than the range around the average 300 ppm atmospheric concentration (16).

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<sup>3/</sup>

Obtained from The Matheson Company, Inc., East Rutherford, New Jersey.

Use of changes in carbon dioxide concentration to measure photosynthetic or respiration rates has many advantages. The measurement is both sensitive and rapid if an infrared gas analyser is used. Certain limitations must be recognized, however. Until additional experiments can be carried out, if one wishes to correct the rate of  $\text{CO}_2$  uptake in illuminated conditions (apparent photosynthesis) for the concurrent  $\text{CO}_2$  evolution (respiration), one is forced to assume that the rate of respiration in light and dark is equal. The total uptake or photosynthetic rate is considered the sum of the apparent photosynthetic rate added to the dark respiration rate at that temperature. Common to measurement of both photosynthesis and respiration by changes in  $\text{CO}_2$  concentration is the assumption that any non-photosynthetic  $\text{CO}_2$  uptake is negligible. Comparisons of respiration rates measured in terms of  $\text{CO}_2$  evolution at different temperatures, ages and for seedlings from different sources implies that the Respiratory Quotient remains the same throughout. No experimental verification of this assumption has yet been made.

## INVESTIGATIONS

While the primary goal of this study was to determine the response of the seedlings to temperature and light, certain other investigations were also necessary. It seemed quite probable that photosynthetic and respiratory rates would vary with the age of the seedling. Also, despite the narrow concentration of carbon dioxide over which the photosynthetic rates were measured, it seemed necessary to show whether there was any difference in the effect of CO<sub>2</sub> concentration on photosynthetic rates for seedlings of the two sources (3).

The decrease in photosynthetic rate from 370 ppm to below 300 ppm CO<sub>2</sub> was found to be essentially linear for seedlings of both sources under the experimental conditions (correlation coefficients of 0.7 and 0.9 for the Vancouver Island and Montana seedlings respectively). The regression coefficients for the slopes of the lines were 0.30 and 0.33 per cent decrease in photosynthetic rate per ppm CO<sub>2</sub>. When tested by covariance analysis, these coefficients were found not significantly different for seedlings of the two sources (Table 7, Appendix). For both sources the photosynthetic rate at 300 ppm CO<sub>2</sub> was approximately 84 per cent of the rate at 350 ppm, mid-point of the range of CO<sub>2</sub> which this study utilized.



## I. Changes in Apparent Photosynthesis with Seedling Age

### Introduction

Deciduous plants present a characteristic pattern of photosynthetic activity in young leaves. Assimilation of  $\text{CO}_2$  is low in very young leaves, increases to a maximum in fully expanded leaves and then decreases as the leaves age (39, p. 451). The increase in photosynthetic capacity has been shown to lag behind chlorophyll development, and also to develop under conditions where chlorophyll concentration is constant. Correction for the decrease in respiration rate during this time does not change this conclusion (10, p. 253). Since chloroplasts from young spinach leaves have less Hill reaction activity than those from old spinach leaves even when the chloroplasts of one are suspended in the cell sap with cytoplasm of the other, the change has been interpreted as occurring within the chloroplast itself (15, p. 126). More recent work with the growing leaves of pea (Pisum sativum) has shown that activities of ribulose-1, 5-diphosphate carboxylase and photosynthetic pyridine nucleotide reductase, both enzymes of the photosynthetic process, parallel the changing rate of photosynthesis in the early stages (43).

If plant dry weight gain per unit leaf area, leaf nitrogen or leaf dry weight is plotted against plant age, a sharp drop in the rate

of gain occurs even before there is significant intra-plant shading, thus illustrating a drop in efficiency. These data were obtained for potato and sugar beet under controlled environmental conditions (48, p. 365).

Since conifer needles may persist several years, one must distinguish between needle age and plant age. Comparisons of 1-year, 2-year, etc. needles of several species have shown the younger needles to have higher photosynthetic rates (19) (28). For newly developing needles of Balsam fir, Abies balsamea, and white spruce, Picea glauca, there occurs a sharp increase in photosynthetic rate over a two-month period until, as the new needles mature, they are apparently the most efficient foliage on the tree (13, p. 61).

Existing data suggest primary needles of young loblolly pine, Pinus taeda, have higher absolute rates than secondary needles of this species (7, p. 204). Differences in needle anatomy in addition to less intra-seedling shading have been given as reasons for the lower light intensities required for saturation of 4-month-old loblolly pine seedlings compared with second- or third-year seedlings.

Some developmental stages of typical Douglas-fir seedlings investigated in the study are illustrated in Figure 1.

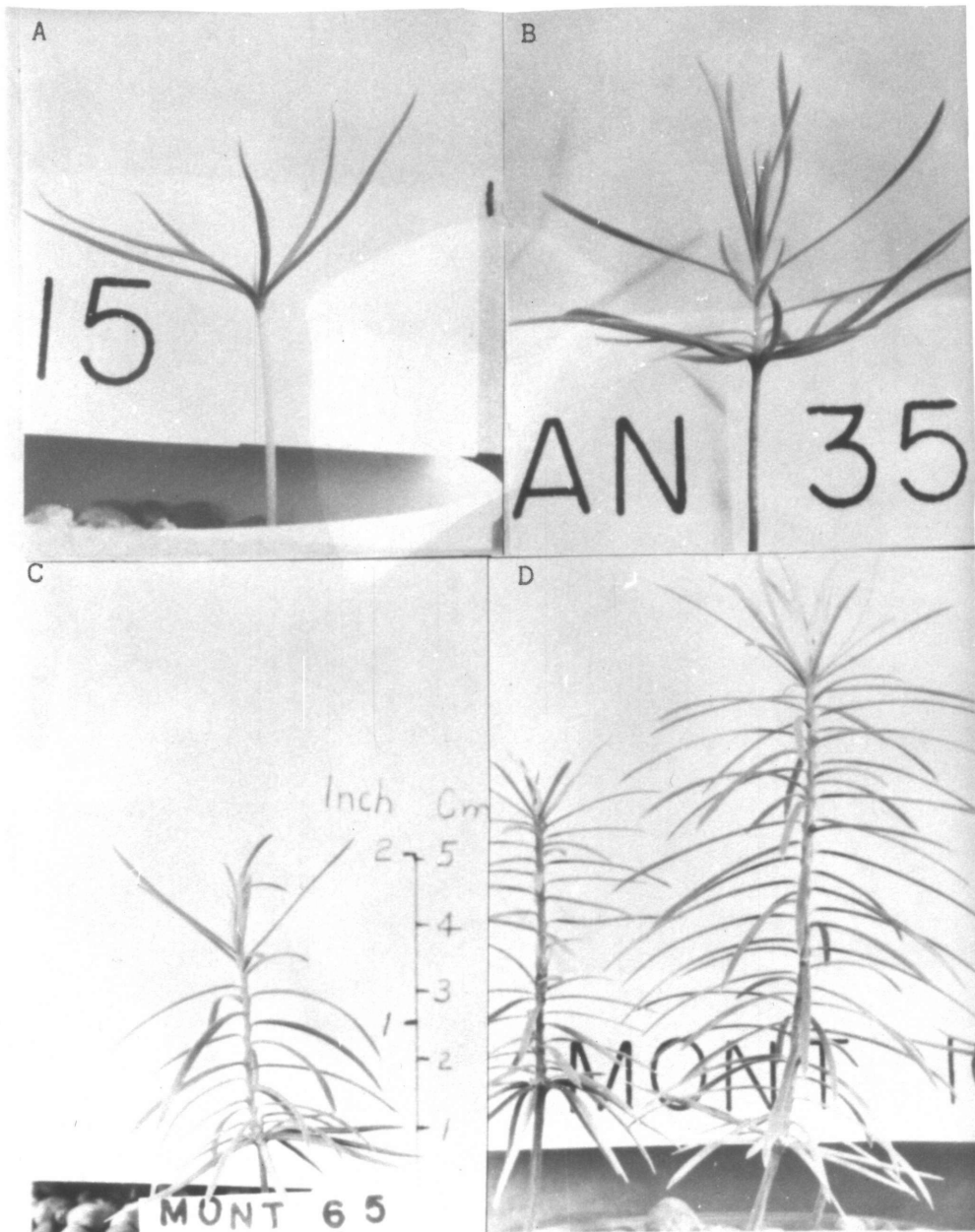


Figure 1. Typical development of Douglas-fir seedlings at various ages. A and B -- Seedlings of Vancouver Island seed source, ages 15 and 35 days from germination, scale 1.5 to 1. C and D -- Seedlings of the western Montana seed source, ages 65 and 100 days, scale 1 to 1.

### Materials and Methods

Photosynthesis at the various ages was measured at saturating light intensity (5000 foot-candles) and 20° C using methods described in a preceding section. Ten separate measurements per source were made at ages 15, 25, 35, 50, 65, 80 and 100 days from germination. Two seedlings which did not shade one another were placed within the cuvette for each measurement at ages 15, 25, and 35 days, while at the other four ages there was one seedling per measurement. Thus the average rates of apparent photosynthesis for the three earliest ages are based on 20 seedlings each, the four oldest on averages of 10 seedlings each for a total of 100 seedlings for each curve (Figure 2).

Using data for average needle moisture content of the seedlings at the various ages (Appendix, Table 3), the photosynthetic curve was replotted on a fresh weight basis to determine whether the interpretation of a rapid early decline would be changed. Chlorophyll content of the needles was also determined at the ages for which the photosynthetic measurements were made (2, p. 92).

Although the surface area of conifer foliage is very difficult to measure, an attempt was made to determine needle surface area of 35-day-old seedlings of both sources, and to correlate this with

needle dry weight. This was to ascertain whether there was any bias toward seedlings of either source when the photosynthetic rates of the seedlings were expressed in terms of dry weight. Moreover, an expression of the photosynthetic rate in terms of needle surface area could be obtained for comparative purposes.

To measure the surface area of the foliage, a seedling was chosen and several standard-size pieces of opaque material were suspended at mid-crown perpendicular to the seedling stem. A vertical picture was taken with the camera set to give maximum depth of field. The fine grain negative was printed at 8 by 10 inches, and the image of the seedling crown and the standards were cut out and weighed. On determining the weight of the known standard area in the picture, the area of the foliage on the picture was then easily calculated from its weight. Only the visible surface of the needles was calculated and no correction was applied for the few overlapping needles. Using this method the area of the foliage at the top of the plant is overestimated while that in the lower portion of the crown underestimated. For comparative purposes the technique would seem satisfactory, however.

To aid in the interpretation of the photosynthetic data, a curve of average total seedling dry weight with age was constructed for

seedlings of the two sources (Figure 5). Seedlings were grown in the controlled environmental conditions described previously and were harvested prior to terminal bud formation.

## Results

### Photosynthetic Rate with Seedling Development

A rapid decline in rate of apparent photosynthesis takes place in the developing seedlings (Figures 2 and 3). The decline occurs regardless of whether  $\text{CO}_2$  uptake is expressed in dry weight or fresh weight although not to the same degree. The rate at 35 days of age for the Vancouver Island seedlings is only 48 per cent of the 15-day rate when both are expressed on a dry weight basis; when rates are expressed in terms of fresh weight, comparison indicates the decline is to 62 per cent. Corresponding figures for seedlings of the Montana source are 45 and 51 per cent. Compared statistically the decreases in rates in the two intervals 15 to 25 and 25 to 35 days of age are both highly significant for seedlings of both sources.

Statistical comparison between sources indicates that Vancouver Island seedlings maintain significantly higher rates of photosynthesis than Montana seedlings at 15, 25 and 35 days of age when photosynthesis is expressed on a dry weight basis (Appendix, Table 10).

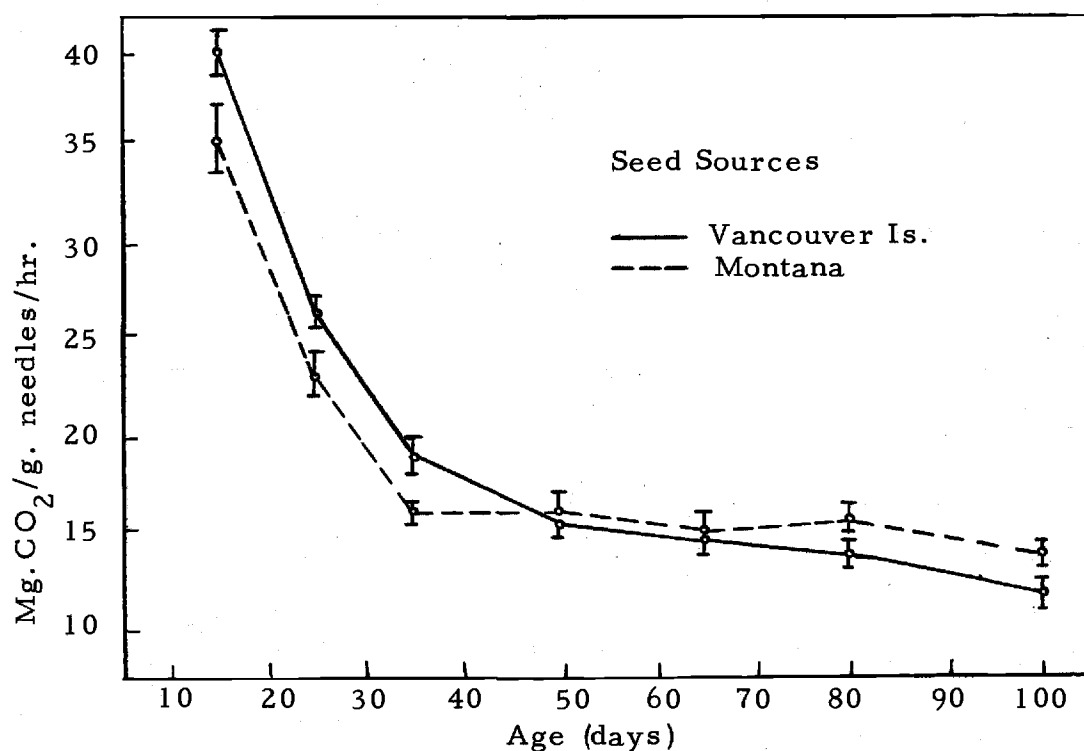


Figure 2. Change in photosynthetic rate with seedling age. Rate calculated on dry weight basis. Bars enclose one Standard Error of the Means.

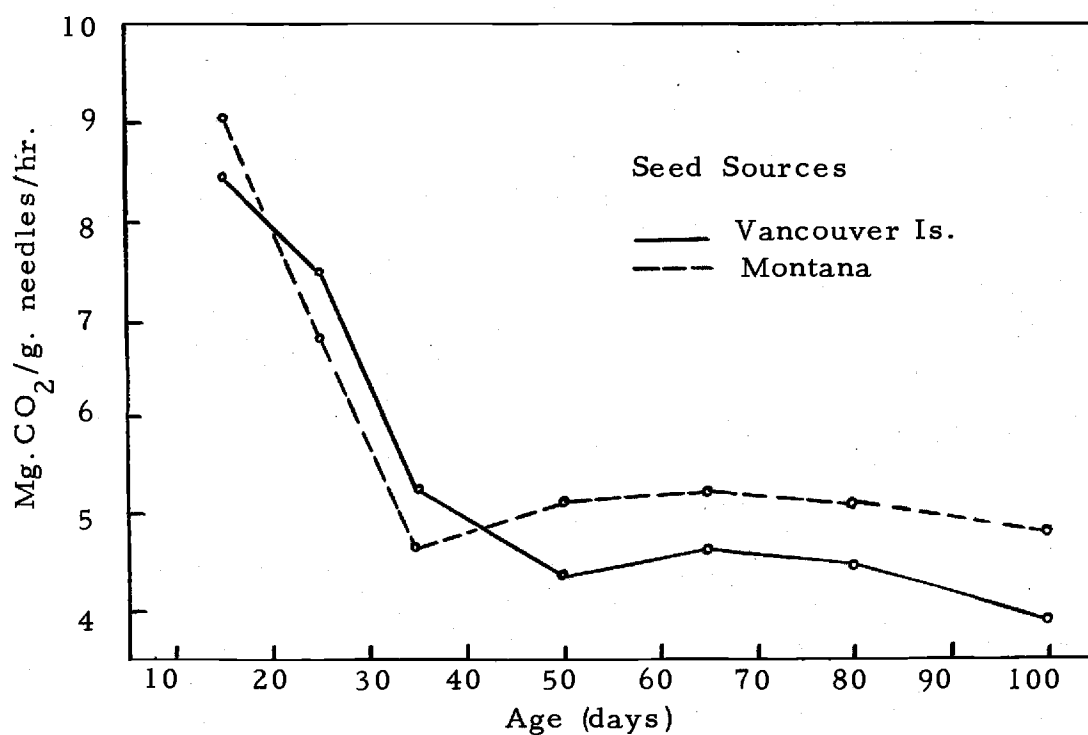


Figure 3. Change in photosynthetic rate with seedling age. Rates calculated from dry weight curve to fresh weight basis.

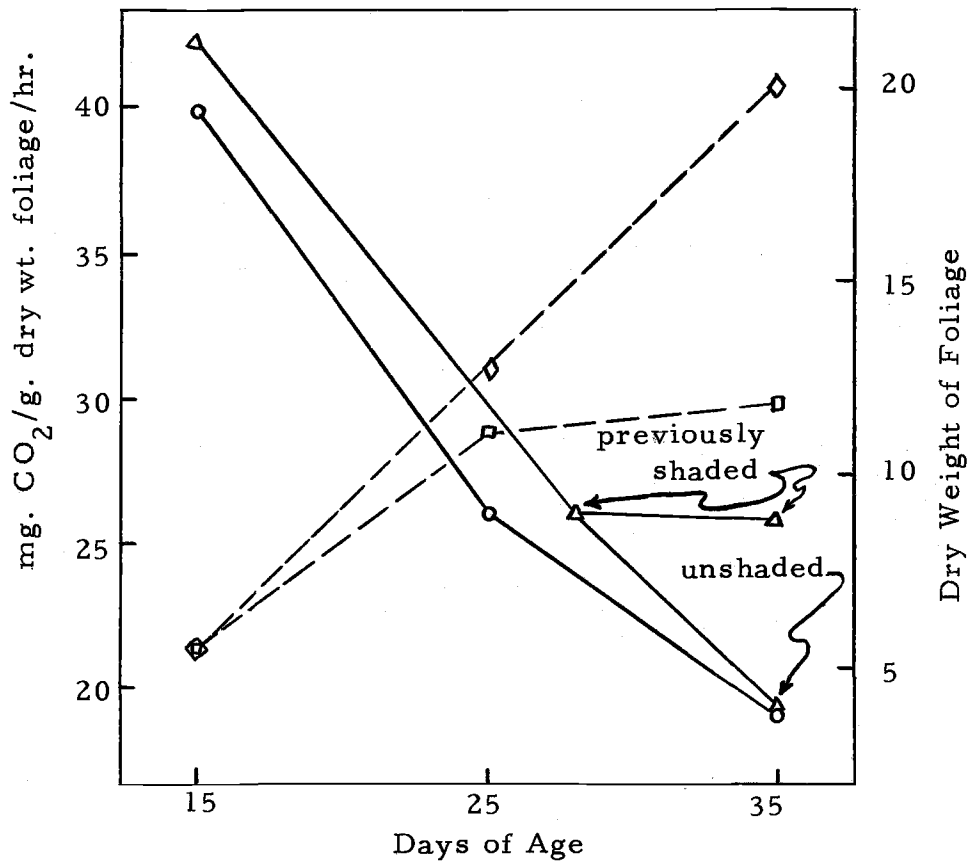


Figure 4. Declining photosynthetic rate of intact and needle-less seedlings, including illustration of the effect of previous shading. Dashed lines show growth of the foliage.

- Intact seedlings
- △—△ Seedlings with cotyledons only
- ◇---◇ Cotyledons and needles
- Cotyledons only



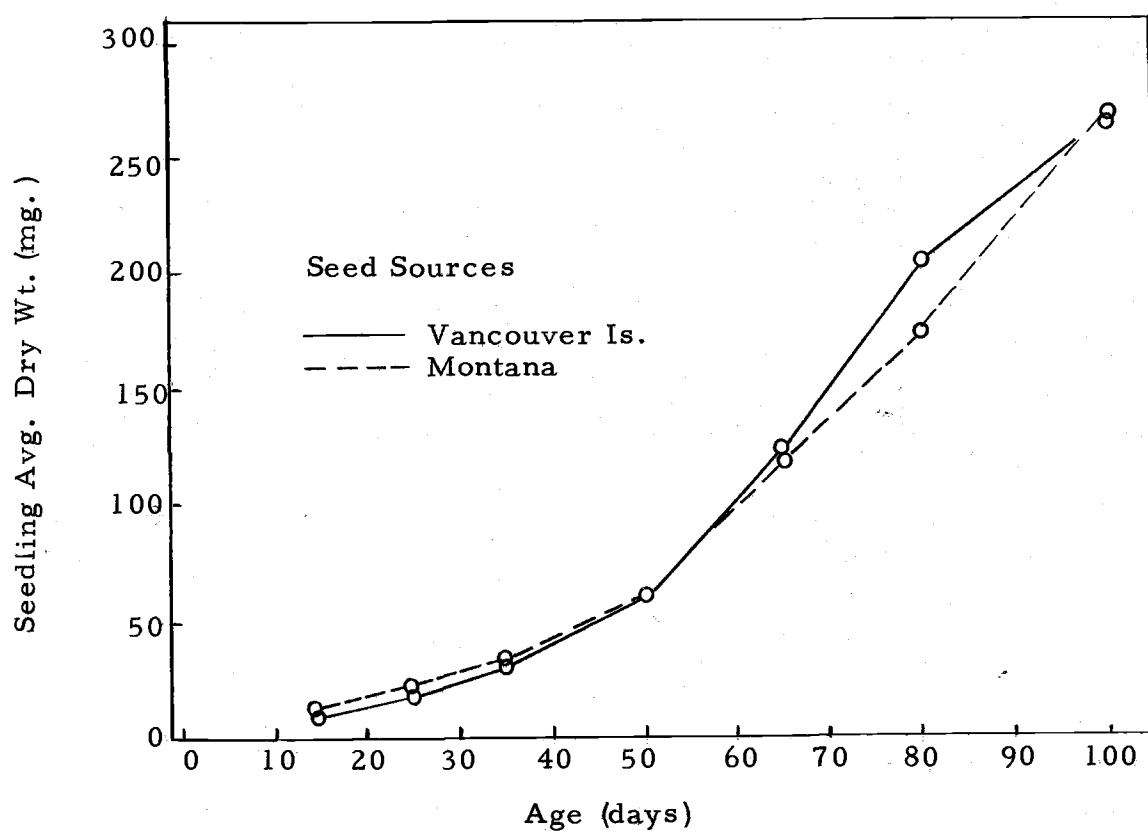


Figure 5. Growth in dry weight of the average Douglas-fir seedlings of the two sources under the conditions described.

At ages greater than 35 days there is no statistically significant difference in rates between the sources when measured under the above conditions.

The photosynthetic tissue of 15-day-old seedlings is essentially limited to the cotyledons. The rapidity of needle development between 15 and 35 days of age can be interpolated from Figures 1A and 1B. As the new needles are rather light green in color, a decline of the average chlorophyll concentration of the total foliage of the seedling is suggested.

Results of analyses of the foliage chlorophyll content show by 35 days a drop to 65 per cent of the 15-day value (Table 1), and one

Table 1. Chlorophyll content of the seedling foliage with age (mg. chlorophyll/g. fresh weight). Values are the results of determinations using a sample of 20 to 100 plants.

Age (days)	Seed Source	
	Vancouver Island	Montana
15	1.67	1.64
25	1.44	1.46
35	1.03	1.13
50	1.12	1.25
65	1.19	1.28
80	1.11	1.17
100	1.21	---

is tempted to conclude that the decrease in chlorophyll concentration is responsible for the early decline in photosynthetic rates. However,

other analyses indicate that the chlorophyll content of cotyledons remains fairly constant in the interval from 15 to 35 days of age.

Somewhat unexpectedly,  $\text{CO}_2$  exchange measurements made with only the cotyledons on the seedlings show that the decline in the apparent photosynthetic rate occurs to about the same degree as for intact seedlings in the period 15 to 25 days of age (Figure 4). The decline in rate continues to 35 days of age under conditions where the needles were clipped from the seedlings at a 2- to 8-day interval prior to measurement. Since clipping off the needles removes a potential "sink" for the 'photosynthate' produced by the cotyledons, the observed photosynthetic rate is perhaps abnormally depressed. However, if the seedlings are shaded for the interval following removal of the needles, the observed rate is similar to that of 25-day-old seedlings but does not approach the observed rate for 15-day-old seedlings.

Dry weight growth of the cotyledons on intact seedlings slows greatly at about 25 days of age (Figure 4) thus removing a "sink" that has been functioning up to that time. The needles of intact plants which might be expected to also act as a "sink" in view of their continuing dry weight increase, are apparently less effective than shading in bringing about higher photosynthetic rates (Figure 4). There is no direct evidence, however, that the accumulation of "photosynthate" is a full or partial explanation for the reduced rates with age.

It was ascertained that the photosynthetic decline with age is not due to increasing respiratory activity (Figure 11). To the contrary, since respiration rate was found to decline with age, the diminished  $\text{CO}_2$  evolution would cause an increase in the apparent photosynthetic rate. Respiration rates of intact 35-day-old seedlings average 2.3  $\text{mg. CO}_2/\text{g. dry weight/hour}$ . Seedlings with cotyledons but no needles respired at 3.4  $\text{mg. CO}_2/\text{g. dry weight/hour}$  based on the average of twelve different seedlings. The decline in photosynthetic rate with age is about 20  $\text{mg. CO}_2/\text{g. dry weight/hour}$ , so this small inequality in respiration rate cannot have much influence on the above observations.

Needle surface area per gram dry weight for intact seedlings of Vancouver Island and Montana was found to be 102.5 and 90.1  $\text{sq. cm.}$  respectively. Covariance analysis of the regression coefficients disclosed that there was no significant difference between the values for the two sources; that is, the needle surface area increases with needle dry weight to the same extent for seedlings of both seed sources.

The apparent photosynthetic rates of 18.9 and 16.0  $\text{mg. CO}_2/\text{g. dry weight needles/hour}$  for seedlings of Vancouver Island and Montana convert to 18.5 and 17.8  $\text{mg. CO}_2/100 \text{ cm}^2/\text{hour}$  when

calculated in terms of surface area. As a comparison, some rates observed in natural conditions also expressed in terms of  $\text{mg. CO}_2 / 100 \text{ cm.}^2 / \text{hour}$  include apple at 20, corn at 10, loblolly pine at 14.3, and tomato at 16.8 (20, p. 250).

### Dry Weight Increase with Seedling Development

In the disease-free environment of the growth chamber where mineral nutrients presumably were not limiting on growth, the dry weight increment should provide a measure of net photosynthesis by seedlings of the two sources under the growth chamber conditions of 1100 foot-candles of light. Data are presented in Table 11 (Appendix) and also plotted in Figure 5.

For the entire 100 day period there appears to be little difference in total growth between the two sources. Distribution of growth between roots and tops of seedlings of the two sources was generally quite similar. The ratio of root to top weight did appear greater for 100-day-old Montana seedlings when compared to 100-day-old Vancouver Island seedlings.

### Discussion

Seedlings of the two seed sources show the same rate of photosynthetic decline at early age although the actual rates (dry weight basis) at ages 15, 25, and 35 days for plants of the Montana source are significantly lower than for those of Vancouver Island. Correction for respiratory  $\text{CO}_2$  would not change the general picture as respiration rate of the seedlings also declines during this period, though to a somewhat lesser extent for seedlings of the Vancouver Island source (Figure 11). Beyond 50 days of age, seedlings of the two sources show no significant difference in photosynthetic rate under the conditions of measurement. Measurement of net photosynthesis as dry weight increase is in good agreement with this result since seedlings of the two sources are found to grow at about the same rate.

The decline in photosynthetic rate of young Douglas-fir seedlings between the ages of 15 and 35 days is very marked when expressed on a dry weight basis, but regardless of the base it appears quite rapid. The decline is apparently much more rapid than the decrease in rate observed for young loblolly pine (7).

The results of  $\text{CO}_2$  measurements indicate that the changes are largely confined to the cotyledons and are little influenced by the

newly developing needles. Analyses of chlorophyll within the cotyledons at 15 and 35 days of age gave no indication that changes in quantity or composition of the chlorophylls are associated with the decreasing rate observed.

The decline in average chlorophyll content of the seedling foliage from 15 to 35 days of age is somewhat misleading. The high chlorophyll content at 15 days is essentially an analysis of only cotyledons since the new needles are not yet in evidence. At 25 and 35 days the newly developing yellow-green needles exert a diluting effect on the total foliage chlorophyll value resulting in the lower figures. The new needles, like those on the new shoot growth of Douglas-fir under natural conditions, rapidly increase in chlorophyll and in 2-3 weeks are quite green in color.

The ecological significance of the contribution by the cotyledons to successful seedling establishment is difficult to assess. It may be noticed from Table 11 (Appendix) that seedling dry weight approximately doubles between 15 and 25 days of age, i. e. the time of maximum cotyledon activity. Photosynthesis by the cotyledons of Lotus corniculatus has been pointed out as a very significant determinant in the ultimate size which the plant attains (42).

## II. Temperature and Apparent Photosynthesis

### Introduction

The classic case of intraspecific temperature adaption for photosynthesis is that of the low- and high-temperature strains of algae. For example, two strains of Chlorella have been found to differ by 7-8° C in their temperature optima for photosynthesis (44). Although apparent photosynthesis is a complex of several processes, all probably affected slightly differently by temperature, their integration provides an interesting subject in a comparison of intraspecific variation.

Under conditions of normal atmospheric CO<sub>2</sub> concentration, a low temperature response by the photosynthetic reaction can be expected since CO<sub>2</sub> is limiting (30, p. 104). Nevertheless, some studies have shown a general correlation of habitat temperature and maximum apparent photosynthesis. For Solidago virgaurea from an alpine area, apparent photosynthesis reached a temperature optimum 4-5° C lower than that of plants from a coastal and an inland source regardless of preconditioning. Though more variable, the inland plants tended toward a higher temperature optimum than plants from coastal climates (4). In this experiment the alpine



plants were not light-saturated while the other plants were. The experiments have apparently been repeated using higher light intensities (5). Plants of a mid-Sierran race of Mimulus cardinalis measured under light-saturated conditions reach maximum rates of photosynthesis at 30° C while 35° C is optimum for plants of a coastal race (21). Later measurements on a second low elevation source showed maximum photosynthesis at 30° C, however (31). Picea excelsa growing at an elevation of 600 meters had a temperature optimum for photosynthesis at 18-19° C while members of the same species sampled at 1340 meters had an optimum at 15-16° C when measured under 30,000 lux illumination (35, p. 540).

Though there was some indication that the photosynthetic rate vs. temperature curve for sun needles peaked at slightly lower temperature than shade needles, data showing the opposite trend have also been obtained (49, p. 164). The light conditions during growth have been found to influence the optimum temperature for photosynthesis unequally for two ecotypes of Solidago (5).

#### Materials and Methods

A saturating light intensity of 5000 foot-candles was provided while photosynthetic rates were measured at each 5° C interval from

10° C to above 40° C. Plants were taken from the 20° C growth chamber and their tops were placed in the cuvette previously brought to the selected temperature. An extensive number of tests showed 20 minutes was adequate for adjustment to a new moderate temperature, i. e. there was no further marked change in photosynthetic rate. For temperatures above 30° C, however, where there was a detrimental effect of length of exposure, 20 minutes was set as the standardized exposure prior to measurement. In determining the temperature compensation point for photosynthesis, plants were placed in the cuvette and the temperature adjusted until there was no net CO<sub>2</sub> exchange for a period of several minutes. Damage occurring to the plants during measurement makes this a rather inexact determination.

Two plants per measurement were used in the case of 35-day-old plants and one plant per measurement for 65-day-old plants. The data for temperature effects on photosynthetic rates of 35-day-old seedlings are based on ten measurements per temperature point except at 10° C and at the temperature compensation point where five measurements were made. Curves for 65-day-old plants are based on five measurements per temperature point except at 15°, 20° and 25° C for the Montana source and 20° C for the Vancouver Island

source where ten measurements per point were made. Thus curves for the 35-day-old plants are based on 60 measurements (120 seedlings) per source; curves for 65-day-old plants on 40 measurements (40 seedlings) and 50 measurements (50 seedlings) for the Vancouver Island and Montana sources respectively.

No difference in temperature response between Montana seedlings with or without terminal buds was observed and the seedlings were used interchangeably.

In a supplementary study, the apparent photosynthetic rate was measured at 20° C and saturating light intensity for ten 35-day-old seedlings from each of two additional seed sources. These were a second seed lot from Vancouver Island labelled Vancouver 500 feet (elevation) and a lot from the Kootenai National Forest collected at 4000 feet elevation at a location north of Libby, Montana. The rates determined were compared with those of the Vancouver Island and Montana seedlings normally used.

### Results

In terms of average rates at 35 days of age, Vancouver Island seedlings have a rather clear but statistically non-significant optimum at 20° C for both apparent and total photosynthesis (apparent

photosynthesis plus dark respiration, Figures 6, 12 and 13) Montana seedlings at this age show only a slightly higher rate of apparent photosynthesis at 25° C than at 20° C. When the dark CO<sub>2</sub> exchange is added, the higher rate is clearly at 25° C (Figure 6). The rate of apparent photosynthesis by Vancouver Island seedlings is significantly greater than that of Montana seedlings at 20° C and 25° C, but not at the other temperatures tested (Appendix, Table 12). There was no significant difference between rates at 20° and 25° C for seedlings of the Vancouver Island source, but the 20° C rate was significantly greater than the 15° C rate and the 25° C rate greater than the 30° C rate. For Montana seedlings there was no significant difference between rates at 15° C, 20° C and 25° C, but the rate at 10° C was significantly less than that at 20° C and the rate at 30° C was significantly less than that at 25° C. From these statistical comparisons, seedlings of the Montana source appears to have a rather broad optimum. Results are shown in more detail in Table 2.

In terms of average rates at 65 days of age, the optimum for the Vancouver Island seedlings is at 20° C for apparent photosynthesis (Figure 7) but if correction for dark respiration is made, the optimum rate shifts to 25° C. Montana seedlings attain maximum rates at 20° C for both apparent and total photosynthetic rates. The

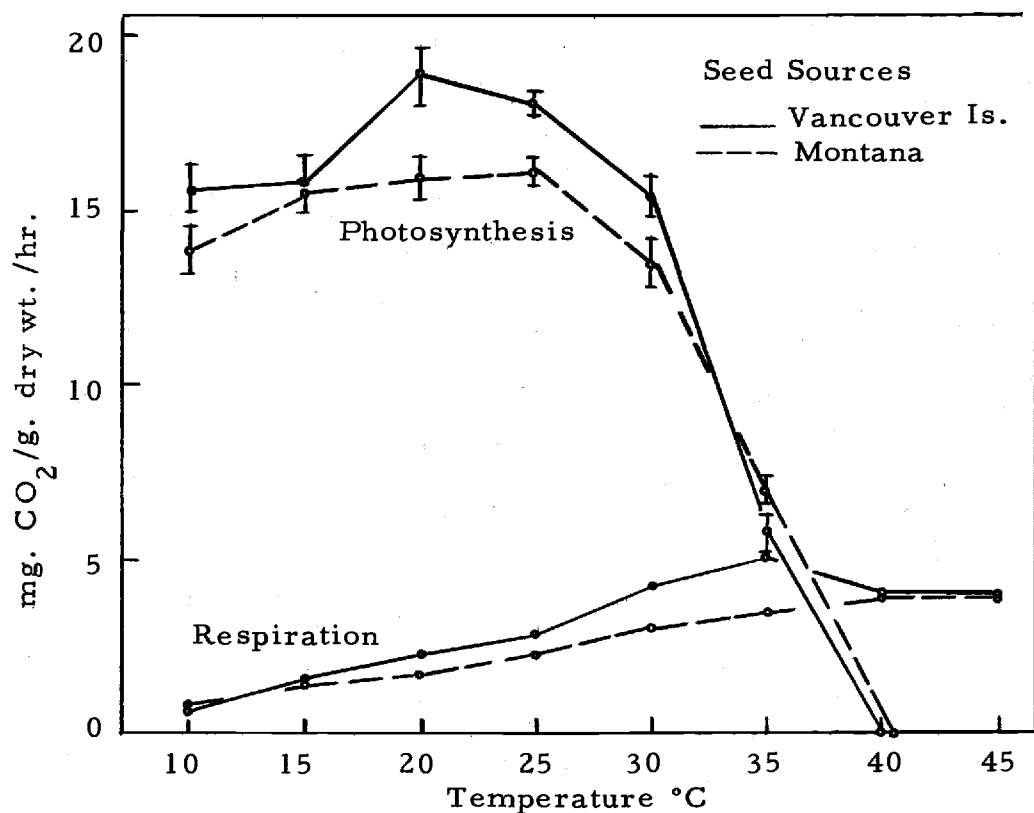


Figure 6. Apparent photosynthesis (needles) and dark respiration (entire tops) with increasing temperature for 35-day-old seedlings. Bars enclose one Standard Error of Means.

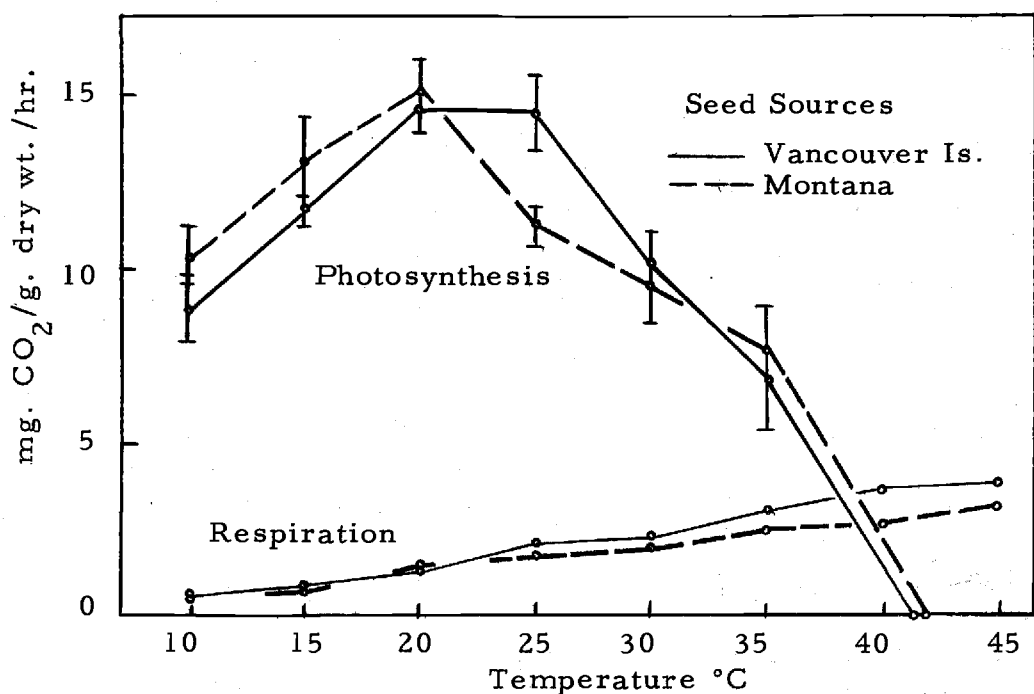


Figure 7. Apparent photosynthesis (needles) and dark respiration (entire tops) with increasing temperature for 65-day-old seedlings. Bars enclose one Standard Error of Means.

Table 2. Statistical analysis of average photosynthetic rates at various temperatures for plants from the same sources.

Age (days)	Temperature Comparison (°C)	Seed Source	
		Vancouver Island	Montana
35	10 vs. 15	--	--
	10 vs. 20	*	*
	15 vs. 20	*	--
	20 vs. 25	--	--
	30 vs. 20	*	--
	30 vs. 25	**	**
	35 vs. 30	**	**
65	10 vs. 15	*	--
	10 vs. 20	**	**
	25 vs. 20	--	**
	30 vs. 20	**	**
	30 vs. 25	*	--
	35 vs. 30	-- (10% level)	--
--	non significant		
*	mean significantly lower at the 95% confidence level		
**	mean significantly lower at the 99% confidence level		

optimum temperatures for seedlings from the two sources are thus reversed from those found at 35 days of age.

There is no statistically significant difference between photosynthetic rates at 15°, 20° and 25° C for 65-day old Vancouver Island seedlings but the rates at 10° C and 30° C are significantly less than that at 20° C (Table 5). While 15° C and 20° C rates are not significantly different for the Montana seedlings, the rate at 25° C is

significantly lower than the 20° C rate. At 10° C the rate was less than the 20° C rate but not the 15° C rate. The photosynthetic rates of seedlings from the two sources differ significantly only at 25° C where seedlings from Vancouver Island are higher.

The temperature compensation point, or temperature at which the net CO<sub>2</sub> exchange was zero, did not differ significantly for seedlings of the two sources (Appendix, Table 12). There was evidence for slightly increased tolerance to temperature with age as seen from the higher values for the temperature compensation point at 65-days as compared to 35 days of age. This difference was significant in the case of Vancouver Island seedlings and highly significant for the Montana seedlings.

The average photosynthetic rate determined for seedlings of the 35-day-old Vancouver 500-foot source, 21.9 mg. CO<sub>2</sub>/g. dry weight needles/hour, was significantly higher than the regular Vancouver Island source. The rate was also significantly higher than for seedlings of the Kootenai source and the regular Montana source. The Kootenai seedlings maintained a significantly higher rate than the regular Montana source seedlings, but there was no difference between the photosynthetic rate of the regular Vancouver source and

the Kootenai seedlings. The photosynthetic rate of the Kootenai seedlings averaged 17.4 mg. CO<sub>2</sub>/g. dry weight needles/hour.

### Discussion

Measurements of the temperature response of photosynthesis made at less than saturating light intensities may lead to an under-estimation of the temperature at which maximum rates are reached (38, Figs. 28.6 to 28.8). Though often satisfactory for comparative purposes, in cases where plants with different requirements for light saturation are compared, such as alpine versus inland and coastal sources of Solidago (4), it is possible that misleading results may be obtained.

Another everpresent and complicating factor is the calculation of total photosynthesis. For three different plant species, one has been found to respire more intensely in light than dark and the other two less (27). Hence, the CO<sub>2</sub> evolution in light and dark seems to be a characteristic of the individual species. Arbitrarily in the present study the CO<sub>2</sub> of apparent photosynthesis and that of dark respiration were added as a measure of total photosynthesis.

If one uses statistics to determine the temperature optima for photosynthesis of these seedlings a very broad range is found,



e. g.  $15^{\circ}$  to  $25^{\circ}$  C. This result may be partly attributed to the variability found in the sample measured. Examination of the data for average rates found (Table 12, Appendix), discloses that  $20^{\circ}$  C or  $25^{\circ}$  C produces the maximum total photosynthetic rate. This temperature range is near or slightly lower than that found for many field plants.

Photosynthesis for 35-day-old Douglas-fir reached a maximum rate at  $20^{\circ}$  C for seedlings of Vancouver Island and at  $25^{\circ}$  C for Montana seedlings, although differences between  $20^{\circ}$  C and  $25^{\circ}$  C were slight in both cases. A plot of photosynthetic rate and temperature data for Vancouver Island seedlings at 65 days of age produced about the same shape curve as for 35-day-old seedlings but with the highest rates occurring at  $25^{\circ}$  C. For 65-day-old Montana seedlings, however, the data showed a rather striking shift compared to the curve for 35-day-old seedlings as the rate at  $20^{\circ}$  C compared to  $25^{\circ}$  C was significantly higher. The physiological and ecological significance of this shift is unknown but it seems very interesting for future investigations.

The Vancouver 500-foot and Kootenai source seedlings maintain the same relationship to each other as the regular Vancouver Island and Montana seedlings; that is, the coastal seedlings have a higher

photosynthetic rate. It is interesting to note that the photosynthetic rate of seedlings of Vancouver 500-feet is significantly higher than that of Vancouver Island seedlings, and that the rate of Kootenai seedlings is significantly higher than that of Montana seedlings.

However, the photosynthetic rates of the Kootenai and the Vancouver Island seedlings are not significantly different. Thus it appears that seedlings from areas in comparatively close proximity may in certain cases differ more than those from widely separated locales.

### III. Apparent Photosynthesis at Different Light Intensities

#### Introduction

Such factors as CO<sub>2</sub> concentration, mineral nutrition and moisture supply are known to influence photosynthetic rate. Two additional considerations are encountered when studying the effect of light intensity--self-shading and the morphological adaption of the needles to the conditions under which they developed.

Light saturation for trees or other tall, large-crowned plants where much self-shading occurs is usually 10,000 foot-candles or greater. For individual leaves, low plants or small seedlings on the other hand, light of one-third this intensity suffices to saturate the photosynthetic process. For example, two-year-old loblolly pine seedlings are not light saturated at 9300 foot-candles although individual needles and 16-week-old seedlings require only about 3000 foot-candles for saturation (7, p. 200).

Leaves of shade plants in the classical conception are of loose structure with a single layer of palisade parenchyma cells. In contrast, leaves of sun plants are usually more compact and have a thicker or several-celled layer of palisade parenchyma. Characteristically, shade developed plants require less light to reach

compensation and are light saturated at lower light intensities than sun plants. Rates of  $\text{CO}_2$  fixation are somewhat greater for shade-developed plants at light intensities below saturation. However, if light intensities are increased above saturation for the shade plants, sun plants are often found capable of photosynthetic rates nearly twice that of shade plants (38, p. 989).

For young seedlings of Pinus resinosa and Pinus strobus developed in 100, 30, 5 and 1.8 per cent of full sunlight, the highest photosynthetic rates at low light were found in the most shaded plants. However, at higher light intensities the maximum rates of shade plants remained higher than for sun plants (9). No marked change could be observed in needle anatomy for the seedlings developed under the above treatments. Shade needles of Abies balsamea and Picea glauca show the characteristically lower rates at high intensity light but also show lower rates at low intensities than do sun needles (13, p. 33). Thus, all types of deviations from the classical picture have been found for conifers. Pinus taeda seedlings developed 16 weeks under two treatments--full sun and 30 per cent of full sun--showed no significant difference in photosynthetic rates at 500 through 8500 foot-candles intensity when compared on the basis of mg.  $\text{CO}_2$  uptake per gram foliage (6).

Despite the many variations noted, in making comparisons between potential conifer ecotypes for response to light intensity it would seem necessary to provide for development of seedlings under identical light conditions.

### Methods

Light intensity was changed by interposition of various numbers of black screens of different mesh sizes accompanied by small changes in the lamp to plant distance. Measurement of light intensity was made with the sensing element held at approximately mid-crown of the seedlings. Only a small proportion of the radiation received by the plant was found to be reflection from the dark copper walls of the cuvette.

Seedlings were given 15 minutes to adjust to each new light intensity before a rate measurement was begun. Beginning at 200 foot-candles intensity, successively higher intensities were applied while measurements were made at 20°C. Though some investigators have used successive light intensities in the order high to low and also in randomized order, a progression from low to high seems preferable. Chlorophyll breakdown, other radiation effects and/or the effect of slow translocation of photosynthate affecting subsequent rate measurements would almost certainly be minimized as

compared to the reverse case. These precautions aside, later experiments have shown only a 6 per cent decrease in photosynthetic rate occurs in 5 hours at 5000 foot-candles.

Five individual 65-day-old seedlings and five pairs of 35-day-old seedlings were measured over the range 200 to 6000 foot-candles for each source. The same number, though not the identical seedlings, were measured to determine the light compensation point. For the latter measurement, the light intensity was adjusted to the point where less than one ppm change in  $\text{CO}_2$  concentration occurred in ten minutes or more.

To assist in evaluating the sun or shade character of seedlings grown under growth chamber conditions, comparisons of needle structure were made with seedlings of the same sources previously grown out-of-doors in full sun except for the early stages when strips of lath gave alternating conditions of sun and shade. Needles were taken from seedlings at two different ages, 10 micron cross-sections made from the central one-third of the needles, and the internal structure evaluated.

## Results

Examination of the needle sections for vertical length and number of the palisade parenchyma cells revealed much variability between sources and between the outdoor versus growth chamber treatments. As a means of characterizing the needles, the percentage of inter-cellular space was measured by projecting a transparency of the needle cross-section upon a grid and counting the squares occupied and unoccupied by cells. The results indicate a slightly less compact needle structure in the case of growth chamber plants, but the difference is not large and a strong approach to a sun needle type structure is suggested (Table 3). Though not always recognized, it seems likely that a continuous gradient probably exists between a sun and a shade type of needle.

Table 3. Percentage of intercellular space in needle cross-sections of the two seed sources grown under differing light conditions.

Pretreatment	Seed Source	
	Vancouver Island	Montana
1100 foot-candles, 35 days old	11.2	13.6
1100 foot-candles, 45 days old	20.3	21.1
Out-of-doors, 45 days old	19.2	15.9

The photosynthetic responses of 35-day-old and 65-day-old seedlings at the higher light intensities were quite similar (Figures 8

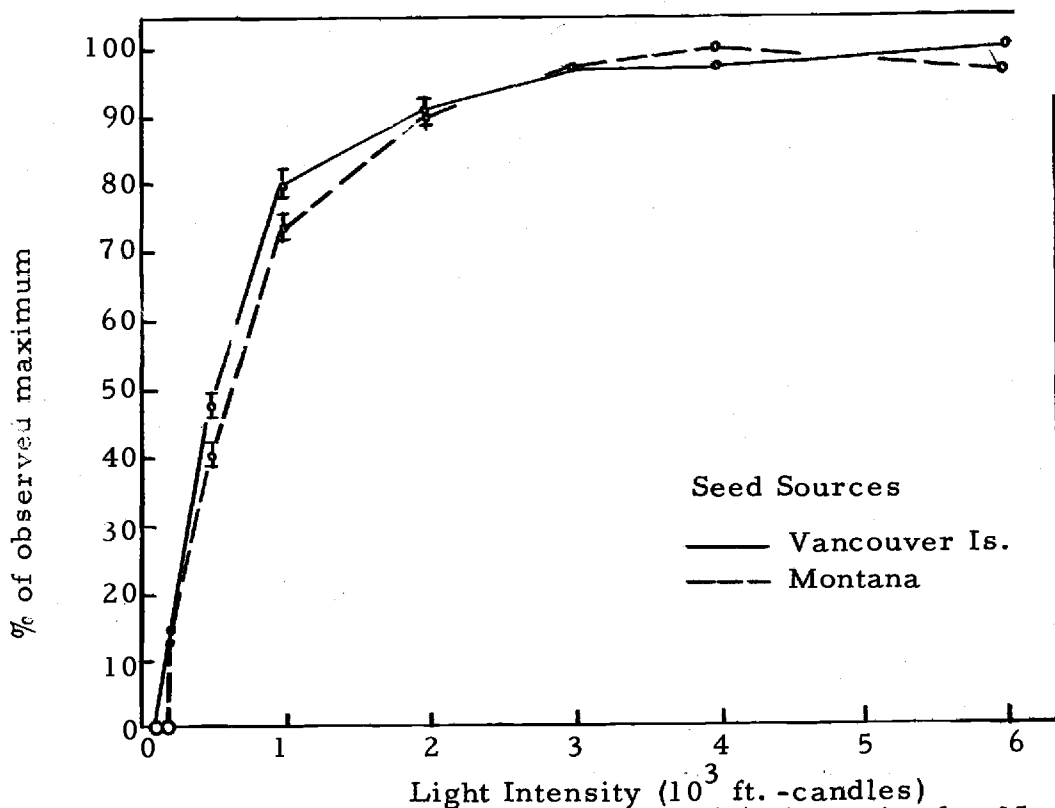


Figure 8. Relative photosynthetic rate with light intensity for 35-day-old seedlings. Bars enclose one Standard Error of the Means.

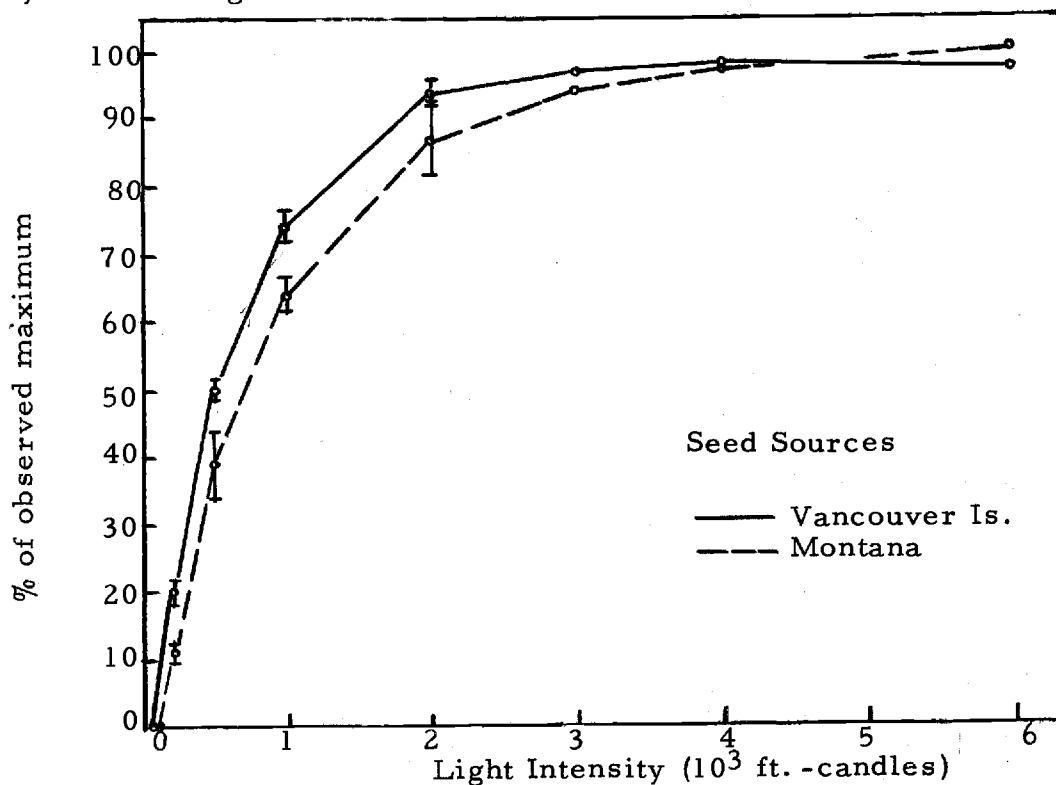


Figure 9. Relative photosynthetic rate with light intensity for 65-day-old seedlings. Bars enclose one Standard Error of the Means.



and 9). For seedlings of both ages and sources, the rate at 3000 foot-candles is nearly 95 per cent of the maximum observed. However, at the lower intensities the photosynthetic response of the Montana source seedlings to corresponding light intensities is less than for Vancouver Island seedlings. The comparative percentage rates for 35-day-old seedlings of the sources are significantly different at 500 foot-candles and differ at 1000 foot-candles at the 1 in 10 confidence level. At 65 days of age, seedlings of the two sources differ significantly at 200 and 1000 foot-candles and at 500 foot-candles at the 1 in 10 confidence level.

A statistical comparison of the percentage rates at the intensities 200, 500, 1000, 2000 and 3000 foot-candles shows that the increase between each interval is significant for seedlings of both sources at both ages with one exception. The rate of 65-day-old Montana seedlings at 3000 foot-candles was not found significantly higher than at 2000 foot-candles intensity.

If the apparent photosynthetic rate expressed in milligrams of  $\text{CO}_2$  per gram dry weight foliage per hour is plotted against light intensity, the same interpretation of the data still applies (Figure 10). The maximum photosynthetic rates at saturation intensity differ, as

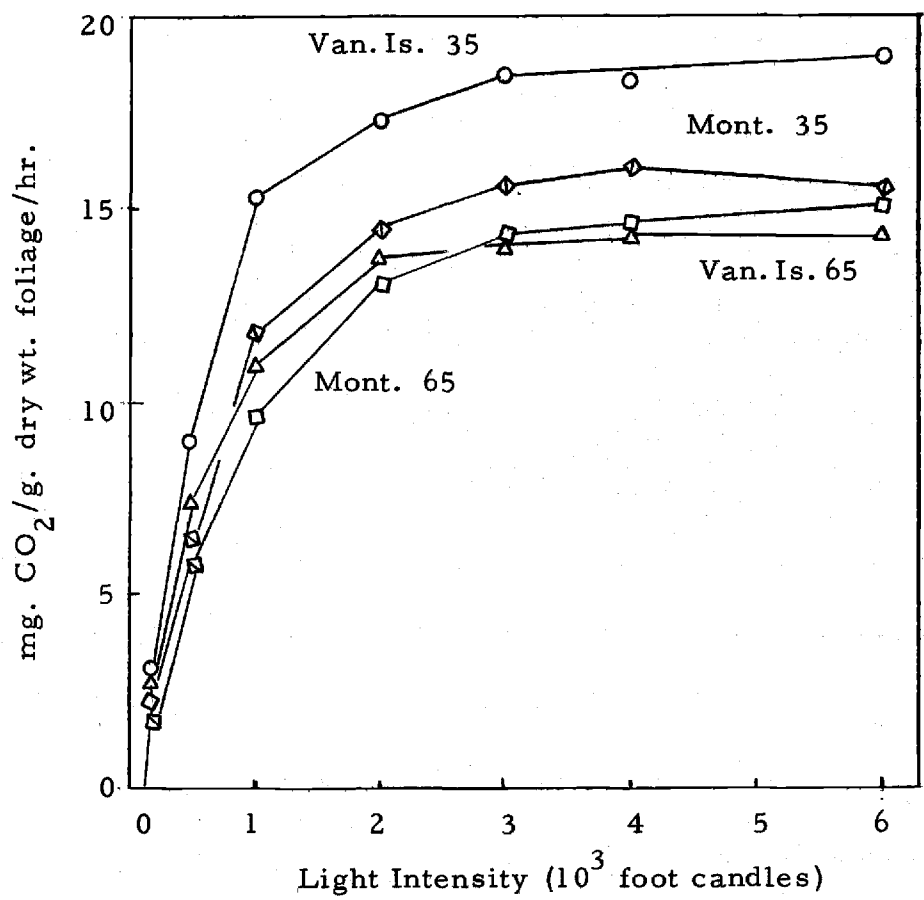


Figure 10. Photosynthetic rate with increasing light intensity for seedlings of the two sources at two ages.

shown previously, being significantly higher for Vancouver Island than for Montana seedlings at 35 days of age (Appendix, Table 12).

The light intensity required at 20° C to bring the seedling tops to the compensation point, i. e. no net CO<sub>2</sub> exchange, is significantly lower for Vancouver Island than for Montana seedlings of both ages. At 35 days of age, an average of 102 foot-candles of light brings the tops of Vancouver Island seedlings to the compensation point while 143 are required for the Montana seedlings. At 65 days of age, the respective figures are 89 and 107 foot-candles. While the difference in light intensity required to reach light compensation for 35- as compared to 65-day-old Vancouver Island seedlings is non-significant, the difference between the two ages for Montana seedlings is highly significant.

### Discussion

In comparison with their maximum potential photosynthetic rate at 20° C, for light intensities below 2000 foot-candles the Montana seedlings have lower rates at the corresponding light intensity than do Vancouver Island seedlings (Figures 8 and 9). Provided seedlings of the same age are compared, curves plotted in terms of actual photosynthetic rates show the same pattern as the

percentage curves with the curve for Montana seedlings below that for Vancouver Island seedlings. A slightly higher photosynthetic rate is attained by 65-day-old Montana seedlings above 3000 foot-candles intensity than by Vancouver Island seedlings.

The Montana seedlings were found to have a slower rate of increase in photosynthetic rate with increasing light intensity than Vancouver seedlings. As might be expected from this observation, significantly more light was also required to bring Montana seedlings to the compensation point. Compensation was reached by 65-day-old Montana seedlings at significantly less light than required by 35-day-old seedlings. Explanation for this latter decrease in the light requirement with age may be due to the decreasing respiration rate. The thickening cuticle on the needles and increasing intra-seedling shading would seem to be creating a higher rather than lower light requirement for compensation.

Ecological significance can possibly be attached to the comparative behavior by seedlings of the two sources toward light intensity. Characteristically in the coastal Pacific Northwest, of which Vancouver Island is typical, seedlings may often germinate and grow in early spring under dark, cloudy skies in situations where a rather lush growth of vegetation may already be established.

Hence, a low light requirement for a reasonably high rate of photosynthesis would be a distinct advantage. On the other hand, Douglas-fir in the northern Rocky Mountains of Montana characteristically grows on south and west slopes where ground vegetation is often less dense due to the drier environment, resulting in less shading and probably less selection pressure for a low light requirement.

From a brief examination of the shade or sun character of the seedling needle structure developed under outdoor and under growth chamber conditions, it was tentatively concluded that in both cases the structure tended to be sun-like and did not differ greatly between seedlings of the two sources. Results of the photosynthetic measurements tend to indicate a slightly more sun-like character for the Montana seedling needles since the response to light at low intensities is less than for Vancouver Island seedlings. Other factors could also cause this same type of comparative response, however. That shade needles do occur in the lower crowns of Douglas-fir trees seems indicated by the finding that maximum assimilation intensity for such foliage was 8000-16,000 lux when measured in the laboratory (36).

The light intensity where maximum photosynthetic rate is reached is near 3000 foot-candles, about the same as that found for other forest seedlings of this size (9). The slightly more gradual

**incline of the curves to the saturating level for 65-day-old seedlings compared to 35-day may reflect the beginning of internal shading within the larger seedlings (Figures 8 and 9).**

#### IV. Rate of Respiration with Seedling Age and as Related to Temperature

##### Introduction

An old study of changes in respiratory rate with age of Helianthus plants still seems to be the most complete available (25). Respiration rates expressed in terms of evolution of  $\text{CO}_2$ /unit dry weight/unit time were found to remain high to 22 days and then decline progressively thereafter to death. Respiration expressed on a "living cell" basis was found to follow a similar trend although in one study a decline of respiration rate was found closely correlated with a decline in protein content of the leaves (39, p. 495).

For short exposures, respiration rates are generally found to increase with rise in temperature from  $0^\circ$  to  $40^\circ$  or  $50^\circ \text{C}$ , although in the higher ranges the rate may decline (24, p. 22). At temperatures much above  $30^\circ \text{C}$ , respiration rates commonly decline with the length of time the plant is exposed to the temperature. Hence it is important for comparative purposes that time of exposure at high temperatures be standardized.

The temperature coefficient for the acceleration of respiration with temperature, referred to as  $Q_{10}$  for a  $10^\circ \text{C}$  temperature interval, generally decreases more or less smoothly from low to high

temperatures (24, p. 27). The pattern of decline does not show any consistent change with age of material or with plants from different climates such as intropical versus arctic (18, p. 242). There is some evidence that plants native to cold climates respire more rapidly than those from warm climates, at least at 20° C (18, p. 254).

### Materials and Methods

Tops of intact seedlings from both seed sources were measured for dark respiration rate at 20° C at the same ages for which photosynthesis had been measured. At 35 and 65 days of age rates were also measured at each 5° C temperature point from 10° C to 45° C.

Tops of two seedlings were sealed inside the cuvette and allowed to adjust to the selected temperature for 20 minutes; then the CO<sub>2</sub> evolved was measured over approximately the same CO<sub>2</sub> concentration range as for photosynthesis. At 35 and 65 days of age, five such measurements were made at each temperature for each source. The same number of measurements were made at 20° C for each age for each source. Thus the respiration rate versus age curve is based on 35 measurements (70 seedlings) for each source. The respiration rate versus temperature curve is based on 40 measurements (80 seedlings) per source per age.



## Results

### Changes in Respiration Rate with Age

Plotted as CO<sub>2</sub> evolved per unit of dry weight, both sources show a progressive decline in rate with increasing age (Figure 11 and Table 13, Appendix). The concavity of the curve for the Montana seedlings appears somewhat greater due to the high rate for 35-day-old Vancouver Island seedlings. The divergence in rates between seedlings of the two sources at the 35-day age was the only difference of significant size.

### Changes in Respiration Rate with Temperature

At 35 days of age the individual seedling respiration rates are quite uniform and several interesting results appear (Figure 12 and Table 4). The trend of curves is upward to 35° C at which point the rate for the Vancouver Island seedlings drops. From 20° C to 35° C the rates of Vancouver Island seedlings are significantly higher than those for Montana seedlings (1% confidence level). At 15° C there is no difference between sources and at 10° C the positions are reversed with respiration rate of Montana seedlings significantly higher than those of Vancouver Island.

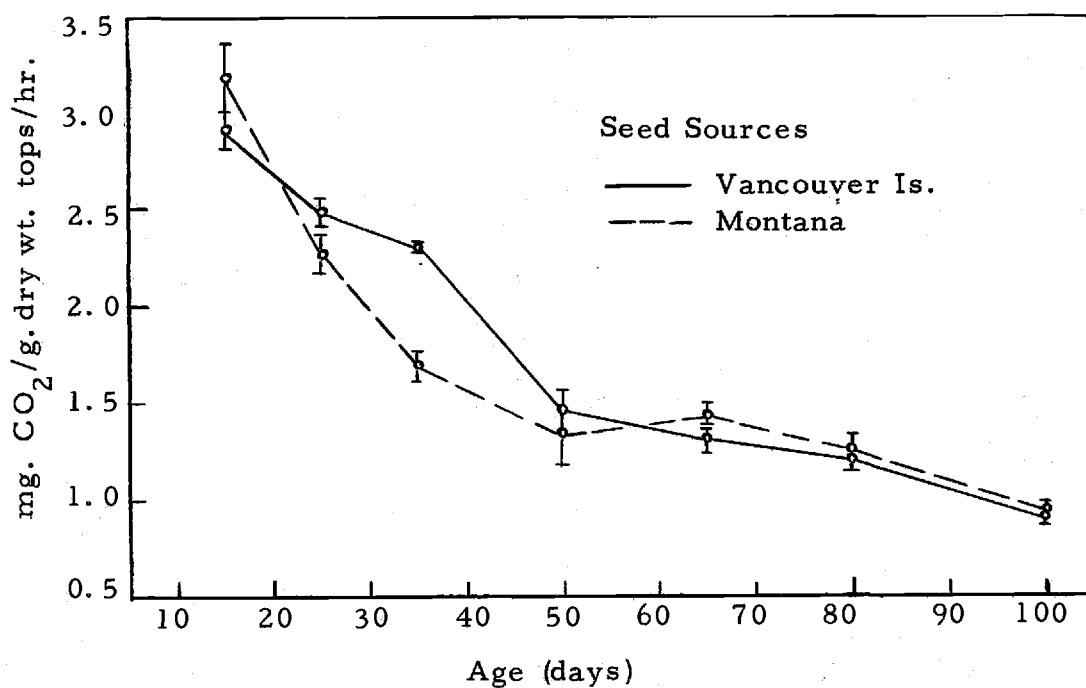


Figure 11. Respiration rate at 20°C with increasing age. Bars enclose one Standard Error of the Means.

Table 4. Respiration rates (mg. CO<sub>2</sub>/g. /hour) of seedling tops with increasing temperature for the two seed sources.

Age (days)	Temperature (°C)	Seed Sources	
		Vancouver Island	Montana
35	10	0.63 ± 0.04	0.84 ± 0.04**
	15	1.58 ± 0.09	1.47 ± 0.08
	20	2.30 ± 0.03**	1.69 ± 0.08
	25	2.85 ± 0.13**	2.23 ± 0.08
	30	4.22 ± 0.09**	3.04 ± 0.08
	35	5.04 ± 0.14**	3.43 ± 0.15
	40	4.52 ± 0.28	4.47 ± 0.13
	45	4.54 ± 0.09	4.45 ± 0.10
65	10	0.61 ± 0.03	0.59 ± 0.17
	15	0.93 ± 0.02*	0.73 ± 0.09
	20	1.31 ± 0.05	1.44 ± 0.06
	25	2.10 ± 0.19	1.77 ± 0.09
	30	2.24 ± 0.12	2.01 ± 0.14
	35	3.02 ± 0.21	2.48 ± 0.25
	40	3.62 ± 0.14**	2.67 ± 0.20
	45	3.77 ± 0.11	3.12 ± 0.29

\* Respiration rate higher (5% confidence level) than that of seedlings of the other source at same temperature.

\*\* Respiration rate higher (1% confidence level) than that of seedlings of the other source at the same temperature.

At 65 days of age there is more variation between seedlings in their respiration rates (Figure 13 and Table 4). Vancouver Island seedlings are again generally higher in respiration rate than Montana seedlings but significantly so only at 15° C and at 40° C (5% and 1% confidence levels respectively).

From Table 14 (Appendix) where  $\Omega_{10}'_s$  are tabulated for the two ages and sources, there appears no strong evidence of any

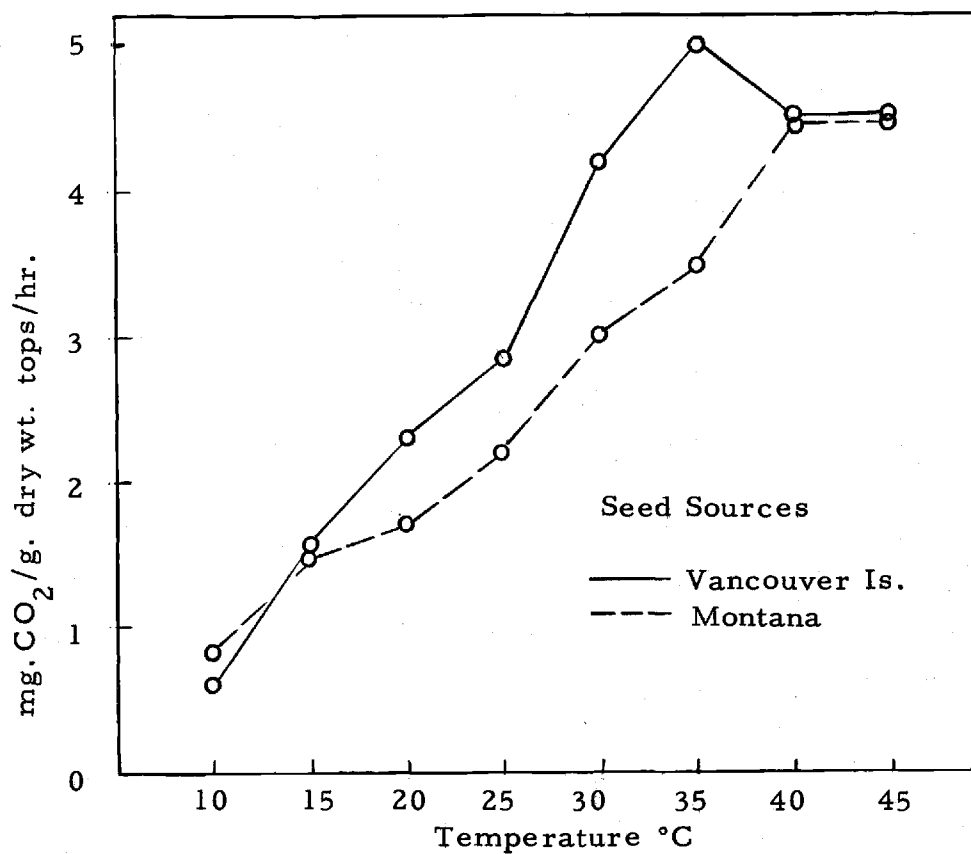


Figure 12. Respiration rates of 35-day-old seedling tops at various temperatures.

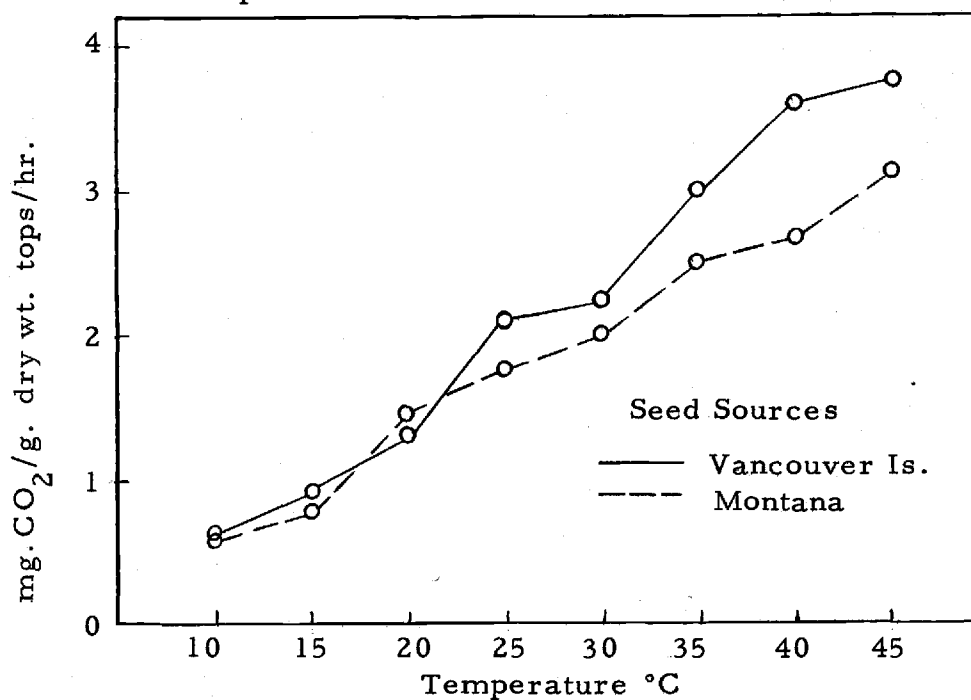


Figure 13. Respiration rates of 65-day-old seedling tops at various temperatures.

difference in temperature response between seedlings of the two sources or any change with age. This interpretation is shown more clearly by the parallel nature of the lines when accumulative  $Q_{10}$  values are plotted against the temperature ranges (Appendix, Figure 17). Examination of the statistical comparison of difference in rates at different temperatures indicates the same conclusion (Table 5).

Table 5. Statistical comparison of respiration rates at various temperatures for Douglas-fir seedlings of the same source and age.

Temperature Comparisons (°C)	Age (days)			
	35 Source		65 Source	
	Vancouver Island	Montana	Vancouver Island	Montana
10 vs. 15	**	**	**	--
15 vs. 20	**	**	**	**
20 vs. 25	**	**	**	*
25 vs. 30	**	**	--	-- <sup>2/</sup>
30 vs. 35	**	*	*	-- <sup>3/</sup>
35 vs. 40	--	**	*	-- <sup>4/</sup>
40 vs. 45	-- <sup>1/</sup>	--	--	--

<sup>1/</sup> 35° C significantly less than 45° C rate. <sup>2/</sup> 25° C significantly less than 35° C rate. <sup>3/</sup> 30° C significantly less than 40° C rate. <sup>4/</sup> 35° C not significantly less than 45° C rate.

-- no significant difference

\* Rates at the lower of the two temperatures significantly less at the 95% confidence level.

\*\* Rates at the lower of the two temperatures significantly less at the 99% confidence level.

### Discussion

Significant ecotypic differences in seedling respiration rates are very easily shown at certain age and temperature combinations. As the seedlings age, any differences between seedlings of the two sources become increasingly more difficult to demonstrate. This observation poses many problems in planning and drawing conclusions in studies of this nature.

Data obtained show the downward trend of respiratory rate with age found by other investigators. Seedlings of the two sources have generally similar respiratory rates although there is a significant difference in the trend at 35 days of age and 20° C where Vancouver Island seedlings have a higher rate (Appendix, Table 13). The drop to the 50-day old rate is steep and the seedlings from two sources maintain about the same rates to 100 days. Since the stem of the seedlings is included in the chamber and contributes something to respiratory CO<sub>2</sub> emission, its weight is included in calculating the respiratory rates. The increase in the proportion of stem with age (Appendix, Table 8) and hence the increase in tissue of low respiration rate may contribute to the gradual drop in respiration rate beyond 50 days of age.

The contention that respiration rates of plants native to cold climates are higher than for those from warm climates receives little support from this study. There is an interesting reversal in relative position between  $10^{\circ}$  and  $20^{\circ}$  C for seedlings of the two sources at 35 days of age (Figure 12), Montana seedlings respiring significantly higher at  $10^{\circ}$  C and significantly lower at  $20^{\circ}$  C than Vancouver Island seedlings. However, at no other temperature or age combination was the Montana seedlings' respiration rate significantly higher than the "warm climate" seedlings. Different results might be obtained at temperatures lower than  $10^{\circ}$  C, however.

The response of respiration rate to temperature at the two ages tested appeared generally similar except toward the extremes. It may be noted that the 35-day-old plants begin to show damage from the heat at  $40^{\circ}$  C as shown by the drop or leveling off in respiration rate, while the 65-day-old seedlings still show no effect at  $45^{\circ}$  C (Figure 13).

## GENERAL DISCUSSION

The ecotype is an ecological or adaptational concept. What constitutes an ecological or ecotypic difference has been variously interpreted and seems largely relative in current thought. Certainly statistics can assist in these interpretations, but nonetheless difficulties present themselves. In this series of investigations several instances of statistically significant differences in photosynthetic and respiratory rates were found for seedlings from a Vancouver Island and a Montana seed source of Douglas-fir. In some instances, however, differences demonstrated at one age and set of conditions are not apparent at another age and the same conditions. Thus two seed sources which would be considered as representing two ecotypes in one instance would go unrecognized in another.

Significant differences in respiration and photosynthetic rate occur mostly in the range of moderate temperature and mostly at the younger ages. The Vancouver Island seedlings maintain a higher photosynthetic or respiratory rate than Montana seedlings at each of the significantly different points except one, Montana seedlings having a higher respiration rate at 10° C. At ages greater than 35 days, the number of cases where any significant difference in photosynthetic



or respiratory rate of the seedlings occurs is few. Perhaps this apparent change to a more similar response pattern as the seedlings age indicates development of greater tolerance to changes in the environment. Young seedlings in a tender vegetative state with a high proportion of meristematic tissue might be expected to show great environmental sensitivity; this may be reflected by the data obtained here.

If within the two environments, coastal and continental, selection takes place most strongly at very early ages, then the use of seedlings as was done in this study may somewhat distort the true picture of the population responses. A certain proportion of these seedlings measured may have shown responses which would lead to their demise in their natural environment.

Lack of significant differences in rate of photosynthesis at  $20^{\circ}\text{C}$  for older seedlings of the two sources is indirectly shown in the dry weight increment curves (Figure 5). The weight increases are almost identical up to three months of age at which time the plants probably lack growing space in the pots. If these two sources are representative, no clear advantage in dry weight growth rate for coastal versus interior seedlings can be shown using young seedlings in active growth at near optimum growth conditions.

One might be misled, however, if seedlings at only very young ages were used. Over a longer period where the effects of dormancy would be operating, differences between sources might appear.

Differences in yield by varieties of annual plants have in general been explainable by differences in "effective leaf area," i. e. differences in phylotaxy, longevity of leaves, rate of chlorophyll loss or accessory organs (1)(11)(50). The characteristic retention of needles by conifers would seem to make them particularly interesting subjects for this type of yield study.

Douglas-fir has long been considered by the forester to be an "intolerant" or light-demanding species. The light levels required for saturation for seedlings of this size, however, could not be considered unusually high. Since the size of these seedlings approximates one-year-old nursery seedlings and also since the  $\text{CO}_2$  concentration levels used are at least as high as for natural conditions, 3000 foot-candles of light intensity can probably be considered as saturating for young Douglas-fir seedlings in the field.

Perhaps the strongest basis for considering representatives of these two seed sources as ecotypes is the comparative photosynthetic response of the seedlings to various light intensities. The light compensation point was higher and the light response curve for the

Montana source seedlings lower than seedlings from Vancouver Island throughout. Such a response may have a physiological basis or may possibly be due to an anatomical difference in the needles of the Montana seedlings. This point was not investigated.

If the rates of photosynthesis obtained under the conditions used here are adjusted to 300 ppm where several other investigators have worked, the average rate for light-saturated apparent photosynthesis by Vancouver Island seedlings would be about 12.5 mg. CO<sub>2</sub>/g. needle dry weight/hour at the 65-day age. This compares with 19 mg. CO<sub>2</sub>/g. needle dry weight/hour reported for Choctawatchee sandpine (Pinus clausa), and 14 mg. CO<sub>2</sub>/g. needle dry weight/hour reported for loblolly pine under what were probably near optimum conditions (33)(26). At the 15-day age where the rate is measured for cotyledons, the average rate of total photosynthesis for seedlings of the two sources adjusted to 300 ppm is 33.9 mg. CO<sub>2</sub>/g. needle dry weight/hour, much higher than any rate reported for conifers.

Statistically significant differences in the photosynthetic responses of seedlings of coastal and interior sources raise speculation as to whether a graded or clinal series of such response may exist in seedlings sampled across the intervening area.

However, a cline is rightfully recognized only after analysis of extensive samples from many localities. For species with obligate cross-pollination, especially where pollen may be carried for many miles, continuous variation is likely to be shown (45, p. 47). The variation in behavior from seedling to seedling will always plague those who work with wild plants, but of course the "flexibility" produced in the species by this variation helps to insure its survival. As pointed out by Clausen, Keck and Heisey, "natural selection is far from a rigid process. Many compromises are tolerated, and fitness of a particular plant depends not so much upon a single character as upon a combination of several. Such a compensatory system of adaption is flexible, for a relative lack of fitness in one character may be compensated by special suitability in another" (14, p. 108).

In some instances one may reduce the variability encountered by propagating certain selected representative individuals vegetatively, by narrowing seed collection areas, by making seed collections from individual trees or by controlling pollination. Depending upon the goal of the study, however, the obvious limitation is that as one narrows his collection, one also narrows the scope of applicability of the results obtained. The balance between

breadth of the sample and the variation which can be tolerated is a very real problem in studies of this type.

## SUMMARY

Douglas-fir seedlings from two seed sources, southern Vancouver Island, B. C. and western Montana, were investigated for their photosynthetic and respiratory response to various temperatures and light intensities. In addition, the changes in photosynthetic and respiratory rates with seedling development were followed from the cotyledon stage to 100 days of age.

Following a steep decline in photosynthetic rate at the early seedling stages, the photosynthetic rate was fairly constant with age. Temperatures of 20° C or 25° C were found to give maximum photosynthetic rates for seedlings of both sources under conditions of saturating light intensity. At the near optimum temperature of 20°, Montana seedlings were found to have a higher light requirement to attain the same degree of photosynthetic response as Vancouver Island seedlings. Respiration rates were generally higher for seedlings from Vancouver Island.

Statistically significant differences between seedlings of the two sources were found for both temperature and light intensity, and they can apparently be considered as "ecotypes" with respect to photosynthetic and respiratory responses.

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**APPENDIX**

Table 6. Composition of the nutrient solution used in growing Douglas-fir seedlings in "controlled environment" chambers at 19-9°C day-night temperature. Media was washed stream-gravel of approximately 3 mm. diameter. After 65 days of daily nutrient solution application plus one tap water flushing each 7 to 10 days, samples of a slurry of the media tested at pH 5.8-6.1.

<u>0.1 Molar Solution</u>	<u>c. c./liter</u>
$\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$	12.5
$\text{KNO}_3$	12.5
$\text{NH}_4\text{Cl}$	0.5
$\text{NaH}_2\text{PO}_4 \cdot \text{H}_2\text{O}$	2.5
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	5.0
$\text{Fe-DTPA}^{1/}$ (0.7% solution)	1.0
A-5 Minor element solution <sup>2/</sup>	0.25

<sup>1/</sup> Fe-DTPA is the iron salt of Diethylenetriaminepentacetic acid (marketed as Sequestrene 330, Giegy Chemical Co.).

<sup>2/</sup> Composition of A-5 nutrient solution is given in reference 20, p. 37.

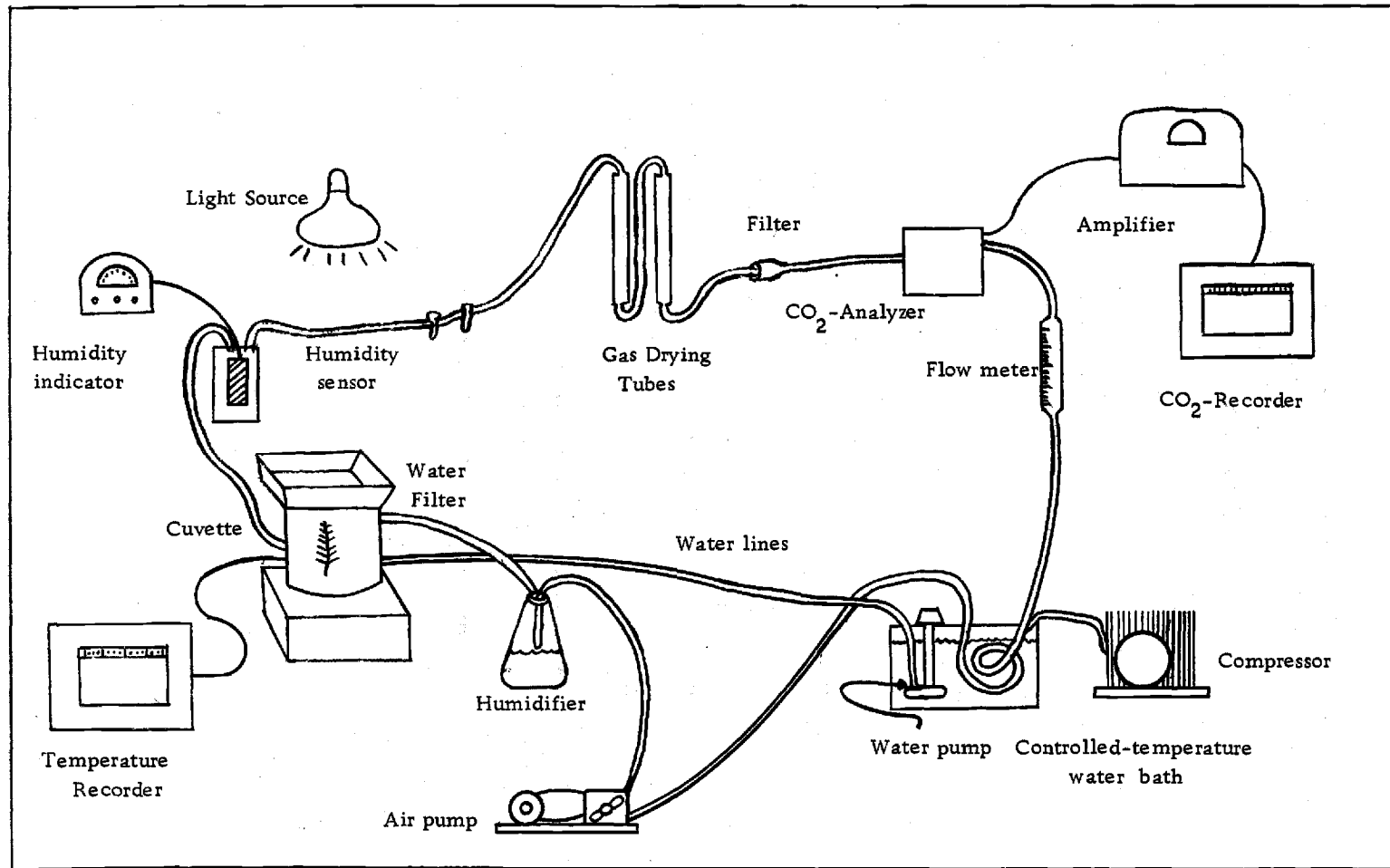


Figure 14. Diagrammatic representation of the experimental apparatus used for the photosynthetic measurements.

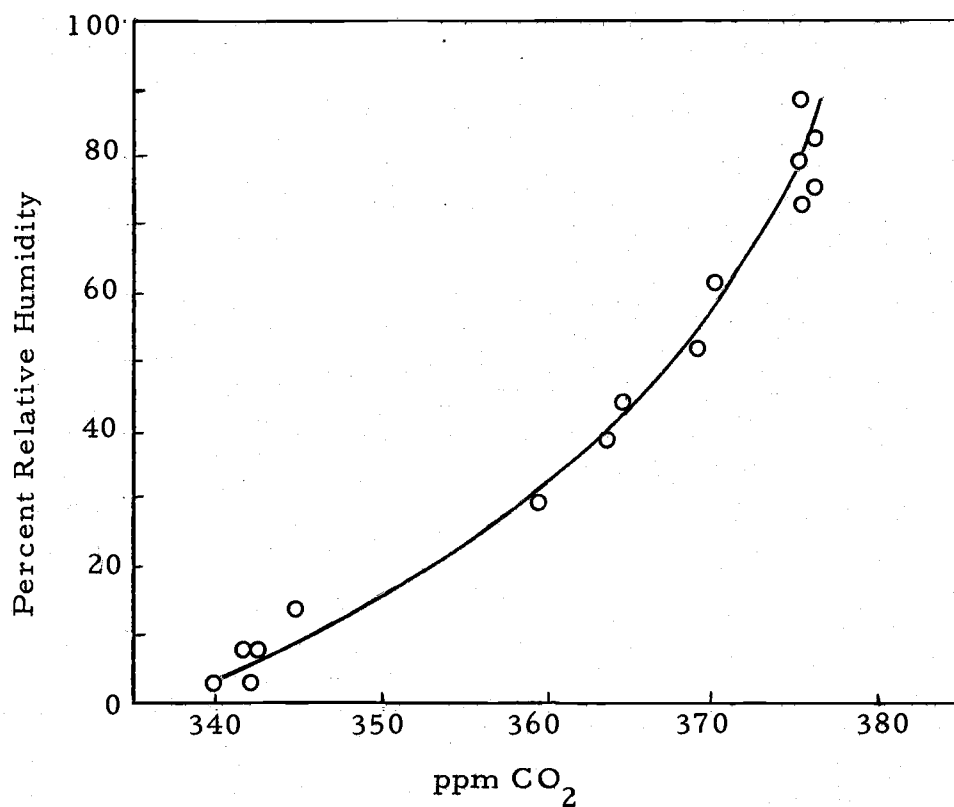


Figure 15. Response of CO<sub>2</sub>-analyzer to changing relative humidities expressed in terms of apparent CO<sub>2</sub> response. Relative humidity measured at 73° F.



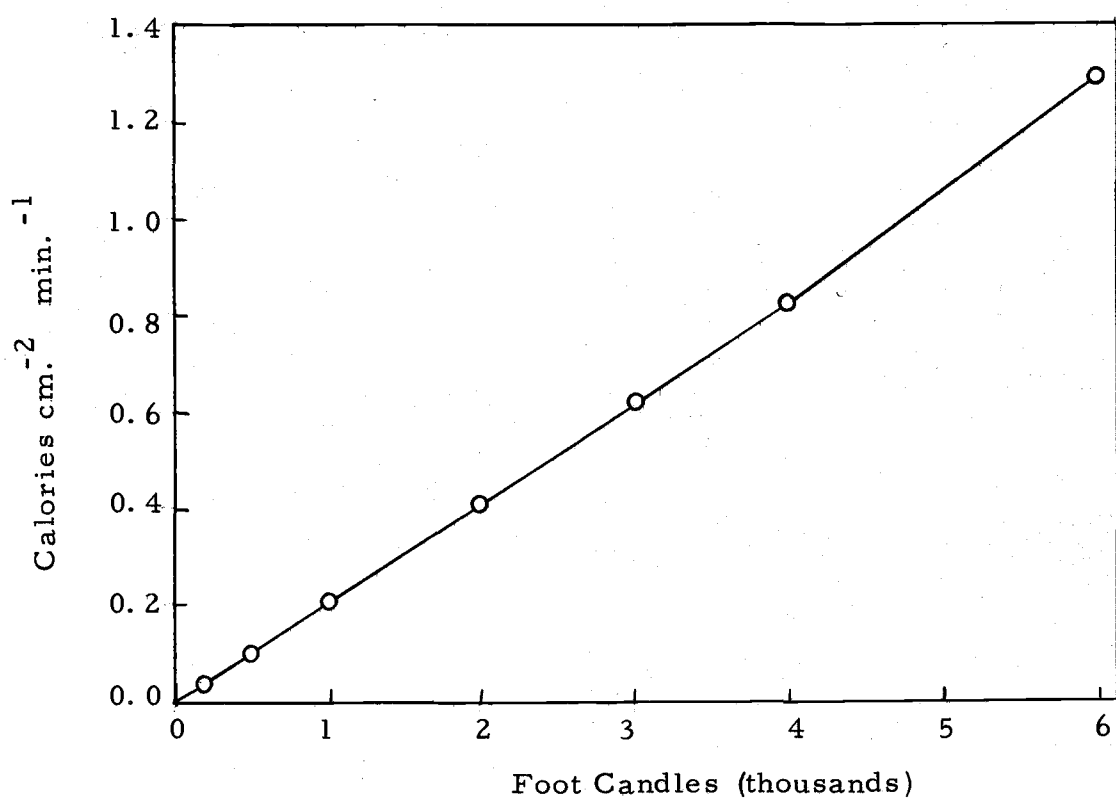


Figure 16. Relation of energy measured by Thornwaite Model REDC net radiometer to foot candles measured by Model 756 (quartz filter) Weston Illumination meter in the photosynthetic chamber. Radiation from 1200 watt Hi Spot incandescent lamp passed through 2.5 mm. of glass and 4.5 cm. of water before measurement.

Table 7. Covariance analysis of the effect of CO<sub>2</sub> concentration on photosynthetic rate of seedlings of the two sources.

Sample	n	SS <sub>x</sub>	SP	SS <sub>y</sub>	b	Regress. SS	df	Resid. SS	df
Van.	5	10,663	3,212	2,029	0.301	967	1	1,061	3
Mont.	5	10,663	3,545	1,061	0.332	1,179	1	375	3
Sum						2,146	2	1,436	6
Pooled		21,327	6,757			2,141	1		
						5.21	1		

$F = \frac{5.21/1}{1436/6} = 0.0218$  w/1 and 6 d.f. No significant difference in the regression coefficients (b values).

Table 8. Average per cent of the weight of actively growing seedling tops contributed by the stem with increasing age for two seed sources of Douglas-fir.

Age (days)	Seed Source	
	Vancouver Island (per cent)	Montana (per cent)
35	9.5	7.9
50	8.0	9.4
65	10.4	9.6
80	10.8	11.9
100	12.7	--

**Table 9. Average moisture content<sup>1/</sup> of foliage of Vancouver Island and Montana source seedlings at various ages.**

Age (days)	Vancouver Island		Montana	
	Moisture Content Per Cent	Basis <sup>2/</sup>	Moisture Content Per Cent	Basis <sup>2/</sup>
15	270	(18, 263)	287	(15, 91)
25	252	(26, 249)	241	( 9, 72)
35	260	(29, 148)	243	(11, 79)
50	253	(12, 57)	216	( 7, 47)
65	218	(14, 62)	190	(10, 40)
80	211	(11, 33)	204	( 9, 28)
100	204	(14, 48)	186	(11, 27)

1/ Moisture content is in per cent of dry weight of needles (100° C drying temperature).

2/ Figures indicate the number of determinations and number of plants used therein for determining average moisture content.

**Table 10. Rate of apparent photosynthesis (mg. CO<sub>2</sub>/g. dry needle weight/hour) at 20° C with increasing age.**

Age (days)	Seed Source	
	Vancouver Island	Montana
15	39.7*	35.2
25	26.3*	23.2
35	18.9*	16.0
50	15.4	16.1
65	14.6	15.1
80	13.8	15.6
100	11.8	13.8

\* Rates significantly higher (95 per cent confidence level) than those for seedlings of Montana source.

**Table 11. Average total seedling dry weight (mg.) with increasing age when under growth chamber conditions. The number of seedlings in the average is shown in brackets.**

Age (days)	Seed Source	
	Vancouver Island	Montana
seed	10 (150)	12 (130)
15	8 (454)	12 (153)
25	19 (270)	23 ( 77)
35	33 (148)	37 (111)
50	65 ( 71)	66 ( 72)
65	124 ( 64)	121 ( 57)
80	207 ( 95)	172 ( 50)
100	266 (102)	268 ( 36)

**Table 12. Apparent photosynthesis (mg. CO<sub>2</sub>/g. dry needles/hour) and respiration (mg. CO<sub>2</sub>/g. dry tops/hour) for the two seed sources with increasing temperature.**

Age (days)	Temp. °C	Seed Sources			
		Vancouver Island		Montana	
		Psn.	Resp.	Psn.	Resp.
35	10	15.6	0.6	13.9	0.8
	15	15.8	1.6	15.6	1.5
	20	18.9*	2.3	16.0	1.7
	25	18.1*	2.8	16.1	2.2
	30	15.4	4.2	13.5	3.0
	35	5.7	5.0	7.0	3.5
Compensation Temperature		40.0° ± 0.6		40.7° ± 0.5	
65	10	8.9	0.6	10.4	0.6
	15	11.7	0.9	13.1	0.7
	20	14.6	1.3	15.1	1.4
	25	14.5*	2.1	11.2	1.8
	30	10.1	2.2	9.5	2.0
	35	6.7	3.0	7.1	2.5
Compensation Temperature		42.6° ± 0.5		43.6° ± 0.6	

\* Vancouver seedling photosynthetic rate significantly higher than Montana.

Table 13. Rate of dark respiration at 20° C (mg. CO<sub>2</sub>/g. dry weight/hour) with increasing seedling age. One Standard Error of the Mean given.

Age (days)	Seed Source	
	Vancouver Island	Montana
15	2.90 ± 0.10	3.17 ± 0.19
25	2.48 ± 0.06	2.27 ± 0.10
35	2.30 ± 0.03**	1.69 ± 0.08
50	1.47 ± 0.12	1.34 ± 0.17
65	1.31 ± 0.05	1.44 ± 0.06
80	1.21 ± 0.07	1.26 ± 0.07
100	0.90 ± 0.03	0.94 ± 0.05

\*\* Rate significantly higher than corresponding Montana rate at one per cent confidence level.

Table 14. Calculated Q<sub>10</sub> values for the temperature response to respiration by Vancouver Island and Montana seedlings of two ages.

Temperature Range (°C)	Age (days)			
	35		65	
	Source		Source	
	Vancouver Island	Montana	Vancouver Island	Montana
10-20	3.64	2.01	2.15	2.42
15-25	1.80	1.55	2.27	2.42
20-30	1.84	1.80	1.72	1.40
25-35	1.77	1.52	1.44	1.40
30-40	1.07	1.50	1.61	1.33
35-45	--	--	1.25	1.26

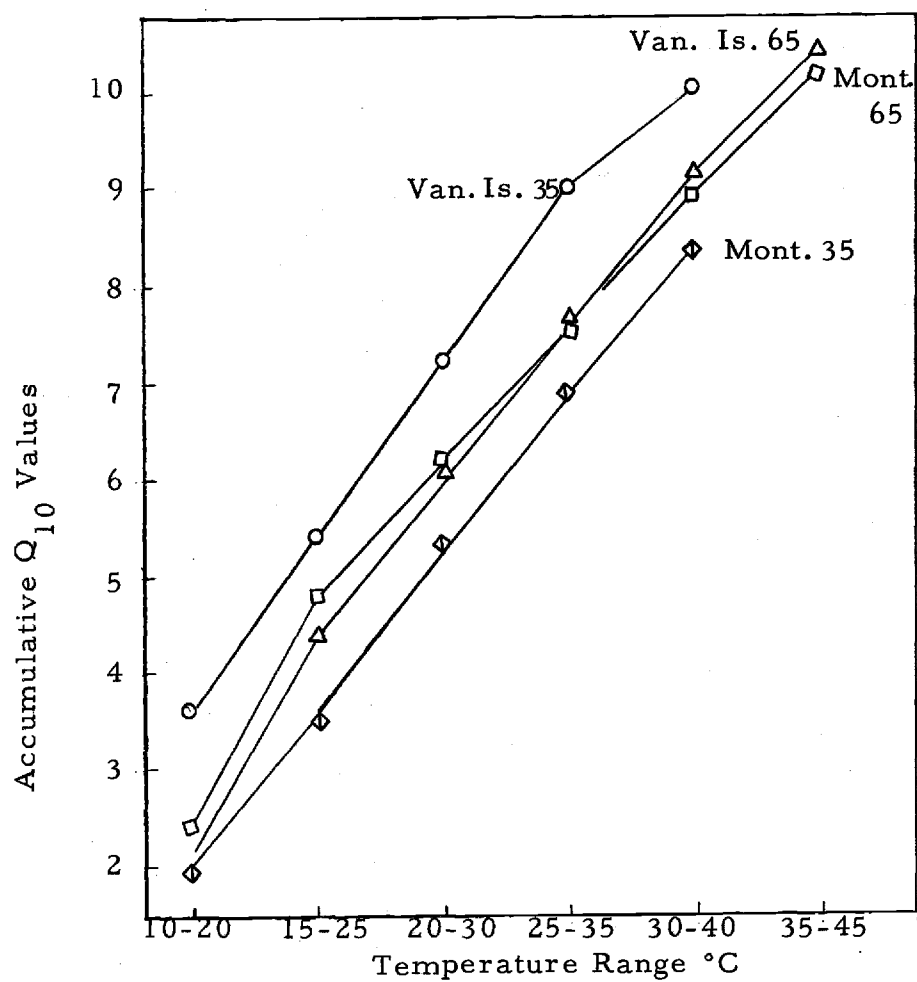


Figure 17.  $Q_{10}$  values for respiration rates plotted as accumulating sums over several temperature intervals. Data shown for seedlings of the two sources at two ages.