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Jaroslav Zavitkovski for the M. S. in Forest Management
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Title THE EFFECT OF DROUGHT ON THE RATE OF
PHOTOSYNTHESIS, RESPIRATION, AND TRANSPIRATION IN
TWO ECOTYPES OF DOUGLAS-FIR (PSEUDOTSUGA MENZIESII
(MIRB.) FRANCO)

Abstract approved Signature redacted for privacy.
(Major professor)

The subject of this study was the determination of the changes in photosynthesis, respiration and transpiration in two ecotypes of Douglas-fir as caused by decreasing soil moisture content. The photosynthetic rate was also correlated with the relative turgidities of needles.

All the above processes were greatly affected by decreasing soil moisture. In general they decreased with the decrease in soil moisture. The transpirational rate was affected relatively more than photosynthetic rate, and the respiratory rate was affected least.

The photosynthetic rates of the two-months-old seedlings of both sources were consistently higher under optimal soil moisture conditions but they were significantly lower (at 1% level) at low soil

moistures than those of the three-months-old plants. There was no significant difference found in the photosynthetic rates between the two sources at two months of age, but significantly higher photosynthetic rate at high soil moistures was found in the three-months-old N. E. Washington seedlings when compared with the Valsetz plants. There is an indication that at very low soil moistures the photosynthetic rate of the N. E. Washington seedlings is higher also but this could not be shown statistically because of the relatively small number of observations.

A good correlation was found between the photosynthetic rate and relative turgidities of needles in both ecotypes. For the same soil moisture a higher relative turgidity was observed in the needles of the N. E. Washington seedlings than in the Valsetz source.

The respiratory rates of the two-months-old seedlings of both sources were consistently higher than those of the three-months-old plants. While the difference in respiratory rates between the two ecotypes was not significant at two months of age, it was significantly higher in the Valsetz source at three months. It is suggested that this difference was due to the relatively larger proportion of the newly developing needles in this ecotype. Contrary to observations made by some researchers no increase in the respiration was determined at the onset of the drought or at the lowest soil moistures

used in this study.

The relation between the soil moisture and transpirational rate was linear in both sources in the range below 12% of soil moisture. In this range the transpirational rates of the Valsetz seedlings were significantly higher (at 1% level) than those of the N. E. Washington plants.

The top/root ratios were found significantly different between the two- and three-months-old seedlings in both sources, and also between the Valsetz and N. E. Washington seedlings at two and three months of age. These ratios decreased in both sources between the ages of two and three months. The ratio of the three-months-old N. E. Washington seedlings was the lowest while that of the two-months-old Valsetz plants the highest.

The lower transpirational rate in the N. E. Washington seedlings is of definite advantage for survival on droughty sites. This survival ability is further increased by their low top/root ratio. There is some evidence that they would suit extreme sites much better than the Valsetz source. It is suggested that the periodical droughts of N. E. Washington exercised a strong selection pressure in that direction while in the relatively mild climate of the Coastal Range in Oregon another ecotype was created.

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IN TWO ECOTYPES OF DOUGLAS-FIR
(PSEUDOTSUGA MENZIESII (MIRB.) FRANCO)

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JAROSLAV ZAVITKOVSKI

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INTRODUCTION

Reforestation of droughty clearcuts, especially when delayed for several years so that undesirable herbaceous as well as woody vegetation has had time to establish itself, may present serious silvicultural problems. A decision sometimes must be made as to which ecotype of certain species would best fit into such situation. Seed of the native origin is usually considered first but it may be rejected due to some undesirable features, and another ecotype must be introduced. Such introduction, to be successful, should be preceded by a careful physiological study.

In a species that extends over a large territory, such as Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) great variations between the extreme ecotypes would be expected. Drought, possibly more than any other ecological factor, and particularly in areas where it occurs periodically, exercises strong selection pressure upon this species. On the other hand in regions with high precipitation and generally mild climate the natural selection is based more on other factors, and another ecotype will result.

The selection of seed sources from Valsetz, Oregon, and N.E. Washington for this study was not accidental but intentional. The Valsetz ecotype grows under optimum conditions of precipitation while the source from N. E. Washington grows in a region known as suboptimal in precipitation with a pronounced period of summer drought.

While this study might well be placed in the category of basic research the main idea was the application of the results to practical problems encountered here on Pacific Coast. Here indeed the selection of an ecotype which will be able to survive and grow on droughty sites may be the crucial point deciding between the success or failure of a given plantation.

Variable soil moisture content is the main factor in this study. No doubt, factors other than drought may occasionally increase or diminish its severity, or they may become even more important than the soil moisture content itself. Light may be insufficient below the canopy, temperature suboptimal at higher elevations, or some biotic agent may be the governing factor in regeneration of Douglas-fir on various sites. But the fact remains that the periodic droughts as they occur in western states are the major ecological factor which limits distribution of Douglas-fir in many areas.

In addition to the main study some preliminary and auxiliary

experiments have been conducted. While some did not contribute to the understanding of the drought problem, others, such as differences in the top/root ratio, seemed to be of great help in explaining, in part at least, different rates of photosynthesis between the two ecotypes under variable soil moisture content.

In the review of literature, which is far from being complete, the main emphasis was placed on similar studies with tree or woody species, but there are some which deal with other kinds of plants as well.

REVIEW OF LITERATURE

In spite of some disagreement among various researchers about the exact point when soil moisture starts to exercise its influence on photosynthesis, respiration, and transpiration, there seems to be no doubt that at soil moistures at which a given species shows first signs of wilting, the rates of the above processes, with possible exception of respiration, are greatly reduced. The majority of workers report steady decrease in the photosynthetic rate at soil moistures between field capacity and wilting point (5; 10; 12; 17; 21; 26) but another group did not find such a decrease until a soil moisture stress developed (1; 15; 28).

Since plant growth is controlled directly by the plant water stress and only indirectly by soil water stress (12) some researchers feel that photosynthesis, respiration, and transpiration should be measured simultaneously with indicators of plant water stress (4). Relative turgidity and particularly diffusion pressure deficit are such indicators and have been used in some studies (4; 26). The main obstacle to more general use of diffusion pressure deficit are the difficulties encountered in its measurement as has been stressed by others (33).

There seems to be no clear evidence relative to the changes

in respiratory rate with decreasing soil moisture. Increase in respiration with decreasing soil moisture was observed by Schneider and Childers (25, p. 575, 580) in apple leaves. Brix (4) obtained in loblolly pine a decrease followed by an increase above normal level and finally decrease below normal level after drought onset but in tomato plants the trend was down all the way. Also Parker (22) reported erratic behavior of respiration in the needles of Austrian pine but disregarding the erratic ups and downs the general tendency was decrease in respiration with decrease in available water in needles.

A certain similarity between decreasing rates of photosynthesis and transpiration with simultaneous decrease in the soil moisture has been found by some scientists (4; 21) but others have reported that transpiration is reduced sooner than photosynthesis (15, p. 522). As pointed out by Kramer (11; 12) the water stress in a plant depends on relative rates of both absorption and transpiration, and not on the soil water supply alone. Besides, plants of different species have widely different transpirational rates. The importance of stomates as regulators of transpiration and also entry of carbon dioxide is stressed by Gaastra (9, p. 63) who thinks that transpiration is relatively more influenced than photosynthesis.

One of the most controversial issues in transpirational studies is ascertaining of the point when the rate starts to decrease. While

the majority of researchers agree that the rate decreases with decreasing soil moisture (26), Veihmeyer and Hendrickson (30; 31) claim that the rate of water extraction from soil by plants is not influenced by the water content so long as it is above the permanent wilting point, and consequently transpiration remains the same whether the soil moisture is high or low.

MATERIALS, METHODS, AND APPARATUS

Two ecotypes of Douglas-fir were used in this comparative study; one from the vicinity of Valsetz in the Coastal Range of Oregon, the other from N. E. Washington.

The seeds of both sources were germinated in petri dishes after a short period of cold stratification, and planted in pint plastic pots in sandy soil. They were grown in an unheated greenhouse for a period of two and three months, from early April 1963. No additional light was provided. Due to rather unfavorable weather during April and part of May, heavy mortality occurred caused by damping-off fungi. The N. E. Washington source was affected particularly. All seedlings received the same treatment; the soil moisture was kept high throughout the period and nutrient solution was applied twice a week to all seedlings that shed their seed coats.

About one month before the beginning of drought treatment, sunflower seeds were planted in some pots and the sunflower plants were later used as a measure of existing soil moisture stress. But the method appeared to be difficult in the sandy soil used in this study, because the two stages in wilting, namely of the lower and upper pairs of leaves, were only about 0.6% of soil moisture apart, an amount that under average environmental conditions was

transpired in few hours. For this reason the method was not used in three-months-old seedlings. In these the daily evaporational loss from the pot was used in estimating the soil moisture content (Figure 1). More detail about this method will be found under the heading "Evaporation from Unsealed Pots".

When the seedlings reached the age of two months, half of them was transferred from the greenhouse to a growth chamber with controlled environment. The watering of these seedlings was discontinued and the photosynthetic, respiratory, and transpirational tests were started. This will be described in more detail in the particular sections. The same was done with the other half of the seedlings when they were three months old.

Closed systems, similar to those used by Krueger (14, p. 4-9) for the measurements of changes in carbon dioxide concentrations, were also used in this study for the determinations of photosynthetic and respiratory rate. The detailed description of these systems may be found in the above paper. The changes in carbon dioxide concentration were measured by an infrared gas analyzer and recorded by a Honeywell recorder, in the range from about 330 to 370 ppm. Light intensity in the cuvette at the seedling level, as measured with Weston Illumination meter, reached 4,500 f. c. and was kept constant in all photosynthetic runs. The temperature in the

cuvette was also kept constant at 20 degrees C in both photosynthetic and respiratory studies. The rates of photosynthesis and respiration were computed from the changes of the carbon dioxide concentration and expressed in milligrams of carbon dioxide absorbed per one gram dry weight of needles per hour. The dry weight of the needles was determined to the nearest 0.1 mg.

The soil moisture contents in each run were computed from changes in weight of the pots which were weighed after the termination of each run to the nearest 0.01 g. The dry weight of the soil was obtained at the end of a series of runs by drying out the soil in the oven at 105 degrees C for 24 hours. At the same time the weights of the pot and plant were also determined and subtracted from the gross weight to obtain the fresh weight of the soil in a particular run. Then the soil moisture content in percent was computed for each run by using the formula:

$$\% \text{ soil moisture} = \frac{\text{fresh weight of soil} - \text{dry weight of soil}}{\text{dry weight of soil}} \times 100$$

Relative turgidity, the ratio of existing water content in the needles to the water content at full turgidity, was also obtained at the time of testing. More detail on this method as well as on the determinations of the transpirational rates will be found under the respective headings.

PRELIMINARY EXPERIMENTS

Some additional experiments were required to obtain a basis for such determinations as transpiration from sealed pots, relationships between soil moisture content and total soil moisture stress, and also to obtain some insight into differences in photosynthetic rates. These experiments were conducted before and during the main study.

Soil data

Sand sieved through a 1/8 inch mesh sieve was the only soil used in the study. The absence of organic matter in the soil made the determinations of available water easier. The data furnished by the Soils department, where the soil moisture stress as related to soil water content was tested, are summarized in Table 1.

Table 1. Total soil moisture stress at several soil water contents of sandy soil sieved through a 1/8 inch mesh sieve.

Soil moisture content % of D. W.	Total soil moisture stress atm.
4.73	0.1
4.12	0.5
3.91	1.0
3.47	2.0
3.33	5.0
2.94	15.0

It is usually assumed that the field capacity of a soil corresponds to 0.1 atm. on a moisture stress scale. Some authors give 1/3 atm. as a closer approximation. However Marshall (16) using tensiometers, obtained in sandy soils a tension of only 0.07 atm. at field capacity. Certainly a somewhat higher soil moisture content corresponds to this lower tension, but for lack of more detailed data, 4.7% of soil moisture was used as field capacity in comparisons of adjusted means of photosynthetic, respiratory, and transpirational rates. It should be noted that 81% relative turgidity corresponds on the average to a soil moisture content of about 4.7%.

Evaporation from unsealed pots

Evaporation from four unsealed pots served as a basis for estimating water loss during the following 24 hours from pots with plants used in photosynthetic and respiratory tests. The four pots were filled with soil, saturated to capacity, placed in a hot chamber in which all plants were kept during the study, and weighed daily for a period of about three weeks. At that time the soil moisture was reduced to a point very close to equilibration with the environmental conditions of the growth chamber, and the water loss by evaporation reached a very low level of 0.02 gm/pot/day. From the data obtained a graph (Figure 1) was constructed in which the evaporational

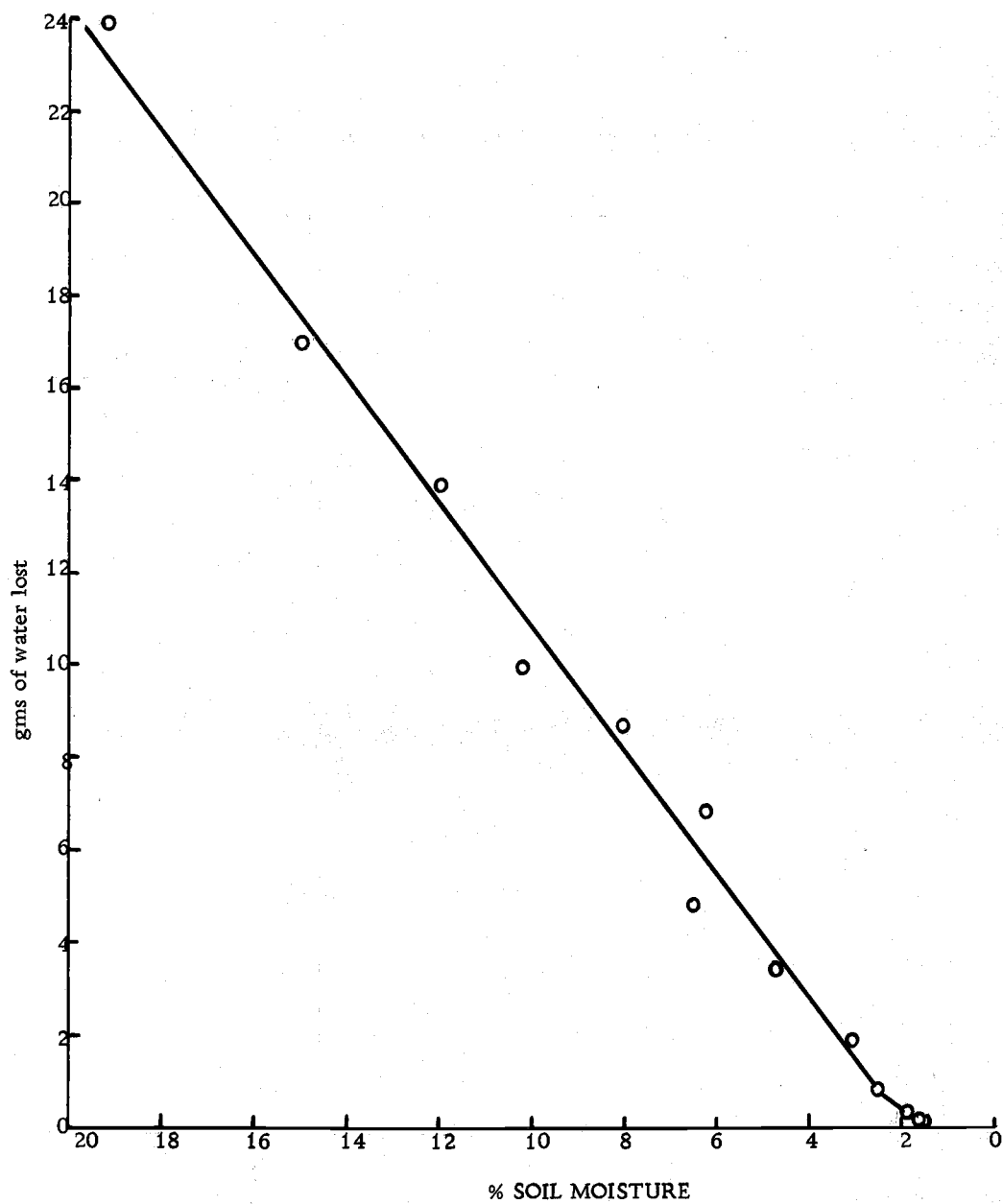


Figure 1. Evaporation rate from unsealed pots. Water loss expressed in gm per day per pot, and related to the initial soil moisture percentage.

loss in grams per day was plotted over the decreasing soil moisture percentage. The graph was used in the study on photosynthesis and respiration, and enabled prediction with a certain degree of accuracy of the soil moisture in the next one or two days. This was found very advantageous in scheduling the photosynthetic and respiratory tests. Inaccuracies were caused mainly by unequal amounts of soil in the pots, by variations in the weight of the pots themselves, and also by changes in relative humidity in the growth chamber.

Evaporation from pots sealed with paraffin

One of the assumptions in the transpirational study was that the pots had been made impermeable and any water loss took place only from the needles. To test this assumption four pots filled with soil of about 6.1% soil moisture, were sealed in the usual way with melted paraffin. Subsequently the pots were placed in a hot chamber and periodically weighed. The seal was carefully checked before every weighing but no cracks were found during the forty days of testing.

As can be seen in Table 2, the water loss from these pots reached on the average 0.025 g/day/pot and this value was used for adjustment of the sealed pots with plants. It should be noted,

however, that this loss could as well be neglected because during the average time required for a transpirational study of about 35 days, the water loss by evaporation reached only 0.15% of soil moisture. Besides, it may be assumed that the loss would be considerably smaller at lower soil moistures.

Table 2. Evaporational loss from sealed pots without plant.

Pot no.	Days	Weight - g		Water loss in g	
		Initial	Final	Total	Per day
1.	40	668.46	667.61	0.85	0.0213
2.	40	657.69	657.03	0.66	0.0165
3.	40	651.69	650.71	0.98	0.0245
4.	40	643.39	641.83	1.56	0.0390
Average				1.05	0.025

Top/root ratio

The ratio of dry weights of the top to the root was obtained from all seedlings used in the study; a total of 160 seedlings was used in the determinations and "t" tests were to show the differences statistically. Significant differences, all at 1% level, have been found in the following tests:

1. Valsetz x N. E. Washington - two months old seedlings
2. Valsetz x N. E. Washington - three months old seedlings
3. Valsetz: two months old seedlings x three months old seedlings
4. N. E. Washington: two months old seedlings x three months old seedlings

The ratio in both sources decreased with age from two to three months. The mean ratio of the Valsetz seedlings decreased from 2.58 at two months to 1.93 at three months of age, and the corresponding values for the N. E. Washington plants were 2.16 and 1.31.

To characterize the development of the seedlings after two months of age, it may be pointed out that both sources produced relatively more roots than shoots. The average weights of tops and roots are given in Table 3.

Table 3. Average weights of tops and roots, and top/root ratios in Valsetz and N. E. Washington Douglas-fir seedlings at the age of two and three months.

Source	Dry weight of top		Dry weight of root		Average Top/Root ratios	
	2 months	3 months	2 months	3 months	2 months	3 months
	mg		mg			
Valsetz	32.66	64.73	14.03	37.10	2.58	1.93
N. E. Wash.	29.35	43.92	14.36	37.51	2.16	1.31

From the table it can be concluded that while the average weight of roots in both sources is almost identical, the weights of the tops differ significantly. Valsetz seedlings almost doubled the weight of the top from two to three months of age but N. E. Washington plants increased their weight by less than 50% only.

The relatively higher rate of growth of roots in the N. E. Washington source may offer a partial explanation for the higher

photosynthetic rate as will be discussed later. From the ecological standpoint the lower top/root ratio is of survival value and this will be explored in more detail in the section on ecological implications.

Photosynthetic rate in seedlings with and without cotyledons

One of the additional studies involved a comparison of the photosynthetic rates in seedlings of both sources on which either all needles except cotyledons, or the cotyledons only were left. The purpose of these experiments was to find possible causes of the different photosynthetic rates observed in the three-months-old seedlings at higher soil moistures. Only a few seedlings were available for this experiment. Each seedling was tested twice: first the entire seedling and immediately after this the same seedling from which either the cotyledons or needles were removed.

It was suspected that the photosynthetic rate in the cotyledons was higher than in the needles (14), and that this would be relatively more pronounced in the N. E. Washington source. In the tests a higher photosynthetic rate actually was determined in the cotyledons of both sources but the increase was about the same in both ecotypes. The most plausible reason for this increased photosynthetic rate was the increased light intensity after the removal of the shade casting needles.

It was also suspected that the photosynthetic rate in the needles of the N. E. Washinton plants might be higher than in the needles of the Valsetz seedlings because of the relatively larger proportion of the new needles in the Valsetz source. But even this was disproved by the results and a moderate increase in the photosynthetic rate was observed in both ecotypes after the removal of the cotyledons.

In the conclusion it may be said that in spite of the fact that the results were consistent they did not furnish the expected clue to solution to the problem. The results are summarized in Table 4.

Table 4. Photosynthetic rates of three-months-old seedlings compared to seedlings from which either cotyledons or needles were removed.

Source	Seedling	Photosynthetic rate mg CO ₂ /g DW/hr.		
		Entire seedling	Cotyledons only	Without cotyledons
Valsetz	A	20.4	28.7	--
	B	17.2	22.2	--
	C	14.7	19.8	--
	D	15.3	23.5	--
N. E. Wash.	35	16.9	25.1	--
Valsetz	31	14.6	--	15.3
	E	15.5	--	15.9
	F	14.5	--	17.5
	G	14.7	--	17.0
N. E. Wash.	33	14.6	--	15.9
	34	15.0	--	16.6

The effect of temporary increase in temperature and of darkness

The following observations actually are not a part of the preliminary experiments. They were observed after the control of the growth chamber went out of order, over the weekend of July 6 and 7. Both the temperature and light were affected; the temperature reached about 44 degrees C, or 9 degrees above the normal, and the light was switched off for unknown length of time. The photosynthesis and respiration were unfavorably influenced both showing a pronounced decrease in rates as shown by dashed lines in Figures 3 and 9. The sequence of readings is summarized in Table 5.

Table 5. Effect of temporary increase in temperature and of darkness on photosynthesis and respiration in three-months-old Valsetz seedlings.

Seedling no.	Readings previous to the mishap	Readings first day after the mishap		
		mg CO ₂ / g D. W. /hour	Readings two or three days later	
Photosynthesis				
1.	14.7	14.4	10.1	10.8
2.	14.6	14.7	8.8	9.7
3.	14.8		11.9	14.0
				13.7
Respiration				
1.	1.29		0.50	0.82
2.	1.29		0.56	0.82
3.	1.35		0.69	0.76

Apparently the physiological processes of the seedlings were affected temporarily after the accident but recovered later. The photosynthetic and respiratory readings obtained on July 8 had to be eliminated from the study.

EFFECT OF DECREASING SOIL MOISTURE ON PHOTOSYNTHESIS

Introduction

There is certain disagreement about the dependence of photosynthesis on the soil moisture as has been discussed in "Review of Literature" but there seems to be no argument about the sharp decrease in the photosynthetic rate at low soil moistures.

Not only drought but also flooding causes reduction in photosynthesis. Loustalot (15, p. 523) reports that the photosynthetic rate of pecan leaves was reduced to $2/3$, and eventually to 11% of the maximum rate after about five days of root submersion, and Clark (5, p. 45-50) observed that the maximum photosynthetic rate in balsam fir and white fir did not occur when the soil was wettest but rather after considerable water loss had taken place. In his as well as in several other studies the maximum rate was observed at soil moistures just below the field capacity (21; 25, p. 578-581). This increase is said to be caused either by the improved soil aeration, by increased stomatal opening, or both (10).

Basically the photosynthesis may be reduced in two ways by a decrease in the soil moisture: directly by reducing the moisture of mesophyll cells, and indirectly by the closure of stomata and

reduction of the leaf area (10;12). Other authors mention, however, that the photosynthesis is relatively less affected by stomatal closure than the transpiration, because the resistance to carbon dioxide diffusion lies both in the stomates and in the mesophyll (4; 8, p. 63).

There seems to be no difference in the minds of various authors between growth and net photosynthesis; some use the first, others the second to describe the changes that take place due to variations in the soil moisture. But the growth in length is reported to occur even after the dry weight of the plant was reduced (26, p. 325-328). This suggests the possibility that the same phenomenon might have been occurring in other experiments where no mention of dry weight was made and only the elongation was observed (1). The reason for such elongation is that the young tissue in some species, due to its higher DPD is able to remove water from older parts of the same plant, and elongate in spite of the fact that the plant as a whole is under a severe moisture stress. According to Kramer (12) water is essential for the maintenance of turgidity which is necessary for cell enlargement and growth. Along the same general lines Martin (17, p. 456, 463) reports that plants grown under a regime of low moisture grew less in the diameter, leaf area, stem height, and also in dry weight.

In both hardwoods and conifers the photosynthetic efficiency of

the leaves changes with age. Richardson (23, p. 448-450) classified the leaves of maples and oaks according to various physiological ages, and observed the lowest net photosynthetic rates in young expanding leaves, the highest in fully-expanded. In conifers Clark (5, p. 54-58) and Krueger (14, p. 50) observed a decreasing photosynthetic rate with the increasing age. In this connection the effect of mutual shading on the photosynthetic rate should be mentioned as reported by Kramer and Clark (13) in loblolly pine. They observed a decrease in the photosynthetic rate with increasing mutual shading.

Materials and methods

The photosynthetic rates of the three-months-old seedlings were obtained by repeated testing of 16 seedlings of each ecotype, while in the two-months-old plants eight seedlings were tested repeatedly and additional single determinations were made on 14 Valsetz and 10 N. E. Washington seedlings. The soil of one half of the seedlings was saturated several hours before the test started, and subsequently three or more photosynthetic readings were obtained within the following seven or eight days. For the other half of seedlings the soil moisture was reduced to lower levels before the testing started. In the two-months-old seedlings this was at the first signs of wilting of the lower leaves in sunflower, which

occurred at about 4.5 to 5.5% of soil moisture. In the three-months-old plants it was found advantageous to start this series of runs at somewhat higher soil moisture so that the overlapping of both series of runs was longer and fitting of the final curve easier.

The restriction of testing to one week was found necessary in order to prevent errors resulting from continuous growth of the seedlings. The assumption made in this study was that the growth was linear during the seven or eight days of testing. Based on this assumption the dry weight of foliage for each particular run was obtained from the formula:

$$\frac{\text{Final dry weight}}{\text{Final age}} \times \text{Age at particular run}$$

The above formula was used in all runs in which the photosynthetic rate was above 3.0 mg CO₂/g DW/hour, while no adjustment was made below this value, assuming that the photosynthesis and respiration during the 24 hours were about the same. It is recognized that the above assumptions may not be exactly correct and actually no experiments were conducted to obtain evidence on this point. However, it is also recognized that the possible errors would be very small and of little consequence for this comparative study.

Before starting a run the seedlings were left about 20 to 30 minutes in the cuvette to equilibrate. This time was found sufficient by Krueger (14, p. 7) for Douglas-fir and approximates the

adaptation period used by Stalfelt (27, p. 396-397) in his studies with lichens and mosses.

The range of carbon dioxide concentration was slightly higher than the average found in the atmosphere. However, Miller and Rusch (19) observed that the concentration of the carbon dioxide in the lower part of stem space remained considerably higher all the time when compared to the outside atmosphere. Readings over 400 ppm are reported in their study, particularly for the layers very close to the surface where the seedlings develop.

The photosynthetic rates obtained were analyzed statistically by an analysis of covariance. In testing the differences of the photosynthetic rates the readings were adjusted to 2.94, 4.7, and 9.5% of soil moisture. The curves obtained by plotting photosynthetic rates over soil moisture contents were found essentially linear if divided into two halves at 3.5% of soil moisture. Then each set of readings was analyzed separately.

Results

Generally, with decreasing soil moisture the photosynthetic rates in both sources at both ages decreased also (see figures 2, 3, 4, and 5 and table 6). Maximum photosynthetic rates were observed at the highest soil moistures used in this study which was

at about 20% of soil moisture. It should be noted however, that the testing at these highest soil moistures took place almost immediately after the seedlings were transferred from the cool greenhouse into the hot chamber so that the higher photosynthetic rate might well be due to a better physiological condition of the seedlings which presumably existed in the greenhouse and would persist for some time even after the transfer. The photosynthetic rates then decreased steadily with the decreasing soil moisture, slowly at first, but in the region between 3 and 4% of soil moisture, the decrease became more pronounced, and the photosynthetic rate in some plants approached zero at about 2% of soil moisture. At soil moistures above field capacity the photosynthetic rates of the three-months-old seedlings from Valsetz were found to be quite uniform, but below field capacity they behaved like the two-months-old seedlings of both sources and the three-months-old N. E. Washington plants.

At 2.94% of soil moisture (15 atm. S. M. S) the photosynthetic rate in all four groups of seedlings was still fairly high, on the average 60% of the observed maximum; and a considerable gas exchange was determined in some seedlings even at very low soil moistures, such as 2%, with unknown soil moisture stress, but estimated in several tens of atmospheres. Figures 2, 3, 4, and 5

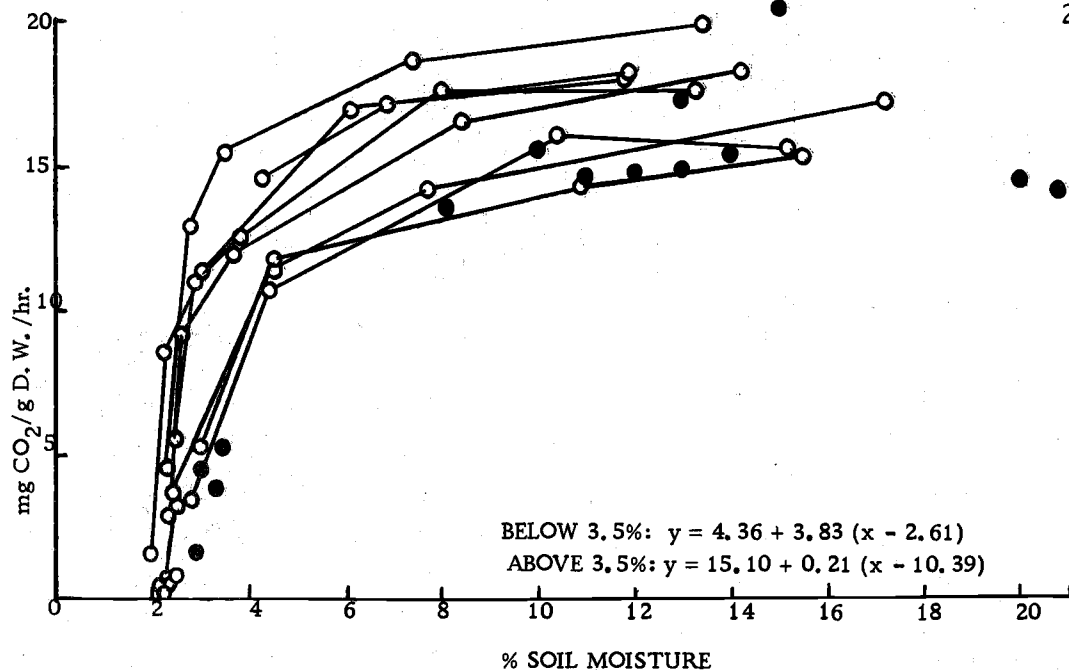


Figure 2. Photosynthetic rate of two-months-old Douglas-fir seedlings from Valsetz at 4,500 f. c. and 20 degrees C as affected by decreasing soil moisture. ● represents single readings, o---o represents repeated readings.

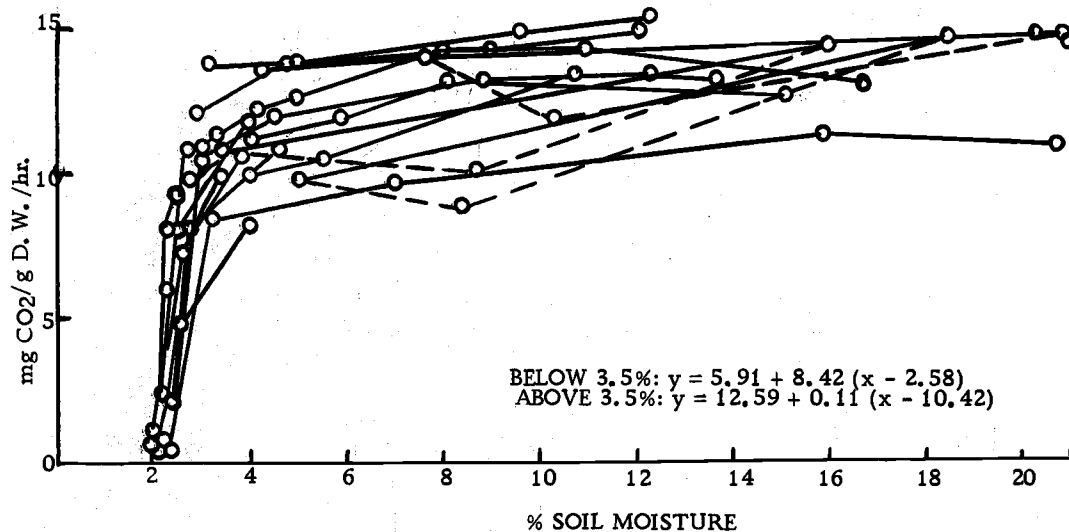


Figure 3. Photosynthetic rate of three-months-old Douglas-fir seedlings from Valsetz at 4,500 f. c. and 20 degrees C as affected by decreasing soil moisture.

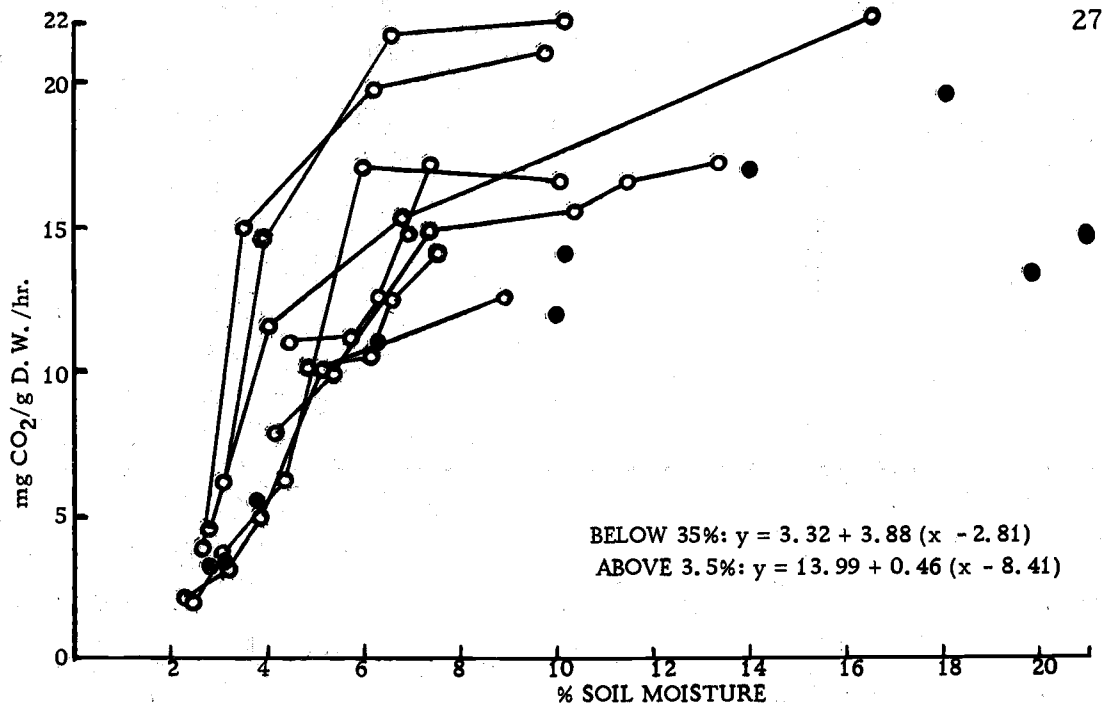


Figure 4. Photosynthetic rate of two-months-old Douglas-fir seedlings from N. E. Washington at 4,500 f. c. and 20 degrees C as affected by decreasing soil moisture. ● represents single reading. o---o represents repeated readings.

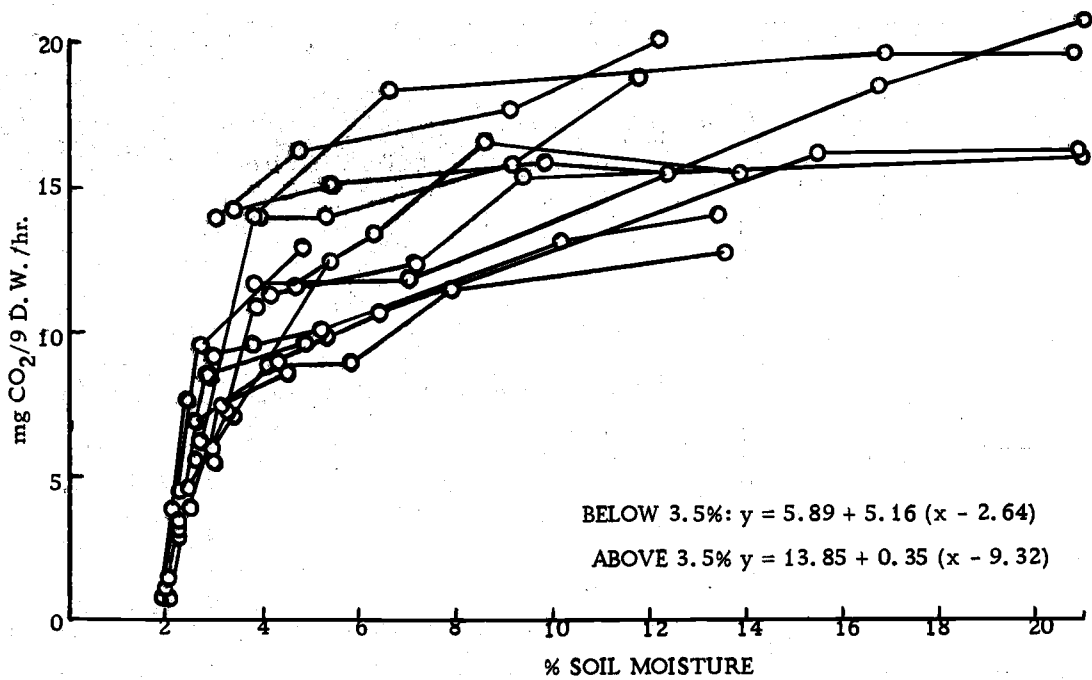


Figure 5. Photosynthetic rate of three-months-old Douglas-fir seedlings from N. E. Washington at 4,500 f. c. and 20 degrees C as affected by decreasing soil moisture.

depict the trends in photosynthesis in the various groups of seedlings, and Table 6 summarizes the various statistical tests performed.

Table 6. Photosynthesis. Results of the analysis of covariance. Expressed in mg of CO₂/g D. W. /hour.

Source tested	Adjusted to Soil moist. %	Adjusted means compared	Adjusted means compared	Level of significance
Valsetz 2 x 3 months	9.5	14.91	12.48	1%
Valsetz 2 x 3 months	4.7	13.93	11.92	1%
Valsetz 2 x 3 months	2.94	5.62	8.94	1%
N. E. Wash. 2 x 3 months	9.5	14.49	13.92	not significant
N.E. Wash. 2 x 3 months	4.7	12.28	12.22	not significant
N.E. Wash. 2 x 3 months	2.94	3.82	7.44	1%
Valsetz x N. E. W. 2 months	9.5	14.91	14.49	not significant
Valsetz x N. E. W. 2 months	4.7	13.92	12.28	not significant
Valsetz x N. E. W. 2 months	2.94	5.62	3.82	not significant
Valsetz x N. E. W. 3 months	9.5	12.48	13.92	1%
Valsetz x N. E. W. 3 months	4.7	11.92	12.22	not significant
Valsetz x N. E. W. 3 months	2.94	8.94	7.44	not significant
Valsetz x N. E. W. 3 months	2.00	1.03	2.59	not significant

In Table 6 it may be seen that the photosynthetic rate of the two-months-old Valsetz seedlings was significantly higher than that of the three-months-old plants, at soil moistures above the field capacity. It should be noted that while the difference in photosynthetic rate between the two- and three-months-old N. E. Washington seedlings was not significant, it was consistently higher in the

two-months-old plants when adjusted to 4.7 and 9.5% of soil moisture.

At lower soil moisture however, the picture changed completely. Thus at 2.94% of soil moisture the photosynthetic rates of the three-months-old seedlings of both sources were significantly higher (at 1% level) than in the two-months-old plants. This indicates that the younger seedlings are more vulnerable under soil moisture stress than the older seedlings, and under field conditions probably would suffer more by drought.

There was no significant difference found in the photosynthetic rate of the two-months-old seedlings, but in the three-months-old plants the N. E. Washington source was on the average more efficient, especially at very high and very low soil moistures. This did not seem to be consistent with the apparent growth of the seedlings because it was the Valsetz source that produced larger tops.

Discussion

One of the characteristic results was the slow but steady decrease in the photosynthetic rate with decreasing soil moisture in all groups of seedlings. No increase in the rate was observed at or slightly below the field capacity as reported by some investigators (5, p. 48; 21; 25). The reason most frequently cited for such

an increase is the improved aeration, while an increase in stomatal openings was suggested by others (10).

In order to explain the rather unusual results obtained in this study, one of the hypotheses was that there existed no aeration problem in the sandy soil even under conditions of full saturation. Before accepting this hypothesis a question should be asked: Why did the photosynthetic rate decrease, in most cases, thereafter? Since the availability of water to the seedlings probably did not change substantially between the highest soil moistures and field capacity, the above hypothesis cannot be accepted.

In the search for another explanation the physiological "shock" caused by a sudden transfer of the seedlings from the cool greenhouse into the hot chamber provides another hypothesis to elaborate upon. Some special attention has been given to a group of the two-months-old seedlings of both ecotypes. While no visible symptoms have been observed in the N. E. Washington source, the actively growing tops of the Valsetz plants showed visible signs of wilting several hours after the transfer, and some did not completely recover until the termination of the experiment. Since the soil moisture was relatively high the conclusion was that the absorption lagged behind the transpiration with the resulting water stress as described by Kramer (12) and others. The optimal conditions under

which the seedlings were tested apparently were too short to cause a reversal and thus both photosynthesis and respiration might have been somewhat subnormal. The absence of any visible signs of wilting in the N. E. Washington seedlings was probably caused by greater stiffness of the newly developing needles but this does not rule out the possibility of the existence of the same phenomena.

The higher photosynthetic rates observed in the two-months-old seedlings at soil moistures above field capacity are in general agreement with the results obtained by Krueger in Douglas-fir, who also found higher photosynthetic rates in younger seedlings in both sources used in his experiments.

From the ecological point of view one of the most important differences found was the significantly higher photosynthetic rate in the three-months-old seedlings of both sources (significant at 1% level). The inability of the younger seedlings to maintain their high photosynthetic rates is definitely a factor in their survival particularly under field conditions.

Rather surprising results were obtained in the three-months-old seedlings where the N. E. Washington plants reached higher photosynthetic rates than the Valsetz seedlings, particularly at higher soil moisture levels (significant at 1% level), but also at very low soil moistures, where the difference was not significant but

indicated very strongly that it probably would if a larger number of determinations were made. This result was the more surprising because exactly the opposite was expected when the apparent growth rates of the tops were considered. One of the possible explanations may be the unequal top/root ratio determined between the sources. Relatively more "photosynthates" have been used in the growth of roots in the N. E. Washington seedlings than in the Valsetz plants. This may constitute the major part of variation but other factors might have been involved too. Among them the relatively higher proportion of the newly developing needles in the Valsetz seedlings probably caused a decrease in photosynthetic rate. As has been shown by various workers (5, p. 54-58; 23, p. 448-450) the photosynthetic rate of developing young leaves and needles is low or even negative for several weeks.

Other experiments have been conducted in order to explain the different rate in the three-months-old seedlings but they were not conclusive and did not furnish conclusive evidence. Reference is made to the part of the thesis which deals with preliminary studies.

RELATIVE TURGIDITY AND PHOTOSYNTHESIS

Introduction

Some researchers feel that a more reliable measure of the plant water stress than that provided by soil moisture determinations, should be used in the growth studies. Kramer (12) thinks that the leaf water content is meaningless by itself because it may represent full turgidity in one species and severe wilting in another. But he sees in the relative turgidity a sensitive measure of the water stress if the critical level is determined for each species separately. Diffusion pressure deficit DPD, is a very valuable measure, superior to the relative turgidity, and should be used whenever possible. Since its determination is difficult, Weatherley and Slatyer (33) suggested a combination of both. To this end the relative turgidity of the needles or leaves is determined by the method first introduced by Weatherley (32). For each species a curve relating the diffusion pressure deficit to the relative turgidity is constructed and used again in the subsequent studies.

Other methods for measuring the plant water content have been introduced lately by Mederski (18) and by Namken (20). The first one uses beta-ray gauging in the measurements of the water status in the leaves, while the other one is based on the electrical

resistance in the leaves. Both methods can be correlated with the relative turgidity and since they do not destroy the plant, and are quickly obtained, they may have more use in the future.

The shortcomings and potential sources of errors in the relative turgidity determinations have been discussed by Weatherley (32, p. 91-94) and Werner (34, p. 7-12). Among them the injection of intercellular spaces during flotation, dew absorption, and increase in dry weight during flotation under bright light are the most important. However, the great diurnal variation in the relative turgidity which according to Werner may reach over 10% under the most favorable conditions of soil moisture, and even more under the decreasing soil moisture, seems to be the major obstacle in obtaining reliable readings (34, p. 37).

Materials and methods

The same seedlings used in the study on photosynthesis and respiration were used in the determinations of the relative turgidity. After completion of a particular photosynthetic run in which two seedlings were tested, one seedling was removed and the needles sampled for the relative turgidity. The remaining seedlings were sampled in the similar way after the termination of all photosynthetic and respiratory runs. Two sets of needles were collected

from each seedling and an attempt was made to obtain identical fresh weights. Inequalities were eliminated by using a correction ratio as introduced by Werner (34, p. 4).

Depending on the size of the seedling, from 12 to 20 needles constituted one set; they were cut so that each set contained about the same number of needles at various stages of development. This procedure minimized the error caused by differences in the relative turgidity in various needles on the same plant (12). Fresh weights of both sets were obtained to the nearest 0.1 mg. Then one set was dried for 24 hours at 105 degrees C and its dry weight determined while the other set was placed in distilled water in vertical position so that the cut bases of needles were about three millimeters below the surface. They were assumed fully turgid after 24 hours under laboratory conditions, removed from the water, rapidly blotted with absorbent tissue and their weight determined. The final weighing was done after 24 hours of drying at 105 degrees C.

The relative turgidity percentage was calculated according to the Weatherley's formula (32) modified by Werner (34, p. 4) as follows:

$$RT = \frac{FW_b}{FW_a} \times \frac{FW_a - DW_a}{FW_t - DW_b} \times 100 \text{ in } \%$$

where: RT is the relative turgidity
 FW_a and FW_b are the fresh weights of set a and b
 FW_a^t is the weight of second set at full turgidity
 DW_a^t and DW_b^t are the dry weights of set a and b

The total number of determinations for each ecotype was 27 after several readings were discarded. The results were then statistically analyzed by an analysis of covariance. The differences in photosynthetic rates were tested after adjustment to 81 and 85% of relative turgidity. It should be noted that the soil moisture contents corresponding to these values were approximately 4.7 and 6.5%.

Results and discussion

A good correlation was found between the relative turgidity of needles and photosynthetic rates in both ecotypes. The correlation coefficient r for the Valsetz seedlings was 0.8, and for the N. E. Washington plants 0.86. The analysis of covariance did not reveal any difference between the two- and three-months-old seedlings in both sources and therefore the readings for both ages in each ecotype were aggregated and an analysis of covariance used for testing the differences in photosynthetic rate between these two ecotypes.

No significant difference was found when the photosynthetic rates of the two sources were adjusted to 81% relative turgidity, but the photosynthetic rate of the N. E. Washington seedlings was

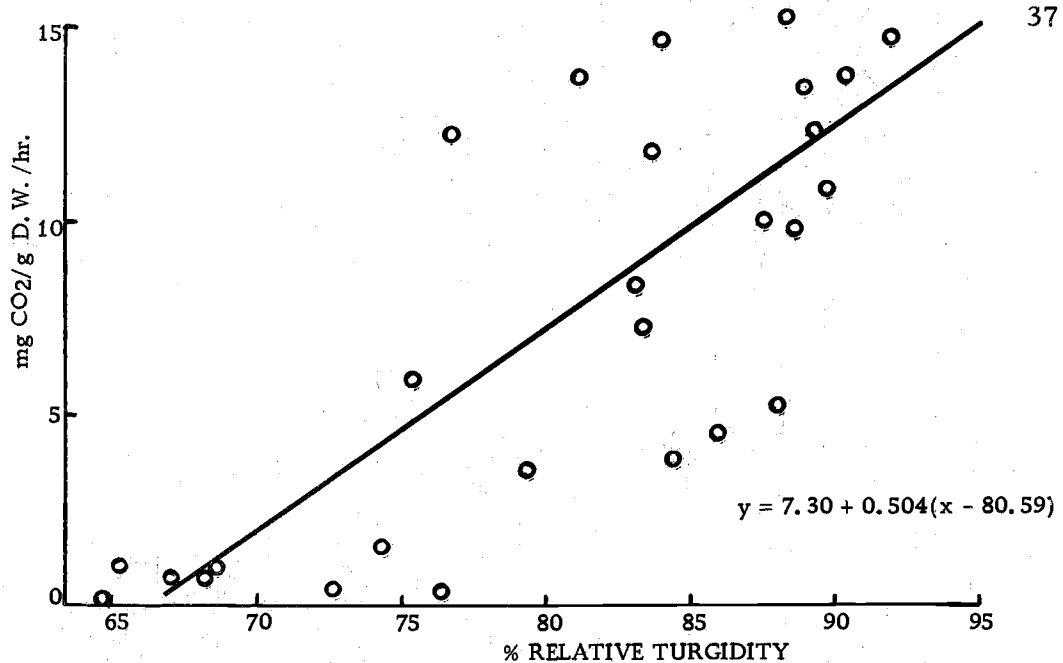


Figure 6. Photosynthetic rate of two- and three-months-old Douglas-fir seedlings from Valsetz at 4,500 f. c. and 20 degrees C as affected by decreasing relative turgidity.

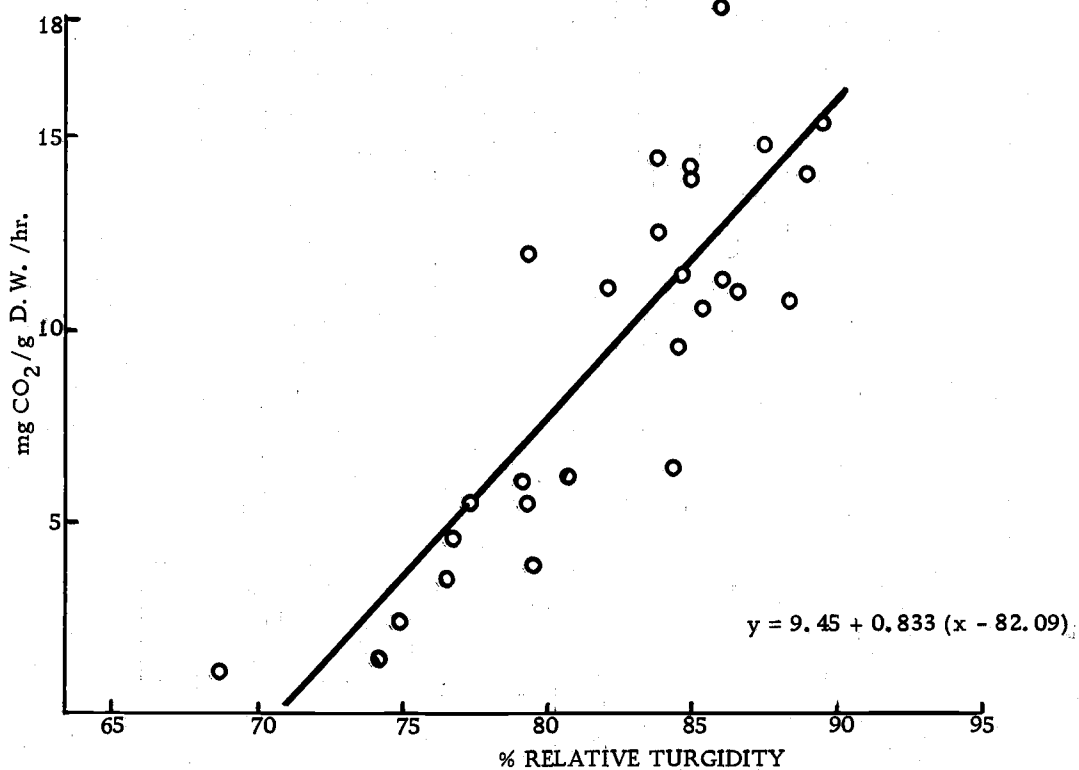


Figure 7. Photosynthetic rate of two- and three-months-old Douglas-fir seedlings from N. E. Washington at 4,500 f. c. and 20 degrees C as affected by decreasing relative turgidity.

found significantly higher (at 2.5% level) than that from Valsetz, when adjusted to 85% R. T; and the tendency was to make the difference even larger with further increase in relative turgidity. Figures 6 and 7 show the trends of the photosynthetic rate in both sources.

The situation at the lower relative turgidities was a little more complicated. Before going into discussion it should be noted that the relation between soil moisture content and relative turgidity was not the same in both sources. Thus at 2% soil moisture the corresponding values on the relative turgidity scale would be approximately 67% in the Valsetz source and about 73% in the N. E. Washington ecotype. In other words the N. E. Washington source was able to maintain higher relative turgidity at such low soil moistures than the Valsetz plants. Under these circumstances it would be misleading to adjust the photosynthetic rates to a very low relative turgidity and test them for differences. They obviously would be in favor of the Valsetz source but they would be irrelevant for this study in which the responses of the seedlings to drought conditions are tested.

The correlation between the relative turgidity and photosynthetic rate was higher in both sources than that between the soil moisture content and photosynthetic rate. The average values

were 0.83 against 0.58. This is in general agreement with the observations made by others. Thus Kramer (12) suggested that the plant growth is controlled directly by the plant water stress and only indirectly by the soil water stress. As for this study it is recognized that the correlation could further be boosted by a careful planning of the experiment so that the confounding effect of the daily fluctuation in relative turgidity would be greatly reduced. There is no doubt that a more realistic and universal evaluation of the internal water status as related to the photosynthetic rate would be obtained by using diffusion pressure deficit as has been stressed by several workers (4; 12; 26). The diffusion pressure deficit of the plant can be readily compared to the total soil moisture stress and it would probably eliminate such misleading results as found at low relative turgidities. But in spite of all its shortcomings the usefulness of relative turgidity cannot be denied as has been lately stressed again by various workers (12; 26; 33) who pointed out its main advantage, namely the ease of its determination.

EFFECT OF DECREASING SOIL MOISTURE ON RESPIRATION

Introduction

The same controversial results reported in photosynthesis exist in respiration. In addition only a few studies with woody species were available and they did not show uniform results. Thus Schneider and Childers (25, p. 575, 580) observed an increase in the respiration with the decreasing soil moisture until a certain equilibration was reached when the respiration levelled off. A very interesting trend in respiratory rate is reported by Brix (4) in loblolly pine. The rate dropped somewhat at the onset of drought but then increased sharply to decrease again after a very high diffusion pressure deficit developed. On the other hand in tomato the trend was different, decreasing with the decreasing soil moisture. Very irregular respiratory rates were observed by Parker (22) in the needles of Austrian pine left to dry out. He also observed a distinct difference between the rapidly and slowly drying needles. However, the general trend of the curves was downward with the decreasing moisture of the needles.

Another issue, still unsettled, is about the existence of "light" respiration as reported by Stalfelt (27, p. 411) and later by Decker (6). Stalfelt found a 50% difference between the respiration in light

and in darkness, the respiration in light being higher. His findings were lately supported by Decker who used Mimulus in his studies.

The "dark" respiration decreased with age in Douglas-fir, as reported by Krueger (16, p. 50 and 51) but it eventually levelled off at about 50 days of age in both ecotypes used in his study.

Materials and methods

The same seedlings used in the photosynthetic study were also tested for respiration. In the three-months-old seedlings of both sources, 14 seedlings were tested two or three times within a period of about one week. In the two-months-old groups eight seedlings were used in the same way but seven more single readings were obtained in addition. These single readings are shown in Figures 8 and 9 by single dots.

As in the experiments on photosynthesis, the respiratory rate was measured in a closed system of 1.63 liters volume by means of an infrared gas analyzer. The cuvette was smaller than for the photosynthetic studies and the top was opaque. The respiratory rate was expressed in milligrams of carbon dioxide released per gram of dry weight of needles per hour.

The seedlings were inserted into the cuvette and an impermeable seal was formed between the inside and outside atmosphere.

After equilibration of about 20 to 30 minutes the increase in carbon dioxide concentration in the system was measured and recorded in the range from about 330 to 350 ppm. However, at very low soil moistures when the respiratory rate decreased to a fraction of its original value, a limit of one hour was established for one single run, and the amount of added carbon dioxide carefully computed.

The results were statistically analyzed in the same way as those in the photosynthetic experiments and the comparisons and their significance are summarized in Table 7.

Table 7. Respiration. Results of the analysis of covariance.

Sources tested	Adjusted to Soil moist. %	Adjusted means	Level of significance
Valsetz 2 x 3 months	4.7	0.96	0.84 not significant
Valsetz 2 x 3 months	2.94	0.64	0.64 not significant
N. E. Wash. 2 x 3 months	4.7	1.02	0.64 1%
N. E. Wash. 2 x 3 months	2.94	0.53	0.43 not significant
Vals. x N. E. W. 2 months	4.7	0.96	1.02 not significant
Vals. x N. E. W. 2 months	2.94	0.64	0.53 not significant
Vals. x N. E. W. 3 months	4.7	0.84	0.64 1%
Vals. x N. E. W. 3 months	2.94	0.64	0.43 1%

Results and discussion

In general the respiratory rates of both sources were decreasing with the decreasing soil moisture (Figures 8, 9, 10, and 11).

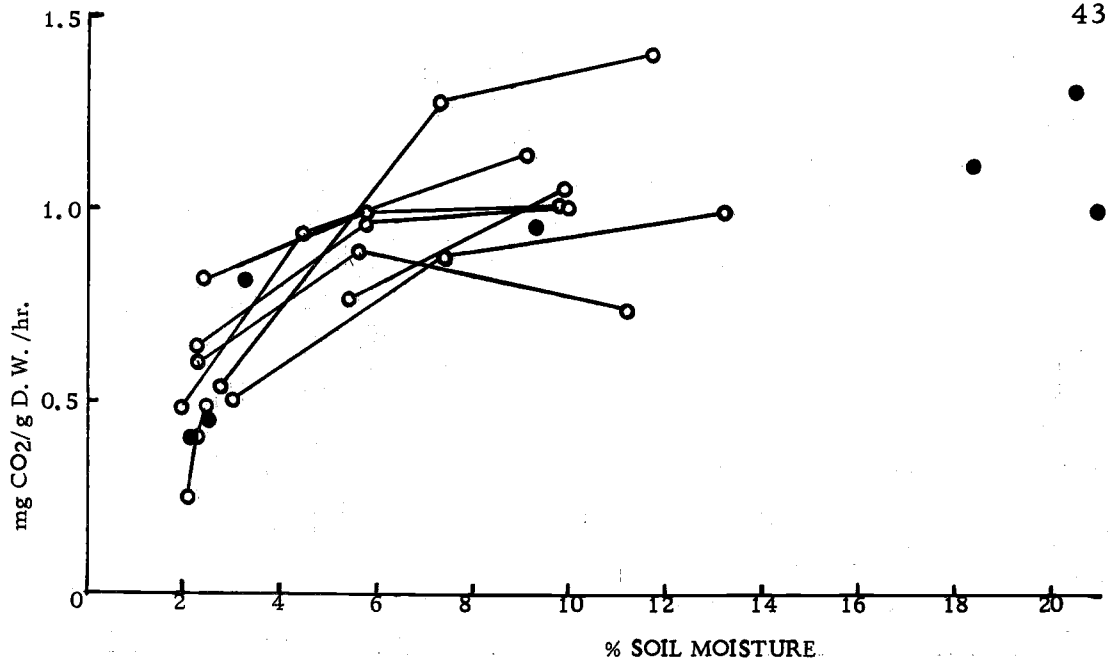


Figure 8. Respiratory rate of two-months-old Douglas-fir seedlings from Valsetz at 20 degrees C as affected by decreasing soil moisture. ● represents single reading; o---o represents repeated readings.

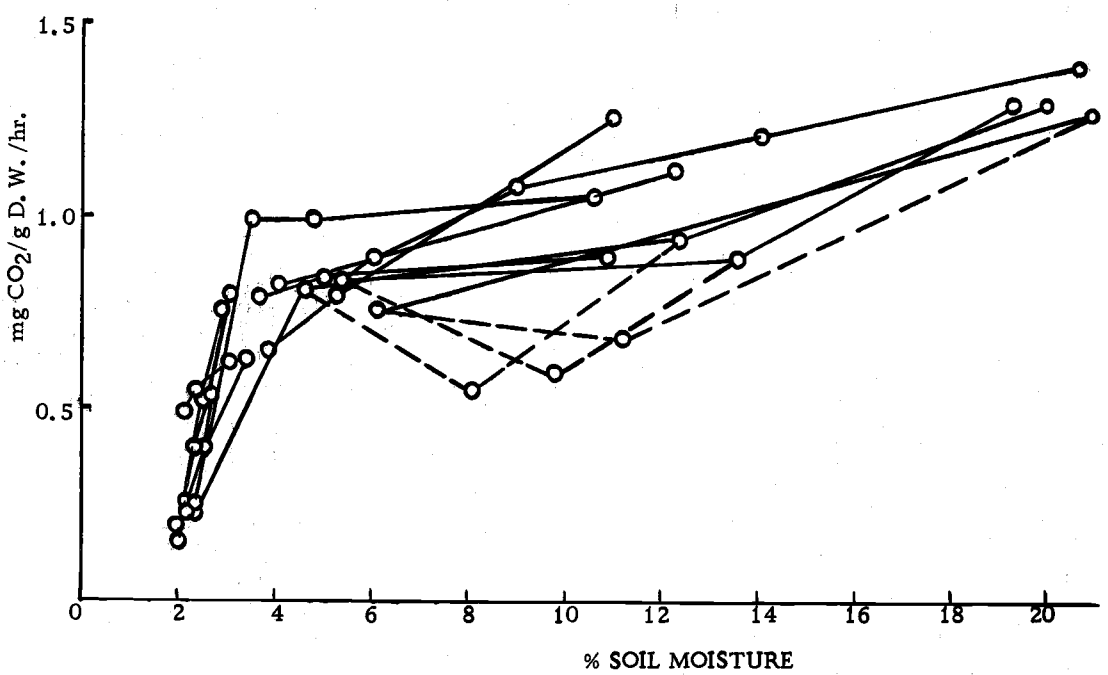


Figure 9. Respiratory rate of three-months-old Douglas-fir seedlings from Valsetz at 20 degrees C as affected by decreasing soil moisture.

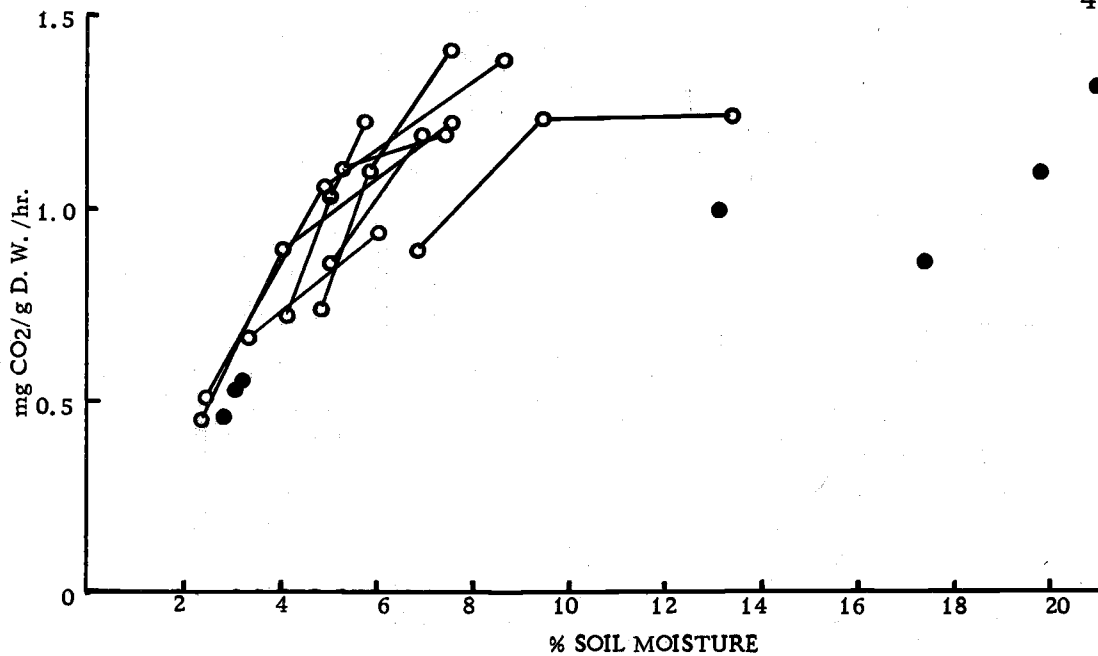


Figure 10. Respiratory rate of two-months-old Douglas-fir seedlings from N. E. Washington at 20 degrees C as affected by decreasing soil moisture. ● represents single reading. o---o represents repeated readings.

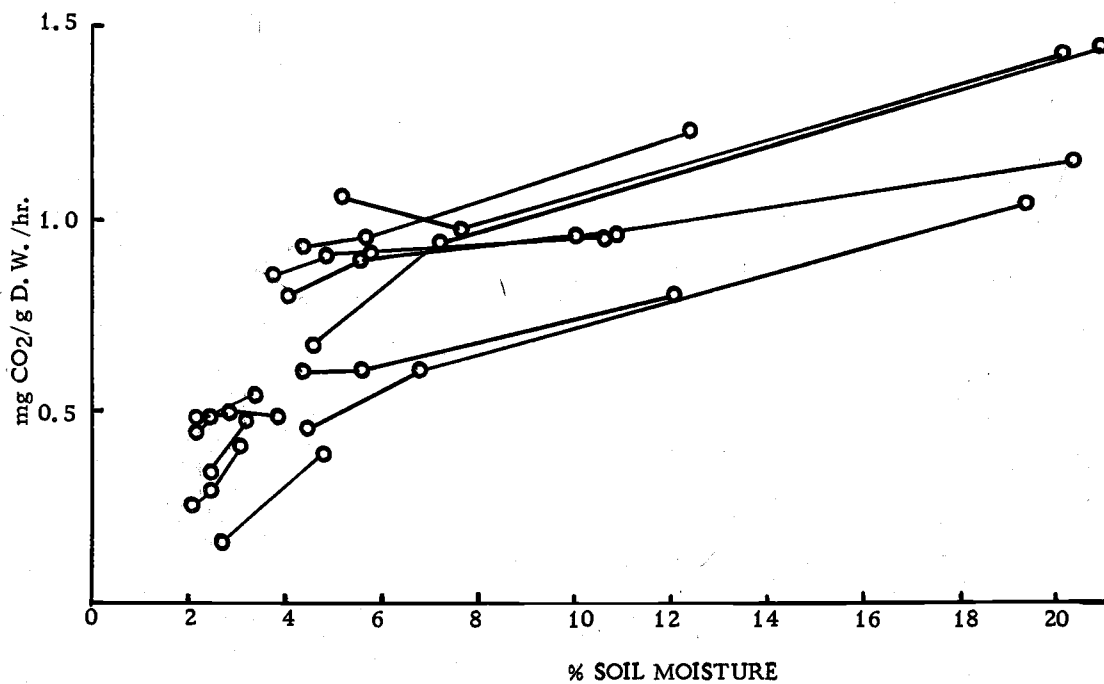


Figure 11. Respiratory rate of three-months-old Douglas-fir seedlings from N. E. Washington at 20 degrees C as affected by decreasing soil moisture.

The analysis of covariance revealed a highly significant differences between the two- and three-months-old seedlings from N. E.

Washington, and between the Valsetz and N. E. Washington seedlings three months old. The various tests performed are summarized in Table 7.

While the higher respiratory rate of the younger seedlings was significant only in the N. E. Washington source at field capacity, it was consistently higher in all remaining tests, namely in the N. E. Washington ecotype at 2.94% of soil moisture, and in the Valsetz source at both soil moistures, 4.7 and 2.94%. These results generally agree with those obtained by Krueger (14) in Douglas-fir as mentioned in the introduction.

A certain consistency was observed also between the respiratory rates of the Valsetz and N. E. Washington seedlings at both ages. At the age of three months the respiratory rates of the Valsetz seedlings were significantly higher (at 1% level) than those of the N. E. Washington plants. Assuming that this "dark" respiration was the true expression of the respiratory activity of the seedlings, then the higher rates of the Valsetz seedlings were very logical especially if the development of the seedlings after two months of age, as discussed in the section on the top/root ratio, is taken in consideration. There it was determined that the Valsetz seedlings almost

doubled the weight of the top from two to three months of age, always having much higher proportion of the newly developing foliage than the N. E. Washington plants. This implies a higher metabolic activity in the tops of the Valsetz seedlings, and the observed higher respiratory rate agrees with the expected value. The results probably would be quite different if the respiratory rates of the entire seedlings were determined because the N. E. Washington source was relatively more active in the root development.

On the average the respiratory rates in both sources at low soil moistures reached about $2/3$ of the values observed at field capacity. The decrease in the respiratory rates was relatively smaller than that in the photosynthetic rates. At higher soil moisture, e. g. at 9.5%, the respiratory rate reached 7.1% of the photosynthetic rate observed at the same moisture content. This proportion did not change appreciably, being about 6.9% at the field capacity and 8.7% of the net photosynthetic rate at 2.94% of soil moisture.

Contrary to the results obtained by Schneider and Childers in apple trees, there was no increase in the respiratory rate at the onset of drought. The rate was decreasing steadily resembling the results which Brix obtained in the tomato plant, or in loblolly pine before very high diffusion pressure deficits were reached.

The excessive decrease in the photosynthetic rate caused by

overheating and darkness in the growth chamber, as discussed in more detail in the section on preliminary experiments, was accompanied by a similar decrease in the respiratory rate. These rates are shown in Figure 11 by a broken line. The normal rate, as in the photosynthetic study, was reached relatively soon, on the following day.

EFFECT OF DECREASING SOIL MOISTURE ON TRANSPIRATION

Introduction

Transpirational rate may be reduced by drought as well as by flooding (10). However, drought seems to be by far the more important and common factor in the transpirational decrease. According to some workers the transpiration is reduced sooner than the photosynthesis (15; 25) but others observed simultaneous decrease and similarity in both (4; 21) at about the same time.

The variation in the transpiration is not caused by the differences in soil moisture only but also by the species itself (11; 13; 26). Generally it is agreed that the transpirational rate decreases with the decrease in soil moisture. Satoo (24) reported a slight decrease at first but once a certain point, specific to a given species was reached, the decrease became sudden. After such a sudden decrease Slatyer (26, p. 325) obtained in privet and tomato a very low level of transpiration that reached about 5% of maximum. This occurred at approximately 30 atmospheres of total soil moisture stress (TSMS) but with further increase in TSMS the transpirational rate did not change appreciably. Martin (17) obtained a decrease in transpiration in sunflower only when 2/3 of the available water was removed. And finally Veihmeyer and Hendrickson (30; 31)

did not find any change in the transpiration between field capacity and wilting point.

The mechanics of transpiration was investigated by Gaastra (8, p. 63) who thinks that transpiration is more dependent on stomatal conditions than photosynthesis because transpiration is limited by the sum of the diffusion resistance in the external air and stomatal resistance only, while carbon dioxide diffusion in addition is dependent on the resistance in the mesophyll cells.

Leaf structure is said to be a poor indicator of transpirational rates but there is some indication that the root system has some influence on total water removed from the soil; shallow-rooted species usually remove less (11) than deep-rooted plants. The absorption is probably a limiting factor in transpiration because even under conditions of high soil moisture, water stress may develop in the plant and reduce the rate (4; 11; 12).

Materials and methods

Twelve Valsetz and fifteen N. E. Washington seedlings were grown in one pint plastic pots for two months. Sandy soil was used as in the previous studies. The soil of about half of the seedlings had been soaked with water 24 hours before the experiment was started while the other half was left unwatered for three days.

Then all the pots were sealed on the bottom and top with paraffin of low melting point and weighed to the nearest 0.01 g. They were placed in a hot chamber with a day temperature of 35 degrees C and night temperature of 20 degrees C. The relative humidity in the chamber was relatively high at night but during the day it dropped to about 60%.

The transpirational loss was obtained by repeated weighing every second or third day. The paraffin seal was always carefully checked for cracks and resealed with a hot wire whenever necessary. Lack of aeration showed up in several seedlings of both sources under the high soil moisture regime and they had to be discarded. But most seedlings survived for one or even two months, and were able to transpire most of the available water from the pot. The transpirational rates were expressed in grams of water per gram of dry weight of needles per day, and are summarized in Figures 12 and 13.

Results

The transpirational rates plotted over the soil moisture content showed a curvilinear correlation, however below 12% of soil moisture the curvilinearity was very small and so analysis of covariance was made for linear regression in this interval. It showed

that the transpirational rates of the Valsetz seedlings were significantly higher (at 1% level) when adjusted to 4.7% of soil moisture, and at 5% level, when adjusted to 2.94% of soil moisture. The corresponding values on the soil moisture stress scale are 0.1 and 15 atmospheres. Actually at any soil moisture content the Valsetz seedlings transpired more than the N. E. Washington plants. The ecological implications of this different rate will be discussed later. From the graphs it is apparent that in both sources the maximum transpirational rates were not reached at the highest soil moistures at the beginning of the experiment but were progressively increasing until the maximum rates were attained at about 12% of soil moisture.

Discussion

A reduced transpirational rate at the highest soil moistures is usually traced back to the lack of aeration, as exemplified by flooding, and desiccation may result if the flooding is prolonged. However, under the conditions of this experiment the aeration was interrupted completely by the paraffin seal at the beginning of the testing, and consequently it would be difficult to explain the lower transpirational rates at the highest soil moistures only in the terms of aeration. Another explanation for this low rate is that it may be

due to continued growth of the seedlings during the experiment. One of the assumptions in this as well as in the previous photosynthetic study was that the growth would be essentially linear between the beginning and the end of the experiment. This assumed growth probably was not too different from the true one in a short-time study, such as was that on photosynthesis. But in this transpirational study the period was very long reaching in some seedlings up to 53 days. If the assumed growth were not linear, and there is some evidence that it actually was not, but curvilinear, so that the weight increase of the seedling at the beginning of its life would be very small but increasing gradually with the age, then by the linear interpolation from the final weight, the weights at all previous ages would be overestimated and at the same time the transpirational rates underestimated. This could be further aggravated if the growth of the seedling after certain time of deprivation from normal oxygen supply slowed down or even stopped completely as shown in Figure 14. Then the computed transpirational rates at the beginning of the study would be excessively small. This very well could have happened in this study and if it actually did, then the initial lower transpirational rates could be explained in these terms.

The difference in the transpirational rate is of ecological importance and brings further evidence for distinguishing Valsetz and

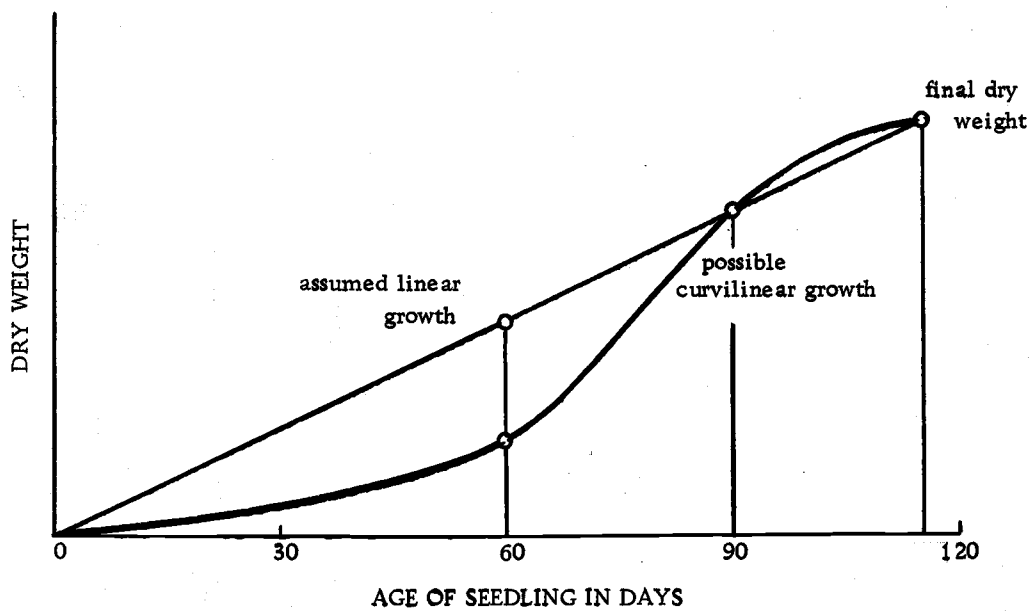
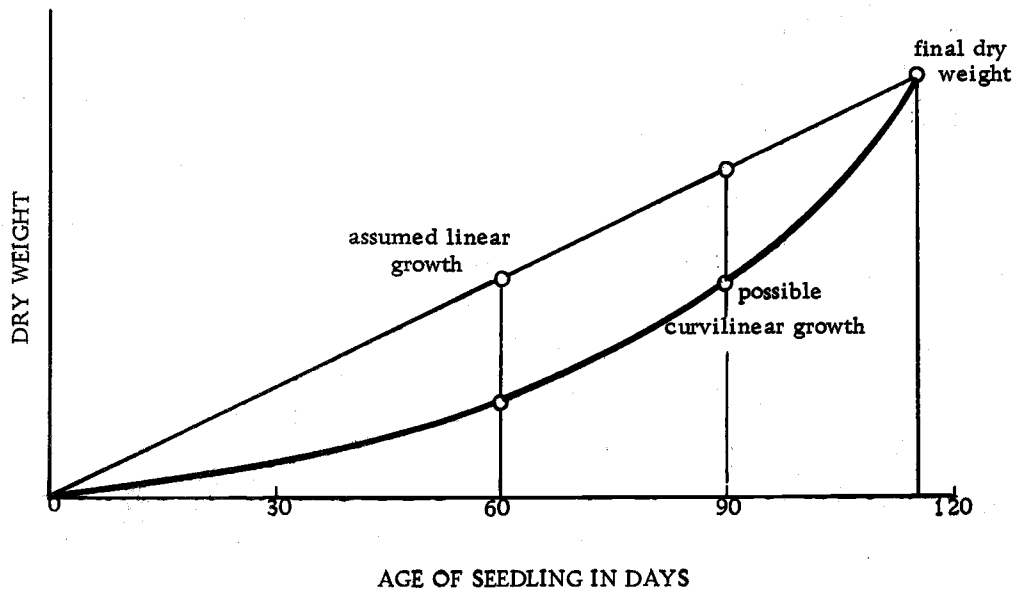


Figure 14. Two possibilities for the curvilinear growth of Douglas-fir seedlings.

N.E. Washington seedlings as two different ecotypes. The Valsetz seedlings used on the average much more water than the N. E. Washington plants in which the periodical drought presumably eliminated individuals with high demands for water. On the contrary the N. E. Washington seedlings use moisture very conservatively which makes them more suitable for droughty sites.

In both sources there was a definite decrease in transpiration from the high to low soil moistures, in accordance with most other studies. A very pronounced decrease in the transpirational rate was observed at soil moistures well above the field capacity, and this decrease remained basically the same even below the wilting point which contradicts the results obtained by Veihmeyer and Hendrickson (30; 31) who did not find any change in transpiration between field capacity and wilting point.

In this study the transpirational rate started to decrease approximately at the same time as the photosynthetic rate. The most important difference between these two processes was the degree of the decrease. The photosynthetic rate was decreasing very slowly at first, but the transpirational rate, disregarding the initial dubious increase, decreased very distinctly and almost linearly from relatively high soil moistures, and continued so to the lowest used in this study.

ECOLOGICAL IMPLICATIONS

Birand (2) in his study on the relation between the root and aerial growth of certain xerophytes came to the conclusion that the structure of the desert plants is deliberately designed to secure a maximum root development for a minimum expenditure of the assimilation products. Actually the natural selection was the driving force; the severity of a desert climate exercised a strong pressure on the plant species eliminating those unfit for the prevailing environmental conditions.

Some results in this study have ecological implications as well, and point to the natural selection as the main causative factor. Thus the top/root ratio and transpirational rate of the N. E. Washington seedlings have been found significantly different from those of the Valsetz plants. We may say that the natural selection in the N. E. Washington source gradually eliminated seedlings with excessive transpiration as well as plants with unfavorable top/root ratio. The lower top/root ratio may be of survival value on many droughty sites because the relatively more numerous roots would provide the moisture necessary for survival much easier than would be the case in seedlings with a high top/root ratio, as found in the Valsetz source. In addition the situation in the Valsetz seedlings is aggravated by

their higher transpirational rate when compared with the N. E. Washington ecotype.

Another observation based on the results of this study involves the differences in the photosynthetic rates between two- and three-months-old seedlings of both sources, at low soil moisture contents. The photosynthetic rate of the three-months-old seedlings was found significantly higher than that of the two-months-old plants (at 1% level). In other words the younger seedlings are more vulnerable under drought conditions, slowing down their growth which under optimal conditions of soil moisture has been found consistently higher than that of the three-months-old plants (see Table 6).

The problems with which foresters have to cope involve the establishment of a new stand on droughty sites. Usually local seed source is said to be the best; and it probably is under natural conditions. But man frequently creates more severe conditions than are those found in virgin forests. Very severe conditions for survival of the seedlings are created by clearcutting the old stands on extensive areas. On such clearcuts the reestablishment of the new stand by planting seedlings obtained from a nearby nursery may not be successful despite the fact that the local seed source was used, which is not always the case. If the forester could better evaluate the conditions under which the seedlings will develop he probably

would reject the local source and use another one which is proved to be more resistant to such critical conditions. No doubt, the potential growth of such a source should also be considered.

The drought, possibly combined with heat, is one of the major obstacles in the establishment of a new plantation on exposed, critical sites. Large amounts are spent on replanting in addition to the original planting cost, and many times special measures are required to make the survival of the seedlings more likely. Among them various protectors of the stem, spraying of the planting areas with herbicides to reduce the competition for moisture, or cultivating of such areas should be mentioned. These measures are sometimes successful. But there is a strong indication that a physiological study of several ecotypes could provide the best answer to the above mentioned problems.

SUMMARY

The effect of the decreasing soil moisture on the rates of photosynthesis, respiration, and transpiration in two ecotypes of Douglas-fir was studied. The photosynthetic rate was also determined in relation to the relative turgidities of needles.

In general with decreasing soil moisture the photosynthetic, respiratory, and transpirational rates also decreased. The photosynthetic rates of the two-months-old seedlings of both sources were consistently higher under optimal conditions of the soil moisture, but they were significantly lower (at 1% level) at low soil moistures than the three-months-old plants. There was no significant difference found in the photosynthetic rates between the two sources at two months of age, but significantly higher photosynthetic rate at high soil moistures was found in the three-months-old N. E. Washington seedlings when compared with the Valsetz plants. While the photosynthetic rates in these plants at very low soil moisture was not significantly different, there is an indication that such a difference would be found if a larger number of seedlings were tested.

The respiratory rates of the two-months-old seedlings of both sources were consistently higher than those of the three-months-old

plants. The difference in respiratory rate between the two ecotypes was not significant at two months of age, but they were significantly higher in the Valsetz seedlings at three months. This was probably due to the relatively larger proportion of the newly developing needles in this ecotype. There was no increase in the respiration observed when the drought set on as reported by some workers.

The relation between the soil moisture and transpirational rate was linear in both sources in the range of soil moisture below 12%. In this range the transpiration of the Valsetz seedlings was significantly higher (at 1% level) than that of the N. E. Washington plants. It was also observed that for the same soil moisture a higher relative turgidity was found in the N. E. Washington seedlings than in the Valsetz source.

The top/root ratios were found significantly different between the two- and three-months-old seedlings of both sources, and also between the Valsetz and N. E. Washington seedlings at two and three months of age. These ratios decreased in both sources between the ages of two and three months, and the ratio of the three-months-old N. E. Washington seedlings was the lowest, while that of the two-months-old Valsetz plants the highest.

The relatively lower top/root ratio in the N. E. Washington seedlings combined with their lower transpirational rates is of

definite advantage for survival on droughty sites. Probably the periodical droughts of N. E. Washington exercised a strong selection pressure in that direction. It is suggested that the use of such drought-resistant seed source on extreme sites would increase the survival.

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