Photosynthesis and growth of Douglas-fir seedlings when grown in different environments

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Douglas-fir seedlings from western Montana and western Oregon seed sources were grown in a cool (18°C day - 4°C night) or warm (36°C day - 21°C night) growth chamber. Photosynthetic and respiratory rates were measured at 20°, 27.5°, and 35°C at cotyledon stage (15 to 18 days old), 55 days old, and 100 days old. Needle, stem, and root dry weights were also determined. Photosynthetic rates declined with age, were higher for Oregon than for Montana seedlings, particularly at lower measurement temperatures, were higher for high-temperature-grown than for low-temperature-grown plants, and were lowest at the highest measurement temperature. Each of these factors was modified by the others in its effect on the photosynthetic rates. Respiration rates declined with age, were slightly higher for Montana than for Oregon seedlings, were much higher for the cold-temperature-grown than for the warm-temperature-grown seedlings, and were highest at the highest measurement temperature. When plants from the two growth environments were interchanged, the photosynthetic rates (measured at 27.5°C only) of the seedlings changed to those of the new environment within 10 days. Comparison of seedlings grown at high and low temperatures showed the latter to have lower photosynthetic rates but higher growth rates, probably as a result of the higher proportion of leaf tissue produced by the low-temperature-grown plants.

Introduction

Douglas fir is a species with a large geographic range in western North America. Seedlings of different geographic origins differ in growth even under common environmental conditions (Ching and Bever 1960; Hermann and Lavender 1968; Sorensen 1967; Sweet 1965). Such growth differences could result from inherent differences in seasonal duration of active growth (Irgens-Moller 1958), from differences in CO₂ exchange rates, or from differences in the distribution of assimilate. The purpose of this paper is to examine some of these factors as they relate to seedlings of two sources growing under two different temperatures.

The results were considered from two points of view. First, the effect of seed source, tempera-
ture at which seedlings were grown, temperature at which CO₂ exchange was measured, and age was analyzed to determine if the sources showed differentiation in temperature patterns of photosynthesis and respiration. Second, photosynthetic rates were related to total plant growth and to growth of needles, stems, and roots. This was done to see how photosynthetic rates were related to growth rates.

Campbell and Rediske (1966), testing 1-year-old Douglas-fir seedlings which were the product of controlled crosses within a natural stand of about 200 ac, found significant differences among families and a moderate heritability for photosynthetic efficiency. Such within-stand variation could lead to formation of varieties or ecotypes with different photosynthetic abilities. However, studies on ecotypic variability, even on seedlings from sources as diverse as northern Rocky Mountains and Pacific Northwest coast, have indicated that ecotypic variability in photosynthetic responses is not present or not equally strong under all measurement conditions (Krueger and Ferrell 1965; Zavitkovski 1964; Zavitkovski and Ferrell 1968, 1970). To have a sample of these interactions in the present investigation, age and measurement temperature variables were included.

Temperature was selected for manipulation because it was easy to control with our facilities, it had been shown to affect Douglas-fir seedling growth (Hellmers and Sundahl 1959), and it was known to exert a strong effect on photosynthetic and respiratory responses of many plants both at the time of measurement and when used as a pretreatment (Semikhatova 1960; Simonis 1960).

Materials and Methods

Tests were run on seedlings from western Oregon and western Montana. Oregon seedlings were collected at 700-ft elevation on McDonald Forest of Oregon State University, 10 mi north of Corvallis. About 10 individual mother trees were represented in a bulked collection. Rocky Mountain seeds were collected from three trees at 4300-ft elevation in the foothills of the Garnet Mountains, 30 mi east of Missoula, Montana.

Seedlings were grown in two controlled-environment chambers which differed primarily in the temperature regimes, a 36°C day - 21°C night (called warm environment) and an 18°C day - 4°C night (cool environment). Day temperature was held for 10 h, night temperature for 8 h, and there were 3-h temperature transition periods in the morning and evening. About 1000 ft-c were supplied by a combination of three types of lights: cool white fluorescent, deluxe warm white fluorescent, and incandescent. Photoperiod was 16 h. During the light period, relative humidity was about 70% in the warm conditions and 90% in the cool conditions.

Plants were watered daily until seed coats were shed. Thereafter, seedlings in both environments were watered heavily once a week and given nutrient solution as required the rest of the week. Because of greater moisture loss, plants in the warm environment received three applications of nutrient solution per week compared with two applications per week to plants in the cool environment.

Carbon dioxide exchange rates were determined at three ages: cotyledon stage (cotyledons horizontal, first needles just beginning to emerge), 55 days after planting, and 100 days after planting. The cotyledon stage occurred 15 to 18 days after planting.

Photosynthetic rates at all ages were measured at 5000 ft-c (saturating light intensity) at 20°, 27.5°, and 35°C. In addition, measurements were made at 12.5° and 42.5°C on 55-day-old plants. Respiratory rates were determined in darkness at the same temperature.

Rates of gas exchange for cotyledon stage and 55-day-old plants were measured on pairs of seedlings free from mutual shading. Photosynthetic rate determinations at the 100-day age were usually made on individual seedlings because it was difficult to avoid mutual shading.

Gas exchange determinations were made in a closed system at CO₂ concentrations between 330 and 370 ppm. Temperature in the plant chamber or cuvette was controlled by an overhead, flowing-water filter of about 4 cm depth and a circulating water heat sink in the walls. Volume of the system used in photosynthetic measurements was 2.95 liters; volume of the system used in respiratory measurements was 1.63 liters. Air movement in the cuvette was sufficient to minimize boundary layer resistance, as demonstrated by lack of change of CO₂ uptake with a 50% decrease in air flow rate in the plant chamber. A more complete description of the apparatus is given in Krueger and Ferrell (1965).

Rates were measured after a 20-min equilibration period in the cuvette at the proper temperature. Two consecutive photosynthetic determinations with a maximum duration of 30 min were made on each seedling to check the adequacy of the equilibration period. The average rate was used in subsequent analyses. The only exception was for determinations at 42.5°C. Here, a prolonged decrease in rate began about 45 min after first exposure to the high temperature, so only one measurement was made. Respiratory determinations took considerably longer, so the two halves of a single run were compared to check if the equilibration time had been long enough.

Rates of gas exchange were determined throughout the second half of the 16-h photoperiod. During the day, there was no indication of change in rate for plants from either the warm or cool chamber.

After measurement, the needles were stripped from the seedlings and weighed after drying for 24 h at 100°C. Photosynthetic and respiratory rates were expressed on the basis of milligrams CO₂ exchanged per gram needle dry weight per hour.

Some of the seedlings were also used for further dry weight determinations. At 18, 55, and 100 days from
planted, about 40 plants of each source from each environment were removed and separated into needles, stems, and roots. This material was dried for 24 h at 100°C and weighed.

Two additional tests involved the transfer of plants from one growth environment to the other. Only Oregon seedlings were transferred; no more Montana seeds or seedlings were available. For the photosynthetic and respiratory measurements, the plants were grown to age 45 days in one temperature chamber, then transferred to the other. CO₂ exchange rates were determined at 27.5°C, 10 days after the transfer. For the growth measurements, the seedlings were grown 28 days in one environment, then transferred to the other. Dry weights of needles, stems, and roots were determined at age 55 days.

Analysis

Gas exchange rates were analyzed according to completely random analyses of variance with fixed treatment effects. Treatments were based on variation of source of seed, age at which gas exchange rate was measured, temperature at which seedlings were grown (called “growth temperature”), and temperature at which gas exchange rate was measured (called “measurement temperature”). Ten seedlings or 10 pairs of seedlings were used to determine photosynthetic rates at each treatment level; 5 seedlings or pairs of seedlings were used for respiratory rates.

In both analyses, variances were found to be heterogeneous when evaluated with Bartlett's test. Logarithmic and square-root transformations were tried but did not successfully remove the heterogeneity. In the analysis of photosynthetic rates, the transformations had little effect on heterogeneity or on test statistics. Consequently, untransformed values were used in the analysis.

Respiratory rate, within fairly wide limits, varied exponentially with temperature. This would lead to interactions between measurement temperature and other treatments if untransformed rates were used. In this analysis of respiratory rates, the log transformation eliminated or greatly reduced interactions involving temperature, although it did not eliminate the heterogeneity of variance. Under these circumstances, the log scale was considered best for presentation of the data (Kempthorne 1957; Mather and Jinks 1971, pp. 56-64) and was used here.

Results

Photosynthetic Rates

Seed source, growth temperature, age, and measurement temperature all had highly significant effects on variation in photosynthetic rates (Table 1, Fig. 1). On the average, the Corvallis seedlings absorbed CO₂ at a rate of 14.4 mg/g needle dry weight per hour; Missoula plants photosynthesized at a rate of 13.5 mg CO₂/g needle dry weight per hour. The effect of the

<table>
<thead>
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<th>Source of variation</th>
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<th>Mean squares</th>
<th>Components of variance*</th>
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</thead>
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<td>0.000</td>
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<tr>
<td>A × G × M</td>
<td>4</td>
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<td>0.39</td>
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<td>Error</td>
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*Components given only for the sources of variation which include effect of seed source.
†Calculated F exceeds 5% tabular F.
‡Calculated F exceeds 1% tabular F.
other treatments was greater. Plants from the cool environment assimilated at an average rate of 11.3 mg CO$_2$/g needle dry weight per hour; plants from the warm environment photosynthesized at an average rate of 16.6 mg CO$_2$/g needle dry weight per hour. Average rates at the three temperatures of measurement (20°, 27.5°, and 35°C) were, respectively, 16.0, 15.3, and 10.5 mg CO$_2$/g needle dry weight per hour. Average rates at the three ages (cotyledon stage, 55 days of age, and 100 days of age) were, respectively, 24.1, 9.5, and 9.2 mg CO$_2$/g needle dry weight per hour.

Several of the interactions were also significant. Seed source × age had the highest component of variance of all the effects involving source (Table 1). Montana and Oregon seedlings had, according to this interaction, different rate-age curves. Oregon seedlings had a higher average photosynthetic rate than Montana plants at the cotyledon stage. By 55 days, Montana seedlings had a significantly higher rate. Oregon seedlings again had the higher rate at 100 days, primarily because of the poor performance of Montana seedlings from the warm environment (Fig. 1).

A source × measurement-temperature interaction resulted from photosynthetic rates of Oregon plants exceeding the rates of Montana plants more at low measurement temperatures than at high temperatures (Fig. 1). Krueger and Ferrell (1965) found the same relationship between coastal British Columbia and Montana seedlings. This interaction was not significantly altered by age or growth temperature.

In general, plants from the warm environment had higher measured photosynthetic rates than plants from the cooler environment. Results from other organisms both agree (Wolede and Jewiss 1969) and disagree (Langridge 1963; Sorokin 1958) with these results. This lack of consistency could be associated partially with the temperatures used or with length of time the plants remained in their respective environments.

Growth temperature interacted significantly with both age and measurement temperature. The growth temperature × age interaction was revealed through a reduced effect of environment on growth with increasing plant age or with the change from cotyledons alone to a mixture of cotyledons and needles. Growth temperature × measurement-temperature interaction occurred because plants grown at low temperature tended to have lower optimum temperatures for photosynthesis (Fig. 1). In fact, the measurement temperature interacted significantly with both age and growth temperature, and an estimate of an optimum temperature or temperature range for photosynthesis would not mean much unless these factors were taken into account.

![Graph showing photosynthetic rates at three ages and three or five measurement temperatures of seedlings from Oregon (open circles) or Montana (solid circles) after growth in warm (solid line) or cool (broken line) environment.](image-url)
Net photosynthetic rates of 55-day-old plants were determined at 12.5° and 42.5°C, in addition to the three temperatures used previously (Fig. 1). Assimilation rates of plants from the high-temperature environment remained higher than those from the low-temperature environment. These results were similar to those reported by Mooney and West (1964), who gave examples of species whose photosynthetic rates at temperatures from 10° to 30°C were greater after acclimation at a “desert station” than after acclimation at a “subalpine station.”

As in most tests of this type (Lyutova 1958; Pisek and Winkler 1958; Rook 1969; Semikhatova 1960; Tranquillini 1957; Woledge and Jewiss 1969), the effect of environment was of short duration. The duration of effect was tested for the Douglas-fir seedlings by growing the plants of the Corvallis source for 45 days in either warm or cool conditions, then moving them to the other environment and determining photosynthetic rates 10 days later. Rates were compared with nontransferred seedlings (Table 2). Seedlings transferred from one chamber to another behaved, with respect to photosynthesis, almost as if they had spent their entire lives in the latter environment. Mooney and Harrison (1970) showed that such changes, involving complex modifications of stomatal, mesophyll, and biochemical behaviors, can occur within a 24-h period.

**Dark Respiration**

When averages were taken over all treatment combinations, there was no difference between seed sources. Average rates for sources were as follows.

<table>
<thead>
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<th>Treatment</th>
<th>Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Warm chamber: 55 days</td>
<td>12.8b*</td>
</tr>
<tr>
<td>Cool chamber: 45 days; warm chamber: 10 days</td>
<td>14.3a</td>
</tr>
<tr>
<td>Warm chamber: 45 days; cool chamber: 10 days</td>
<td>7.4c</td>
</tr>
<tr>
<td>Cool chamber: 55 days</td>
<td>8.1c</td>
</tr>
</tbody>
</table>

*Any two means with different letters are significantly different at the 0.05 level by Duncan's new multiple range test.

**Table 2**

Photosynthetic rates at 27.5°C of transferred and nontransferred 55-day-old seedlings of the Corvallis source; rates are in mg CO₂ absorbed/g needle dry wt. per hour.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Missoula: 55 days</td>
<td>2.53 mg CO₂ evolved/g needle dry wt. h</td>
</tr>
<tr>
<td>Corvallis: 55 days</td>
<td>2.46 mg CO₂ evolved/g needle dry wt. h</td>
</tr>
</tbody>
</table>

Effects due to age were highly significant, with the rate dropping rapidly with age.

| Cotyledon stage: 55 days old | 2.33 mg CO₂ evolved/g needle dry wt. h |
| 100 days old                | 1.51 mg CO₂ evolved/g needle dry wt. h |

Environment in which the plants were raised also had a strong effect on their subsequent respiration. Plants from the cool environment respired almost twice as rapidly as plants from the warmer environment.

18°C day – 4°C night, 3.43 mg CO₂ evolved/g needle dry wt. h
36°C day – 21°C night, 1.81 mg CO₂ evolved/g needle dry wt. h

Difference between measurement temperatures was 7.5°C. Average respiratory rates at the three temperatures for all plants were as follows:

| 20°C: 1.60 mg CO₂ evolved/g needle dry wt. h |
| 27.5°C: 2.57 mg CO₂ evolved/g needle dry wt. h |
| 35°C: 3.78 mg CO₂ evolved/g needle dry wt. h |

The only significantly different response involving seed source was with environment in which the plants were grown. Missoula plants respired more rapidly than Corvallis plants after growth at cool temperatures; and Corvallis plants, more rapidly than Missoula plants after growth in warm temperatures.

The only other significant interaction was between age and growth temperature. Plants in the cool chamber respired more rapidly than plants in the warm chamber at all ages, but the difference was greater at the cotyledon stage than at older ages.

**Dry Weight**

In general, high growth temperature decreased rate of dry matter accumulation, the difference increasing with advancing age up to 100 days. On the basis of whole plant dry weight, seedlings of the two sources were similar when grown in
the 18°C-4°C environment but quite different when grown in the 36°C-21°C regime (Fig. 2).

All plants in the cool environment had about the same weight distribution of needle, stem, and root tissues up to age 55 days (Fig. 3). By 100 days, the Missoula plants had lower needle weight and greater stem and root weight than the Corvallis plants, apparently as a result of Missoula seedlings in cool environment setting buds between 55 and 100 days. Bud set did not affect photosynthetic rates (Fig. 1) but did stop terminal elongation, which in turn reduced needle dry weight increment. Excess of photosynthate apparently went to roots and stems and increased their growth rate. Missoula plants in the cool environment added little photosynthetic tissue, which reduced their total increment relative to nondormant Corvallis seedlings.

**Discussion**

**Photosynthesis**

The main features of the photosynthetic results related to seed source may be summarized as follows. First, Oregon plants had higher photosynthetic rates than Montana plants at the cotyledon stage (Fig. 1). This relationship changed with age and led to a significant source X age interaction (Table 1). Second, Oregon seedlings had higher rates at low measurement temperatures (Fig. 1), and this interaction was also significant. Third, photosynthetic rates of the two sources responded differently to the prolonged exposure to high growth temperatures, as shown by the significant source X growth temperature X age interaction (Table 1).

In general, growth environment had a much greater effect on net photosynthesis than did seed source. Rates of warm chamber plants were higher than those of cold chamber plants at all measurement temperatures, with greatest differences at higher measurement temperatures. Summed over all treatments, average net photosynthetic rates of warm chamber plants exceeded those of cool chamber plants by 47%.

On the average, Oregon seedlings had rates about 5% higher than the Montana plants. Larger differences between sources emerged when other factors were considered. For example, the biggest differences were in the cotyledon stage, when rates for Oregon seedlings were 12% higher than rates for Montana seed-
The differences between the sources essentially disappeared with increasing age. The non-persistent early differences could have been due to maternal effects. Short-lived maternal effects could be of significance in establishment of seedlings in their respective environments but would not seem to be of significance to long-term growth.

Relationship Between Photosynthesis and Growth

Increment in the warmer environment was considerably less than in the cooler conditions. Yet for the entire 100 days that the plants developed, all material from the warm chamber, when measured under the same conditions as plants from the cooler chamber, assimilated more rapidly than the latter plants. For example, at 55 days of age, seedlings from the warm environment were 13% lighter in total dry weight than seedlings from the cool environment. The difference was even greater at 100 days. But in their comparative photosynthetic rates, the warm-chamber plants were about 50% higher. Others have reported similar results for other species (Neuwirth 1967; Hanson 1971). In attempting to explain this seeming paradox, we considered five contributing factors.

1. The plants were grown at about 1000 ft-c light intensity, but photosynthesis was measured at a saturating light intensity of 5000 ft-c. If initial slopes of the light intensity curves were greatly different for plants from the two environments, the photosynthetic rate at saturating light intensity might be a poor indicator of what was occurring in the growth chamber light intensity.

2. Photosynthetic rates for warm-chamber plants were always higher than rates for cool-chamber plants when compared at the same temperatures. But the proper rate comparison for growth should be at the particular temperatures being used in the growth chambers.

3. Respiration at night for plants from the two environments might have been different.

4. Root respiration may have been different for the two environments.

5. Distribution of photosynthate to needle and nonneedle tissue was different and would have contributed to the difference in plant size.

We will show the effect of these five points in turn, using 55-day-old plants as a specific example.

Effect of Light Intensity

One early study (reported in Lyubimenko 1963) indicated that light intensity required for light saturation became lower as the growth temperature became higher. To test this for the warm and cool environments used here, two groups of Corvallis seedlings were grown to 55 days, one in each temperature regime, then light intensity curves were determined from photosynthetic rates measured at 500, 1000, 2000, and 5000 ft-c. Warm-chamber plants were tested at their day-growth temperature of 36°C, cool-chamber plants at their day-growth temperature of 18°C. For warm-chamber plants the photosynthetic rate at 1000 ft-c was 80% of the rate at 5000 ft-c; for cool-chamber plants, the figure was 65%. As a result, the photosynthetic rate of warm-chamber plants at 1000 ft-c turned out to be almost twice the rate of cool-chamber plants. The absolute difference in milligrams CO2 assimilated/g needle dry weight per hour between plants from the two chambers was almost the same at 1000 ft-c as at 5000 ft-c.

Effect of Measurement Temperature

During the 16-h photoperiod in each chamber, the seedlings were 10 h at the maximum temperature and 3 h morning and 3 h evening in a transition between maximum and minimum temperatures. Thus, warm-chamber plants spent 10 h at 36°C and 6 h in changes between 36°C and 21°C. Cool-chamber seedlings spent 10 h at 18°C and 3 h twice daily in transition between 18°C and 4°C. Average transition temperature was 28.5°C for the warm environment and 11°C for the cool environment.

When photosynthetic rates were calculated for 55-day-old plants at these temperatures, the following hourly and daily accumulations were obtained: (1) for warm-chamber seedlings, 10 mg CO2 absorbed/g needle dry weight per hour for the 10 h at 36°C and 13.6 mg/g per hour for the transition periods; (2) for cool-chamber plants, 8.7 mg/g per hour at 18°C and 7.3 mg/g per hour during the transition periods. On the basis of grams needle dry weight per day, warm-chamber plants absorbed 182 mg CO2 and cool-chamber plants, 131 mg. These rates were at 5000 ft-c. When they were adjusted to 1000-ft-c light intensity, comparative daily photosynthate accumulation amounted to 145 and 85 mg CO2 absorbed per gram needle dry weight per day for warm- and cool-environment seedlings, respec-
Effect of Seedling-top Respiration

Net photosynthetic rates have been used, so only the respiration rates for the 8 h of darkness had to be subtracted from the light CO₂ absorption totals. Respiration rates were estimated from rates used for Fig. 15 in Sorensen (1964) and were 1.1 mg CO₂ evolved/g needle dry weight per hour for warm-chamber plants (at 21°C) and 0.3 mg/g per hour for cool-chamber plants (at 4°C). For the 8 h of darkness, this amounted to 9 mg and 2 mg, respectively, on the basis of grams needle dry weight per day. This accounts, in a small way, for the discrepancy between growth rates and photosynthetic rates; however, the difference on a seedling-weight base is not this large because the cool-environment plants were a little heavier.

Effect of Root Respiration

It seemed possible that root respiration for warm-chamber plants was higher than for cool-chamber plants. However, no separate measurements of root respiration were made. It was assumed that, on a tissue-weight basis, root respiratory rates were equivalent to seedling-top respiratory rates.

Using warm-chamber temperatures of 10 h at 36°C, 6 h at 28.5°C, and 8 h at 21°C and cool-chamber temperatures of 18°C, 11°C, and 4°C, respectively, the estimated daily evolution of CO₂ by the roots was 20 mg CO₂/g needle dry weight per day for the former and 9 mg/g per day for the latter. This again accounts for part of the discrepancy between photosynthetic rates and growth rates.

Effect of Photosynthate Distribution

In spite of the “roughness” of some of the estimates, it seemed certain from these figures that on a needle-dry-weight basis the warm-chamber plants were indeed assimilating more rapidly than the cool-chamber plants, although the latter had a more rapid dry weight increment.

One of the most striking differences between plants grown in the two temperature environments was the relative amount of needle or photosynthetic tissue. At the cotyledon stage, when the seedlings had just shed the nutritive tissue of the female gametophyte, the cool-chamber plants had a slightly smaller proportion of needle tissue. At both 55 and 100 days of age, the cool-chamber plants had, relative to total plant weight, 20% more needle tissue. Presumably this adjustment is only another example of the adjustment of plant growth to the environment (Blackman and Wilson 1954). However, it is apparent that a 20% larger photosynthetic apparatus plus a continual channeling of more photosynthate into more photosynthetic tissue could compensate for a lower photosynthetic rate.

Borsdorf (1967), Brix (1967), Sweet and Wareing (1968), Ledig and Perry (1969), and Ledig (1969) had similar results; they found that it was necessary to take leaf-weight/plant-weight ratios or some equivalent into consideration to make growth predictions from photosynthetic rates.

Because of the apparent influence of photosynthetic distribution on growth rate, we were interested to determine if a certain distribution, once started, was stable if the environment changed. To test this, seedlings were planted and grown in either a warm or cool environment for 27 days, then transferred to the other environment and harvested 28 days later. Plants which spent the last half of the time in the cool environment had a needle proportion of 0.58; those grown last in the warm environment had a needle proportion of 0.52. Needle proportions for plants which had been raised all 55 days in either cool or warm environments were 0.61 and 0.50, respectively.

Thus, various plant tissues of the seedlings seemed to respond to different environments. In one environment, this was a relatively small top or needle portion; in another environment, a relatively small root. But in both cases, the photosynthetic rate was apparently somewhat dependent upon some desirable or fixed relationship of needle to nonneedle tissue.

Table 2 shows that photosynthetic rates adjusted quite rapidly when the plants were moved from one growth environment to another. If we look more closely at the assimilation rates of transferred and nontransferred seedlings, we can see that the average assimilation rate of the plants transferred into the warm environment was higher than that of the regular warm-

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chamber plants (14.3 mg CO₂ absorbed/g needle dry weight per hour and 12.8, respectively), and that the average assimilation rate of plants transferred into the cool environment was lower than that of the regular cool-chamber plants (7.4 and 8.1, respectively). This indicated that the transferred plants not only were adjusting the distribution of current photosynthate to suit new environmental conditions but also were growing toward some fixed balance between the different tissues. Plants which spent half their lives in both environments had needle:nonneedle weight ratios quite similar to expected ratios for the second environment. This could hardly have occurred if there had not been at least a temporary overadjustment by the transferred seedlings in distribution of photosynthate.

In this test it was not possible, because of insufficient Montana seed for some of the final comparisons, to relate racial differences in photosynthetic rate to differences in photosynthate distribution. But Zavitkovski (1964), using Douglas-fir seedlings from northeastern Washington and western Oregon, measured photosynthetic rates at 2 and 3 months after exposing plants to various moisture stresses. If only measurements made under favorable moisture conditions were considered, photosynthetic rates for the two sources were equivalent at 2 months, and rates at 3 months for the seedlings from northeastern Washington were higher than the rates for the plants from western Oregon. Nevertheless, western Oregon seedlings were 7% heavier than northeastern Washington seedlings at 2 months and 25% heavier at 3 months. Again, this reverse relationship between photosynthetic rate and growth seemed to be reasonable only when distribution of plant weights was taken into account. Northeastern Washington plants at 2 months had an average top-root ratio of 2.16, western Oregon plants, a ratio of 2.58. At 3 months, the top-root ratios were 1.31 and 1.93, respectively. Thus, the higher photosynthetic rate of the northeastern Washington seedlings was not a reflection of faster top growth but probably of faster root growth relative to top growth.


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