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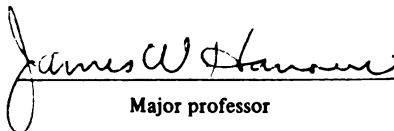
The Effect of Drought Stress on the Growth, Development,
Photosynthesis and Transpiration of Six Species of
North American Spruce

presented by

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ABSTRACT

THE EFFECT OF DROUGHT STRESS ON THE GROWTH, DEVELOPMENT, PHOTOSYNTHESIS AND TRANSPIRATION OF SIX SPECIES OF NORTH AMERICAN SPRUCE

By

Bruce Allan Rottink

Drought stress influenced numerous parameters of size in six-month old greenhouse grown seedlings, as well as survival. In any seedlot the percentage of seedlings which formed dormant apical buds was in most cases independent of water treatment level.

The net photosynthetic rate of blue spruce (Picea pungens Engelm.), a species native to arid areas, is not depressed as much by a reduction in soil water potential as is the net photosynthetic rate of Sitka spruce (P. sitchensis [Bong.] Carr.), a species native to moist areas. The net photosynthetic rate of Sitka spruce seedlings also recovered less completely and more slowly following a post-drought watering than species native to more arid areas. Seedlots which are most drought resistant tend to alter their transpiration rates more in response to changes in

soil water potential than seedlots which are less drought resistant.

Drought stress appeared to have little influence on the development of needle surface waxes. The few changes that were observed were not consistent within a species. There were no obvious differences in needle surface waxes between the species of spruce.

In some instances, the relative sizes of the plant organs varied with water treatment. Plants growing under dry conditions tended to have heavier stems, at the expense of needle production. As needles are the principle water-losing organs, this change could have adaptive significance.

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PHOTOSYNTHESIS AND TRANSPIRATION OF SIX SPECIES
OF NORTH AMERICAN SPRUCE

By

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INTRODUCTION

Seven species of spruce including white spruce (Picea glauca [Moench] Voss), black spruce (P. mariana [Mill.] B. S. P.), red spruce (P. rubens Sarg.), blue spruce (P. pungens Engelm.), Engelmann spruce (P. engelmannii Parry), Sitka spruce (P. sitchensis [Bong.] Carr.) and Brewer spruce (P. breweriana S. Wats.) are native to the United States and/or Canada (Harlow and Harrar, 1958). All species except Brewer spruce, which has an extremely limited distribution, are of commercial importance.

The habitats occupied by the various species differ greatly, especially in degree of aridity.

This study was undertaken to determine the responses of the various species to drought stress and, by comparing their responses to determine ways in which the various species have adapted to the water regime of their native habitat. The responses studied were:

1. Growth and development of the seedlings.
2. Exchange of carbon dioxide and water vapor between the plant and the atmosphere.
3. Development of epicuticular waxes on leaf surfaces.

Data on rates of seedling emergence were also collected to determine if this characteristic is of adaptive significance.

This study was conducted entirely with seedlings because:

1. A variety of species can be assembled for study at a single location with a minimum of preconditioning effects if seed is collected and the plants grown at a single location.

2. The seedling stage has been widely recognized as the most crucial stage in the development of a plant (Bates, 1924; Clark, 1961; Cleary and Waring, 1969).

The results of this study are of potential interest to:

1. Phytogeographers seeking information about factors which may influence the distribution of the North American spruces.

2. Physiologists concerned with changes in the plant caused by drought stress.

3. Geneticists and tree breeders who desire to understand the variability within the genus Picea.

CHAPTER I

EFFECT OF DROUGHT STRESS ON GROWTH AND DEVELOPMENT OF SIX SPECIES OF NORTH AMERICAN SPRUCE

Included among the many ways in which a species of plant might adapt to drought stress are the following:

1. Swift passage through drought sensitive stages of development.
2. Alteration of form to a more drought resistant type.

The purpose of this experiment was to:

1. Determine which species of the genus Picea (spruce) studied were drought resistant and which were not.
2. Determine the rates of seedling emergence.
3. Compare seedling form to determine if this was altered by drought to a more drought resistant form, or if differences in form which have adaptive significance exist between seedlots.

Materials and Methods

Seed of six species of spruce were collected from native stands. Two collections were made for each species from geographically diverse areas (Table 1). In each

TABLE 1. Seedlots of Picea used in this study.

Seedlot	Species	Origin	Seed-weight	MSU Accession Number
Blu-SS	<u>P. pungens</u>	Steamboat Springs, Colorado	4.7mg	8429
Blu-GS	<u>P. pungens</u>	Glenwood Springs, Colorado	5.1mg	8181
Eng-Col	<u>P. engelmannii</u>	Steamboat Springs, Colorado	3.5mg	8425
Eng-Mont	<u>P. engelmannii</u>	Selway-Bitterroot Wilderness, Montana	2.7mg	8589
Wh-Alas	<u>P. glauca</u>	Fairbanks, Alaska	2.6mg	8517-23
Wh-Mich	<u>P. glauca</u>	Barbeau, Michigan	2.7mg	8550-54
Sit-Alas	<u>P. sitchensis</u>	Juneau, Alaska	2.3mg	8555
Sit-Ore	<u>P. sitchensis</u>	Otis, Oregon	2.6mg	8562-66
Bla-BC	<u>P. mariana</u>	Ft. Nelson, British Columbia	1.2mg	8573-77
Bla-Mich	<u>P. mariana</u>	Barbeau, Michigan	1.3mg	8583-87
Red-Que	<u>P. rubens</u>	Portneuf County, Quebec	3.4mg	8603
Red-WVa	<u>P. rubens</u>	Marlinton, West Virginia	4.9mg	8597

stand, seed was collected from four or more trees, mixed, and weighed before sowing.

About 40 seeds were sown to a uniform depth in plastic pots 22 cm tall and 16 cm in diameter in a glass-house in June 1972. They were grown in a soil mixture of

shredded peat and sandy loam. The following equation relating percent of moisture in the soil to soil water potential was determined experimentally using a soil pressure membrane apparatus:

$$\log_{10} (\% \text{ soil moisture}) = 1.847 - .207 (\log_{10} [-\text{soil water potential (lbs.)}]).$$

Continuous fluorescent lighting supplemented natural daylight.

Seedlings were thinned to 14 per pot 2 to 5 days after emergence, and to 7 per pot two weeks later.

One blue spruce seedlot and one red spruce seedlot germinated very poorly. Seedlings in these lots were pulled out and seed from lots Blu-GS and Red-WVa were planted as replacements two weeks after the other lots were sown. For this reason, these two seedlots are treated separately in most of the analyses.

The soil was kept continually moist for the first month after sowing, at which time watering was halted to allow establishment of different water regimes. Because the seedlings began to die rapidly, watering was resumed 10 days later and continued for an additional two weeks. At this point, trees were thinned to three uniformly spaced seedlings per pot.

The pots were then allowed to begin drying out again, and three watering regimes were established. The

pots were weighed daily and sufficient water was added to saturate the soil when the moisture content of the soil declined to 45%, 32% and 25% for the wet, medium and dry treatments, respectively. These treatments are the equivalent of -0.6 , -3.4 and -8.3 atmospheres soil water potential. These levels were selected on the basis of results from a preliminary glasshouse test to determine maximum tolerable levels of drought stress and a review of previously reported experiments (Babalola, Boersma and Youngberg, 1968; Boyer, 1965; Jarvis and Jarvis, 1963; Larson and Schubert, 1969; Larson and Whitmore, 1970; Sands and Rutter, 1959; Stransky and Wilson, 1964). This schedule resulted in the "wet" treatment being watered once every two or three weeks when the seedlings were small. Obviously all treatments were quite dry.

There were six pots in each seedlot-water level treatment combination.

Six months after sowing, the trees were harvested. Measurements taken on the seedlings included: stem diameter immediately below the cotyledons (calipered to the nearest $.01$ cm), total height (to the nearest $.1$ cm), fresh and dry weight of the root system, fresh weight of the shoot, dry weight of needles, dry weight of stem plus branches (all weights to nearest $.001$ grams), length of the longest root from the groundline to the tip (to the nearest $.5$ cm), and the mean length of five needles picked from the stem

at uniform intervals (to the nearest .1 cm). Simple correlations were calculated for all possible combinations of the measured parameters. The presence or absence of a dormant apical bud at the time of harvest was also noted.

Data on seedling size were analyzed by a factorial design analysis of variance with seedlots and water levels used as factors, pots as replicates and seedlings within pots as subsamples. Significance of differences between means of various seedlot-water level treatment combinations was determined using Tukey's HSD test (Steel and Torrie, 1960).

The logarithms of the dry weights of the needles, stems, and roots were individually regressed on the logarithm of the total dry weight of the seedling for each seedlot-water level treatment combination. This was done separately for those seedlings which had apical buds and those which did not. Differences in the regression coefficients were tested by the method described in Steel and Torrie (1960, p. 173).

Seedling emergence was determined by taking a daily count of emerged seedlings in each pot. Counts continued for ten days after the emergence of the last seedling. "Days to 50% emergence" was that day on which 50% of all seedlings in a pot had emerged. A one-way analysis of variance was performed on these data and differences between seedlots were tested by Tukey's HSD test.

Survival of seedlings in each pot was calculated at harvest as a percentage of the trees alive when differential watering was initiated. These data were analyzed by a factorial design analysis of variance, with seedlots and water levels as factors, and pots as replicates.

Differences in percentages of trees having a dormant apical bud were analyzed by computing Chi-squared values in a contingency table for all possible pairs of seedlots and water levels.

Results and Discussion

Species considered to be from moist habitats (Sitka and red spruce) emerged significantly more slowly than species considered to be from more xeric areas (blue and Engelmann spruce). In every instance, the more southerly of the two seedlots of a species emerged more slowly than did the northern-most seedlot (Table 2). These results are consistent with the results of previous studies which have indicated that blue spruce germinates more rapidly than white spruce (Hanover and Wilkinson, 1969), and that red and Sitka spruce germinate more slowly than white, blue, black or Engelmann spruce (Heit, 1961). A correlation between rate of emergence and seed weight was found to be nonsignificant.

In xeric areas it would seem advantageous for a seed to germinate and become established as rapidly as

TABLE 2. Number of days from planting required for emergence of 50% of seedlings.

Seedlot	Days to 50% Emergence
Sit-Ore	14 ¹ a
Red-Que	13ab
Sit-Alas	12bc
Wh-Mich	12bc
Bla-Mich	11cd
Wh-Alas	11cd
Bla-BC	11cd
Eng-Col	10de
Blu-SS ²	10de
Eng-Mont	9e

¹Each entry is the mean of 18 pots, 20 to 40 seedlings per pot. Numbers not followed by a common letter are statistically different at the 5% level as determined by Tukey's HSD test.

²Seedlot Blu-GS was sown slightly later than these seedlots and so germinated under somewhat different conditions. Days to 50% emergence for Blu-GS was 9.

possible following the onset of favorable conditions, as these conditions might be of short duration.

Both seedlot (Table 3) and water treatment level (Table 4) are significant factors determining survival of seedlings. The interaction of seedlot and water treatment level is not significant at the 5% level. Of the two seedlots with significantly lower survival rates, Sit-Alas had a very low survival rate in the dry treatment, thus

TABLE 3. Percent of seedlings surviving after six months.

Seedlot	Percent Survival
Wh-Alas	94.4a ¹
Wh-Mich	92.6ab
Eng-Col	90.7abc
Red-Que	88.1abc
Eng-Mont	80.9abc
Sit-Ore	76.9abc
Blu-SS	75.9abc
Bla-Mich	68.5abc
Sit-Alas	66.7bc
Bla-BC	64.3c

¹Percentages not followed by a common letter are statistically different at the 5% level as determined by Tukey's HSD test.

TABLE 4. Percent of seedlings surviving after six months under three watering regimes.

Water Regime	Percent Survival ¹
Wet	85.3a ²
Medium	83.7ab
Dry	71.3b

¹Average of all seedlots except Blu-GS and Red-WVa.

²Percentages followed by a common letter are not statistically different at the 5% level as determined by Tukey's HSD test.

lowering overall seedlot survival percentage, while seedlot Bla-BC had poor survival rates at all water treatment levels.

Six months after sowing, the percentages of seedlings possessing dormant apical buds varied significantly between seedlots (Table 5), but not between water levels averaged over all seedlots (Table 6). Testing all possible pairs of water treatment levels by individual seedlots, the only significant difference found was in seedlot Wh-Mich, where 53% of the seedlings in the dry treatment had apical buds, but only 6.2% of the seedlings in the medium treatment had apical buds.

Taken as a whole, the data indicate that drought stress does not have a strong influence on the formation of dormant apical buds. The formation of an apical bud, with the attendant halt in height growth, may, however, be of some significance in survival under drought conditions. The two seedlots possessing the largest percentage of seedlings with apical buds also had the highest survival rate.

Within any given seedlot-water level treatment combination all measures of seedling weight were consistently and highly correlated with total dry weight of the seedling ($r^2 \geq .85$). Therefore, of all the measures of seedling weight, only total dry weight is presented (Figure 1). The dry weights of seedlots Wh-Alas, Wh-Mich, Eng-Mont, Red-WVa, Sit-Alas and Sit-Ore are averaged and presented as

TABLE 5.--Percentages of seedlings in each seedlot which did not possess an apical bud six months after sowing.

Seedlot	% Not Possessing An Apical Bud
Bla-Mich	100.0a ¹
Sit-Ore	100.0a
Blu-SS ²	95.1a
Eng-Mont	92.3a
Eng-Col	91.8a
Red-Que ²	90.2ab
Sit-Alas	88.2ab
Bla-BC	83.3ab
Wh-Mich	66.0ab
Wh-Alas	17.6b

¹Any values followed by a common letter are not statistically different at the 5% level when tested in a contingency table with the Chi-squared statistic.

²Seedlots Blu-GS and Red-WVa were planted slightly later than these seedlots. Values for Blu-GS and Red-WVa are 94.3% and 94.4%, respectively.

TABLE 6. Percentages of seedlings not possessing apical buds six months after sowing.

Water Regime	% Not Possessing An Apical Bud
Wet	82.4 ¹
Medium	83.3
Dry	72.1

¹None of the values are significantly different at the 5% level when tested in a contingency table with the Chi-squared statistic.

TABLE 7. Significance levels for differences between various measures of growth for ten seedlots of spruce at three watering levels.

Parameter	Water Level	Seedlot	Seedlot X Water Level
Total dry weight	***	***	***
Stem diameter	***	***	N.S.
Shoot height	***	***	***
Needle length	*	***	***
Root length	**	***	**

* $p < .05$

** $p < .01$

*** $p < .001$

N.S. Non significant at the 5% level.

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Figure 1.--Mean total dry weights of seedlings of twelve seedlots of spruce grown under three watering regimes. Differences in seedling dry weight significant at the 5% level include:

Blu-SS wet > Blu-SS dry.
 Blu-GS wet > Blu-GS dry and medium.
 Bla-Mich wet > Bla-Mich dry and medium.

Within the:

Wet Treatment

Blu-GS>Eng-Col, Eng-Mont, Wh-Alas, Wh-Mich, Sit-Alas,
 Sit-Ore, Bla-BC.
 Bla-Mich>Eng-Col, Eng-Mont, Wh-Alas, Wh-Mich, Sit-Alas,
 Sit-Ore.
 Red-Que>Sit-Alas, Sit-Ore.

Medium Treatment

Blu-GS>Wh-Alas, Sit-Alas, Bla-BC.

Dry Treatment

No significant differences.

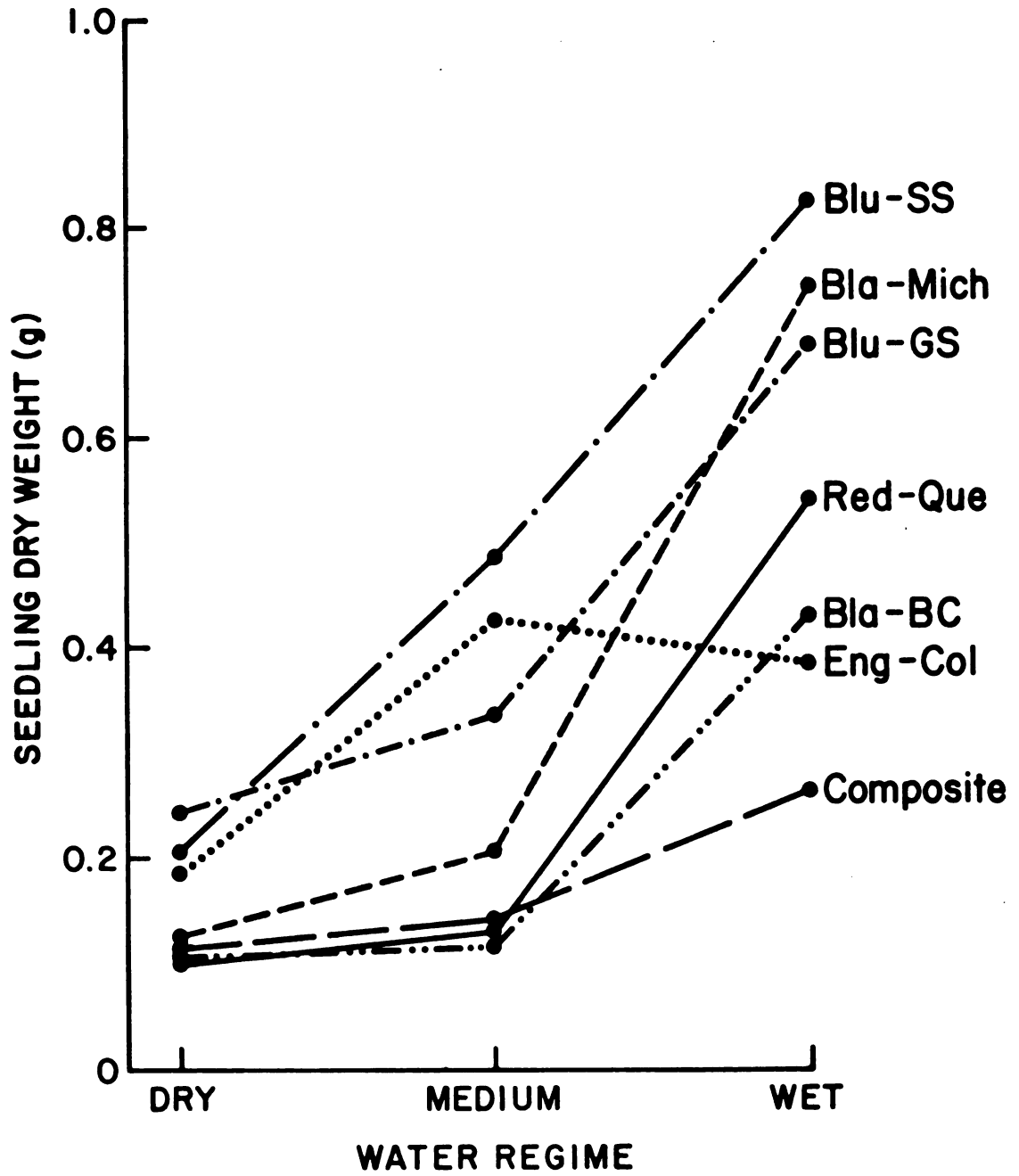


Figure 1

a composite line because they responded nearly identically to all treatments.

Judging from the climatic conditions at the point of origin of the various seedlots, other experiments (see Chapter II), and the growth of seedlings under "normal greenhouse conditions," it is evident that the drought resistant seedlots were those in which the size of the seedlings varied with water treatment levels. Apparently, the seedlings from wet habitats were so stressed at all water treatment levels that little growth could occur.

It should be noted that some of the difference between total dry weight of the seedlings from the various seedlots was due to differences in seed weight. The correlation of mean seedling dry weight for each seedlot and seed weight was significant at the 5% level (with a correlation coefficient of .61) for the dry treatment. The correlation of seedling dry weight and seed weight was not significant for the medium and wet treatments, however. Correlation of the other size parameters with seed weight indicated that with the exception of needle length, there was no significant correlation between any parameter of seedling size and seed weight at the wet treatment level. At the medium treatment level, only needle length and stem diameter were correlated with seed weight. At the dry treatment level all size parameters were significantly correlated with seed weight.

Based on the number of significant differences within a seedlot caused by water treatment level, the parameters

of growth in decreasing sensitivity to drought stress are:
stem diameter > shoot height > total dry weight > root
length = needle length (Tables 8 through 11).

The impact of drought stress on needle length is much more dramatic than Table 10 indicates. Visual observation indicated that the needles elongating and/or forming immediately after a pot was watered were long, straight and "normal" in appearance. Needles elongating and/or forming while the plant was under drought stress were considerably shorter and oftentimes twisted in a helical coil around the plant stem. Following watering, these twisted and coiled needles did not alter their appearance. Examples of this coiling behavior were observed in seedlots Blu-SS, Blu-GS, Eng-Col and Wh-Mich. The technique of averaging the lengths of five needles per tree doubtless helped to obscure these differences, by including needles formed under both wet and dry conditions.

The depth of the soil the seedlings were growing in was about 20 cm, and it is evident that in most cases the roots extended to the bottom of the pot. It is possible that when the root tip encountered the bottom of the pot, the growth of the root may have been altered in an unnatural manner, and for this reason the root lengths are of dubious significance.

Analyzing the linear relationships that exist between the logarithms of dry weights of different plant

TABLE 8. Stem diameters of spruce seedlings grown under three watering regimes.

Water Regime	Seedlot											
	Blu- SS	Blu- GS	Eng- Col	Eng- Mont	Wh- Alas	Wh- Mich	Sit- Alas	Sit- Ore	Bla- BC	Bla- Mich	Red- Que	Red- WVa
							cm					
Wet	.18a ¹	.17 ²	.15ab	.15ab	.14ab	.15ab	.13b	.12b	.14ab	.15ab	.15ab	.12 ²
Medium	.14a	.12 ^{2,*}	.13ab	.11abc	.08c*	.09bc*	.09abc	.08bc	.03bc*	.09abc*	.10abc*	.09 ²
Dry	.11a*	.10 ^{2,*}	.16a*	.09a*	.07a*	.08a*	.08a	.07a	.08a*	.07a*	.08a*	.09 ^{2,*}

¹Values within a row followed by a common letter are not significantly different at the 5% level.

²Not tested against other seedlots at the same water level because of difference in sowing time.

* Significantly different at the 5% level than the wet treatment of the same seedlot.

TABLE 9. Shoot heights of spruce seedlings grown under three watering regimes.

Water Regime	Seedlot											
	Elu- SS	Elu- GS	Eng- Col	Eng- Mont	Wh- Alas	Wh- Mich	Sit- Alas	Sit- Ore	Bla- BC	Bla- Mich	Red- Que	Red- WVa

¹Values within a row followed by a common letter are not significantly different at the 5% level.

²Not tested against other seedlots at the same water level because of differences in sowing time.

* Significantly different at the 5% level than the wet treatment of the same seedlot.

TABLE 10. Mean needle lengths of spruce seedlings grown under three watering regimes.

Water Regime	Seedlot											
	Blu- SS	Blu- GS	Eng- Col	Eng- Mont	Wh- Alas	Wh- Mich	Sit- Alas	Sit- Ore	Bla- BC	Bla- Mich	Red- Que	Red- WVa
Wet	15 ¹	17 ²	10bc	10bc	11b	10bc	8c	9c	10bc	10bc	11b	11 ²
Medium	13c	13 ²	11ab	10bc	10bc	9bc	8c	8c	8c	8c	8c	9 ²
Dry	10a*	13 ² *	10a	9a	10a	9a	8a	9a	8a	8a	9a	10 ²

¹Values within a row followed by a common letter are not significantly different at the 5% level.

²Not tested against other seedlots at the same water level because of differences in sowing time.

* Significantly different at the 5% level than the wet treatment of the same seedlot.

TABLE 11. Mean root lengths of spruce seedlings grown under three watering regimes.

Water Regime	Seedlot											
	Blu- SS	Blu- GS	Eng- Col	Eng- Mont	Wh- Alas	Wh- Mich	Sit- Alas	Sit- Ore	Bla- BC	Bla- Mich	Red- Que	Red- WVa
Wet	24c	29 ²	26c	24bc	29c	26c	16a	18ab	21abc	24bc	26c	23 ²
Medium	25ab	23 ² *	27a	24ab	21abc	21bc	14d	15cd	18bcd	22abcd	19abcd	18 ²
Dry	23a	24 ²	22ab	22ab	24a	21abc	13c	11bc	17abc	20abc	17abc*	20 ²

¹Values within a row followed by a common letter are not significantly different at the 5% level.

²Not tested against other seedlots at the same water level because of differences in sowing time.

* Significantly different at the 5% level than the wet treatment of the same seedlot.

organs has been shown to be the most meaningful way to study the distribution of dry matter in plants (Ledig, Bormann and Wenger, 1970). The smaller the regression coefficient of the regression of the logarithm of the dry weight of a plant organ on the logarithm of the total dry weight of the plant, the slower the organ is growing compared to the rate at which the whole plant is growing.

In this study, equations of the form:

$$\log_{10}(\text{dry weight of an organ}) = a + b (\log_{10}[\text{total dry weight of seedling}])$$

related the two dry weights in such a way that the regression was usually significant at the 0.1% level, with $r^2 > .85$ (Tables 13 through 15).

Seedlot-water level treatment combinations containing sufficient seedlings possessing apical buds to construct regression equations and allow comparison with regression equations for seedlings which did not possess apical buds were: Blu-SS (dry), Wh-Alas (dry, medium and wet), Wh-Mich (wet and dry) (Table 12).

The equations in Table 12 indicate that changes in the relative growth rate of the organs of a plant sometimes occur when the plant produces an apical bud and stops height growth.

Seedlots within a water treatment level which had significantly different regression coefficients for the

TABLE 12. Regression equations for water-level X seedlot treatment combinations in which the slopes of the regressions are different for seedlings possessing an apical bud and those without an apical bud.

Seedlot	Water regime	Variables	Seedlings Without Apical Buds	Seedlings With Apical Buds	Significance Level
B11-51	Medium	$X = \log_{10} \text{ total dry weight}$	$Y = -.196 + 1.150X$	$Y = -.688 + .609X$	*
		$Y = \log_{10} \text{ needle dry weight}$			
W11-195	Wet	$X = \log_{10} \text{ total dry weight}$	$Y = -.692 + 1.217X$	$Y = -.888 + .799X$	*
		$Y = \log_{10} \text{ shoot dry weight}$			
W21-N100	Wet	$X = \log_{10} \text{ total dry weight}$	$Y = -.716 + .677X$	$Y = -1.276 - .189X$	**
		$Y = \log_{10} \text{ root dry weight}$			

* $P < .05$

** $P < .01$

TABLE 13. Regression coefficients for the regression of $\log_{10}$ needle dry weight on $\log_{10}$ total dry weight.

Seedlot	Water Regime		
	Wet	Medium	Dry
Blu-SS	.974a ¹	1.073b	.964ab
Blu-GS	1.054a	1.139a	1.150a
Eng-Col	1.098a	1.007a	.833b
Eng-Mont	.967ab	1.058a	.796b
Wh-Alas	.989a	1.092a	--
Wh-Mich	1.153a	1.009a	.965a
Sit-Alas	.979a	.986a	1.016a
Sit-Ore	.981a	.938a	.812a
Bla-BC	.939a	1.007a	.916a
Bla-Mich	.966a	1.043b	1.014ab
Red-Que	1.023a	.832a	.694a
Red-WVa	1.011a	1.118a	.739a

¹Any values in a row followed by a common letter are not significantly different at the 5% level.

TABLE 14. Regression coefficients for the regression of $\log_{10}$ stem dry weight on $\log_{10}$ total dry weight.

Seedlot	Water Regime		
	Wet	Medium	Dry
Blu-SS	1.216a ¹	1.049b	1.097ab
Blu-GS	1.136a	1.136a	1.217a
Eng-Col	1.186a	1.083a	1.128a
Eng-Mont	1.249a	1.065a	1.095a
Wh-Alas	1.217a	1.311a	--
Wh-Mich	1.046a	1.084a	1.157a
Sit-Alas	.808a	.865a	.892a
Sit-Ore	.886a	1.077a	1.042a
Bla-BC	1.129a	1.560b	1.135a
Bla-Mich	1.128a	1.136a	1.093a
Red-Que	1.180a	.764b	.894ab
Red-WVa	.847a	1.209a	.893a

¹Any values in a row followed by a common letter are not significantly different at the 5% level.

TABLE 15. Regression coefficients for the regression of $\log_{10}$ root dry weight on $\log_{10}$ total dry weight.

Seedlot	Water Regime	
	Wet	Dry
Blu-SS	.930a	1.001a
Blu-GS	.839a	.734a
Eng-Col	.784a	1.257b
Eng-Mont	.917a	1.198b
Wh-Alas	.912a	--
Wh-Mich	.677a	.988a
Sit-Alas	1.292a	1.029a
Sit-Ore	1.099a	1.361a
Bla-BC	1.136a	1.029ab
Bla-Mich	1.041a	.921ab
Red-Que	.855a	1.491ab
Red-WVa	1.048ab	1.530b

¹Any values in a row followed by a common letter are not significantly different at the 5% level.

regression of $\log_{10}$ needle dry weight on $\log_{10}$ total dry weight were:

Wet Treatment

Blu-GS, Wh-Mich>Blu-SS, Bla-BC, Bla-Mich.
Eng-Col, Red-Que>Bla-BC.

Medium Treatment

Blu-SS, Blu-GS, Eng-Mont>Red-Que.

Dry Treatment

Blu-GS>Eng-Col, Eng-Mont, Red WVa.
Sit-Alas, Bla-Mich>Red-WVa.
Bla-Mich>Eng-Mont.

Seedlots within a water treatment level which had significantly different regression coefficients for the regression of $\log_{10}$ stem dry weight on $\log_{10}$ total dry weight were:

Wet Treatment

Blu-GS, Blu-SS, Eng-Col, Eng-Mont, Wh-Alas, Bla-BC,
Bla-Mich, Red-Que>Sit-Alas.
Blu-SS, Red-Que>Sit-Ore.

Medium Treatment

Bla-BC>Blu-SS, Blu-GS, Eng-Col, Wh-Mich, Sit-Alas,
Sit-Ore, Bla-Mich, Red-Que.
Blu-GS, Wh-Alas, Bla-Mich>Sit-Ore, Red-Que.
Wh-Alas>Eng-Col>Red-Que.

Dry Treatment

Blu-GS>Eng-Col, Eng-Mont, Red-WVa.
Sit-Ore, Bla-Mich>Red-Que.
Bla-Mich>Eng-Mont.

Seedlots within a water treatment level which had significantly different regression coefficients for the

regression of $\log_{10}$ root dry weight on $\log_{10}$ total dry weight were:

Wet Treatment

Sit-Alas, Sit-Ore, Bla-BC, Bla-Mich>Blu-GS, Eng-Col,
Wh-Mich, Red-Que.
Blu-SS, Wh-Alas>Wh-Mich.
Sit-Alas, Bla-BC>Blu-SS.
Sit-Ore, Bla-BC>Wh-Alas.

Medium Treatment

Red-Que>Blu-SS, Blu-GS, Eng-Col, Wh-Alas, Bla-BC,
Bla-Mich.
Eng-Col, Sit-Alas, Sit-Ore>Blu-GS.
Sit-Ore>Wh-Alas.

Dry Treatment

Red-WVa>Blu-SS, Blu-GS, Eng-Mont, Wh-Mich, Sit-Alas,
Bla-Mich.
Eng-Col, Eng-Mont>Blu-GS, Bla-Mich.

For simplification, four seedlots are selected for direct comparison of responsive and non-responsive seedlots. Of the ten seedlots sown at the same time, Bla-Mich and Blu-SS are responsive seedlots, while Wh-Mich and Sit-Alas were selected to represent non-responsive seedlots. The selection of Wh-Mich and Sit-Alas were made on the basis of their having the lowest ratio of dry weight of seedlings grown in the wet treatment to dry weight of seedlings grown under the dry treatment. Seedlot Eng-Col was ignored in view of the fact that the dry weight of the seedlings varied in an atypical manner with water treatment level. Comparisons were made at the wet treatment level only because it is at this level that the greatest differences

in total dry weight were found. The responsive seedlings (those adapted to drought stress) apportioned equal or smaller quantities of dry matter into needles, and equal or larger quantities of dry matter into stems than did the seedlings adapted to moist conditions. There are no clearcut trends with regards to dry matter apportioned into root production.

It has long been argued that the relative sizes of the water absorbing organs (roots) and the water losing organs (leaves and possibly stems) are of great importance in determining the water balance of the plant. The data presented here indicate that by apportioning lesser quantities of material into needles, the plants adapted to drought stress may be adapting to the conditions of the environment in which they live.

The recent recognition of the ontogenetic shift in relative sizes of plant organs has led to a re-examination of old data (Ledig and Perry, 1965) and the construction of new experiments (Ledig, Bormann and Wenger, 1970), all of which have failed to demonstrate the ability of drought stress to alter the relative sizes of plant organs. Perhaps this failure was the result of not using severe enough drought conditions.

Summary

The speed of seedling emergence of the spruce seedlots appears to be of adaptive significance in that

seedlots from arid areas emerge faster than seedlots from moist areas. In arid areas, this might be advantageous in that favorable conditions might be of short duration.

Drought stress significantly reduced seedling survival, but appeared not to affect the tendency for a seedling to produce a dormant apical bud. Drought stress also reduced growth of the seedlings.

Drought stress also proved effective in causing a change in the relative size of some plant organs in certain seedlots. These differences were largely in an increase in stem weight at the expense of increased needle production. As needles, but not stems, are water losing organs, the changes could have adaptive significance.

CHAPTER II

THE EFFECT OF DROUGHT STRESS ON PHOTOSYNTHESIS AND TRANSPIRATION OF SPRUCE SEEDLINGS

Drought stress affects several physiological processes within plants; including decreasing net photosynthesis, growth, and transpiration (Sands and Rutter, 1959; Jarvis and Jarvis, 1965; Pallas, Michel and Harris, 1967; Babalola, Boersma and Youngberg, 1968). Aside from a study on two ecotypes of Douglas-fir done by Zavitkovski and Ferrell (1968), few studies have compared the impact of drought stress on these physiological processes using closely related species of trees.

This study was designed to measure and compare the effect of an imposed drought on rates of photosynthesis and transpiration in several species of spruce native to North America.

Materials and Methods

Two seedlots of each of six species of spruce as previously described in Table 1 were used in this study. Trees were grown from seed in plastic pots 16 cm in diameter and 22 cm tall. The soil was 91% sand and 9%

of a standard greenhouse mixture of sandy loam and shredded peat.

The following equation was derived experimentally using a soil pressure plate membrane apparatus which relates soil moisture content to soil water potential:

$$\log_{10}(\% \text{ soil moisture}) = .630 - .174 (\log_{10}[-\text{soil water potential}][\text{lbs.}]).$$

This equation was derived to allow the results to be presented in the more useful terms of soil water potential.

Thirty to forty seeds were sown per pot and one to two weeks after germination the seedlings were thinned to five uniform trees equally spaced in each pot. Trees were grown under continuous artificial light provided by 40 watt cool white VHO fluorescent bulbs at an intensity at soil level of 200 microeinsteins $\text{m}^{-2} \text{ sec}^{-1}$. The pots were watered daily so that the soil water level never dropped below field capacity.

Five and a half months after sowing, when the trees were actively growing, the soil surface was sealed with wax, and all watering was discontinued.

All pots were weighed daily from the time of sealing until a pot stopped losing weight. When this point was reached the trees were removed from the pot and the weight of the pot and the wax determined. The soil was oven-dried and weighed. The trees were oven dried and the needles

stripped off and weighed. The loss of water through unsealed drainage holes in the bottom of the pot was corrected for by noting weight losses of wax sealed pots containing no trees. Transpiration was then computed on the basis of water loss per unit of dry weight of needle per day.

Three seedlots, Blu-SS, Wh-Alas, and Sit-Alas were simultaneously used to determine photosynthetic rates as the soil in the pots dried. The net photosynthetic rate of the seedlings in each of four pots for each seedlot was determined either daily or on alternate days, depending on the rate of change of the photosynthetic rate. Measurements were made in a closed plexiglass chamber system connected with a Beckman CO₂ infrared gas analyzer equipped with a strip chart recorder. Net photosynthetic rates were determined from the rate of depletion of CO₂ in the system from 330 to 270 ppm. Illumination was provided by a 400 watt Mercury lamp, giving an intensity of 600 microeinsteins m⁻² sec⁻¹ at the top of the seedlings. Temperature in the chamber was 22° ± 1.5°C. Photosynthetic rates were expressed on the basis of dry weight of the needles. Photosynthetic measurements were repeated until the rate reached zero or less. At that time, the wax seal was punctured, the soil thoroughly watered and the pot resealed. Measurements were then resumed until two conditions were satisfied. First, the photosynthetic rate had to demonstrate an increase from

the previous day. After that, measurements were continued until the net photosynthetic rate declined for two consecutive days.

Results

Photosynthesis

From the time that excess water had drained from the pot after the final pre-sealing watering until the soil had dried to field capacity, the photosynthetic rate was relatively constant. This constant rate was used as a "basal rate" of photosynthesis under conditions of no water stress, and all subsequent rates are expressed as percentages of this "basal rate" (Figure 2).

The slope differences between the Blu-SS and Sit-Alas seedlots are significant at the 2% level. No other differences are significant at the 5% level.

Seedlings in lot Blu-SS recovered to their maximum rate of post-drought photosynthesis significantly faster than Sit-Alas seedlings, while Wh-Alas seedlings recovered to a significantly higher percentage of their "basal rate" of photosynthesis than did Sit-Alas seedlings (Table 16).

Transpiration

Like photosynthesis, transpiration per unit dry weight of needle was relatively constant for a given pot of seedlings from the time the pot ceased draining after

Figure 2.-- Relationship between soil water potential and photosynthetic rate in blue spruce, white spruce and Sitka spruce.

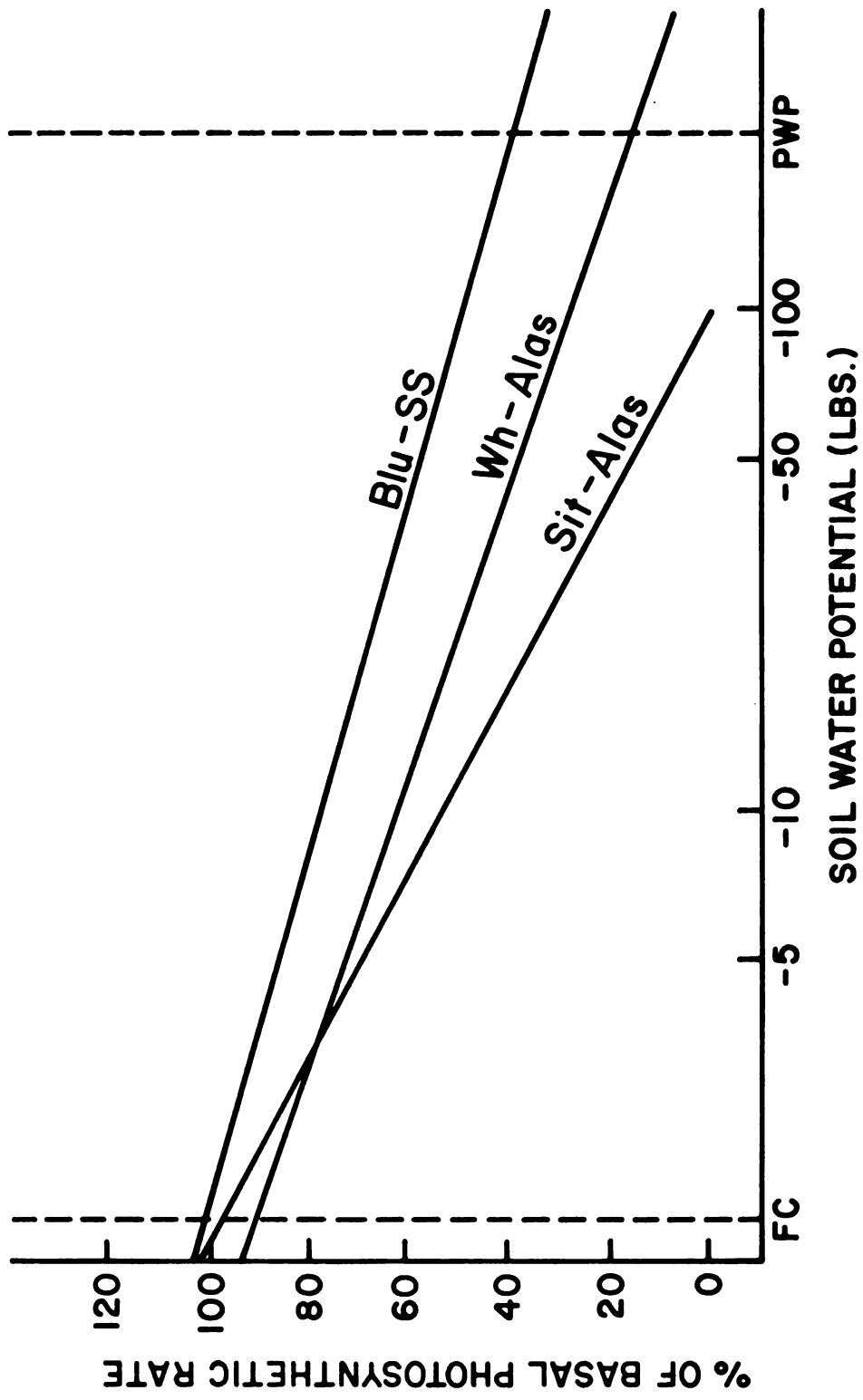


Figure 2

TABLE 16. Characteristics of post-drought recovery of photosynthetic rate.

Seedlot	Mean Days to Highest Recovery of Photosynthetic Rate Following an Imposed Drought	Best Post-Drought Rate of Photosynthesis as Percent of Basal Rate
Blu-SS	2.0a ¹	30.8ab
Wh-Alas	3.7ab	85.8a
Sit-Alas	5.0b	2.8b

¹Any values in a column followed by a common letter are not significantly different at the 5% level as determined by Tukey's HSD test.

the final pre-sealing watering until it reached field capacity (Table 17). Significant differences were found in the regression coefficients for different seedlots when the $\log_{10}$ of the transpiration rate was regressed on the $\log_{10}$ (-soil water potential) for values of soil water potential between field capacity and permanent wilting point (Table 18). Although in certain seedlots a relationship other than the log-log relationship between transpiration and soil water potential gave a slightly higher r^2 value, the log-log relationship presented here was in general superior.

A rank correlation value significant at the 1% level was found which indicates that the more a seedlot transpired per unit dry weight of needles under conditions of no drought stress, the more it altered its transpiration rate in response to decreasing soil water potential. A

TABLE 17. Transpiration rate in grams of water lost per gram dry weight of needles per hour when soil moisture level was between saturation and field capacity.

Seedlot	Transpiration Rate
Blu-GS	.60a ¹
Eng-Col	.46ab
Bla-BC	.44ab
Eng-Mont	.43ab
Bla-Mich	.40b
Wh-Alas	.40b
Sit-Alas	.38b
Wh-Mich	.34b
Blu-SS	.32b
Sit-Ore	.30b

¹Transpiration rates followed by a common letter are not significantly different at the 5% level as determined by Tukey's HSD test.

TABLE 18. Regression coefficients for the regression of $\log_{10}$ transpiration rate (grams water lost per gram needle dry weight per hour) on $\log_{10}$ (-soil water potential).

Seedlot	Regression Coefficient
Blu-GS	-.62a ¹
Eng-Col	-.59ab
Bla-Mich	-.59ab
Bla-BC	-.56b
Eng-Mont	-.46c
Sit-Alas	-.41cd
Red-Que	-.39cd
Red-WVa	-.36cd
Wh-Mich	-.34d
Wh-Alas	-.34d
Sit-Ore	-.33d
Blu-SS	-.28d

¹Regression coefficients followed by a common letter are not significantly different at the 5% level.

rank correlation value significant at the 1% level was also found between those seedlots having the highest rate of transpiration under conditions of no water stress and those seedlots having the lowest rates of transpiration when the soil water potential reached -15 atmospheres.

Discussion

Blue spruce is native to areas that appear to be quite dry, although the species mostly occurs near streams and other moist microclimates (J. W. Hanover, personal communication). Sitka spruce is native to moist West coast areas. White spruce is native to areas that are intermediate in terms of aridity. This study indicates that there are at least three ways in which a species adapts to drought conditions. First, its photosynthetic rate can be less sensitive to changes in soil water potential, secondly it can recover rapidly from a drought stress, or thirdly, it can recover, after a drought stress, to a photosynthetic rate nearly equal to its pre-drought photosynthetic rate.

From the results presented here, white spruce and blue spruce are not significantly different in their adaptation to drought. However, earlier tests (see Chapter I) indicated blue spruce is much better adapted to drought stress than white spruce. The most reasonable explanation of this is that in the earlier tests all seedlings were

subjected to an equal level of stress before rewatering. Speed of recovery and extent of recovery may well be dependent on the soil water potential at which the trees are rewatered. A different response might occur if all of the seedlings in this study were rewatered at a constant soil moisture content rather than when the net photosynthetic rate of the seedlings in a pot fell to zero.

The seedlots whose seedlings alter their transpiration rates most in response to changes in soil water potential, Blu-GS, Eng-Col, Bla-Mich and Bla-BC, appear to be the most drought resistant of the twelve seedlots tested (see Chapter I). Two exceptions to this pattern are: (1) Seedlot Red-Que, which appeared to be somewhat drought resistant in earlier tests, but which alters its transpiration rate only slightly in response to lower soil water potentials. However, the transpiration data for this seedlot are based on the results of a single pot, rather than on four pots as in the other seedlots. The reliability of this measurement may be low. (2) Seedlot Blu-SS which changes its transpiration rate least in response to changes in soil water potential, but appears to be the most drought resistant of all seedlots. Perhaps it is so well adjusted to drought that its transpiration rate was never restricted.

It seems reasonable that drought resistant trees should be able to alter their transpiration rates in

response to soil water potential. If drought resistant trees had continually high transpiration rates, drought conditions would probably be fatal as the foliar tissues would dessicate and die. As both CO_2 and water vapor are exchanged through the stomates, continuously low transpiration rates would probably be coupled with continuously low photosynthetic rates. If this were the case, the plants would be unable to take advantage of periods of adequate moisture, and this would be detrimental in their competition with other species.

The suppression of photosynthesis by soil moisture levels above field capacity has been noted in some studies (Clark, 1961; Pallas, Michel and Harris, 1967; Schneider and Childers, 1941). Another study failed to find this suppression (Zavitkovski and Ferrell, 1968). It has been suggested by Clark (1961) that this suppression is due to poor soil aeration at very high soil moisture levels. A very sandy soil, such as that used in this study, might allow for better aeration at high soil water potentials than would a heavy soil (Buckman and Brady, 1967). It appears that in cases where a sandy soil was used no suppression of photosynthesis by soil moisture levels above field capacity was observed, while experiments using heavier soils consistently demonstrated suppression of photosynthesis when soil moisture contents were above or at field capacity.

The extent and speed of recovery of the net photosynthetic rate following relief from drought stress reported here for white spruce agrees quite well with values previously reported (Clark, 1961).

This study indicates that species native to dry areas differ significantly from a species native to a wet habitat in at least three ways: (1) The net photosynthetic rate is less sensitive to changes in soil water potential. (2) Photosynthetic rates of species native to xeric areas recover faster following relief from a drought stress than a species native to a moist habitat. (3) Species adapted to dry areas recover a greater proportion of their pre-drought photosynthetic rate than species adapted to wet areas.

Transpiration rates are apparently not correlated with drought resistance. However, those species having the highest rates of transpiration under conditions of no water stress tend to have the lowest rates of transpiration under conditions of high water stress.

CHAPTER III

THE EFFECTS OF DROUGHT STRESS ON SURFACE WAX DEVELOPMENT IN SIX NORTH AMERICAN SPECIES OF SPRUCE

The plant cuticle, located at the interface of the leaf and the atmosphere, plays an important role in the regulation of plant water relations. Scanning electron microscopy allows the easy examination of the cuticular surface for studying the adaptive characteristics of various cuticular features.

The leaf surfaces of many plants including a wide variety of conifers are covered with epicuticular waxes, at least some of which take the form of rods, fibers, spheres or plates. The epistomatal chamber appears to be at least partially plugged with wax in many conifers (Hanover and Reicosky, 1972).

The development of this structural epicuticular wax (or bloom) which contributes to the "blue" coloration of leaves is apparently under both genetic and environmental control (Denna, 1970; Cameron, 1970; Hallam, 1970; Banks and Whitecross, 1971). Heavier wax blooms have been observed more often in individuals of a given species growing in arid regions than on individuals in more mesic

areas (Daly, 1964). It has been shown that the removal and/or disorganization of this structured wax results in higher rates of water loss from plant organs (Possingham, et al., 1967; Hall and Jones, 1961; Denna, 1970).

Theoretical calculations (Jeffree, Johnson and Jarvis, 1971) would seem to support the idea that epicuticular waxes are an adaptive advantage in dry regions.

Rook, et al. (1971) found that the imposition of drought stress on Pinus radiata did not alter the appearance of needle surface waxes.

In this study, the epicuticular waxes of six North American species of spruce were examined after they had been growing under alternating dry and wet conditions.

Materials and Methods

Seed from each of the twelve previously described seedlots (see Table 1) were sown in plastic pots in a sandy loam soil enriched with shredded peat to 20% organic matter on January 9 in a glasshouse. The plants received natural daylight as well as continuous artificial illumination from fluorescent bulbs from the time of seedling emergence through the end of the experiment. Through April 1 the pots were kept well watered. Watering was done so as to avoid wetting the foliage. The height of the trees was measured at that time. The trees were then left unwatered until May 2, at which time the height of each tree was

again measured. The plants were watered on May 2 and as needed thereafter to avoid further drought stress throughout the remainder of the experiment. Six to eight weeks following the end of the drought period, observations were made of the epicuticular waxes of the needles from representative trees.

Needles growing on those parts of the main stem that were formed before, during and after the drought period were examined. Cotyledons and the needles immediately above them were not used, nor were very young succulent needles. The magnitude of the drought stress was sufficient to kill more than 50% of the trees in two seedlots.

Needles were picked fresh from the trees and prepared for observation under the scanning electron microscope within one hour. Needles were gold coated prior to examination in an Applied Science Laboratory EMX-SM instrument. Photographs were taken by a Polaroid camera at 1000X magnification except as noted. Care was taken to photograph a "typical" section of each needle. Needles were examined during six different sessions over a two week period.

Results

In most cases, the surfaces of all needles, regardless of species or position on the stem looked basically

alike. Common features include the presence of a large amount of wax in the epistomatal chamber which resembled filaments joined together in a three dimensional fishnet type of configuration (Figure 3a). Clusters of wax filaments are spread across the needle surface. Between these are areas of varying size which contain little or no structured wax (Figure 3b,c).

Some exceptions to this general uniformity of the material were noted. Occasionally, a needle was observed in which the epistomatal chamber was free or nearly free from filamentous wax (Figure 3d,e). A lack of clusters of filamentous wax on the surface of the needle was invariably associated with this condition. Instead, the surface exhibited an undulating appearance which was in sharp contrast to the relatively smooth surface normally observed between filamentous wax clusters (Figure 3f). This condition was very consistent in seedlot Eng-Col on needles formed prior to the drought and was also observed on some of the needles in the Sit-Ore seedlot that were formed prior to the drought (Figure 4a).

Needles of seedlot Wh-Alas formed prior to the drought appeared to have either fewer but considerably thickened wax filaments in the epistomatal chamber (Figure 4b), or the chamber appeared to be completely occluded with what appeared to be molten wax (Figure 4c,e,f). In these cases, the clusters of fibrous surface wax were less

Figure 3.--Surface waxes of spruce foliage, Part I (a, pre-drought Blu-SS 3125X; b, post-drought Eng-Col 625X; c, pre-drought Red-WVa 625X; d, post-draught Eng-Col 625X; e, pre-drought Sit-Ore 625X; f, pre-drought Eng-Col 625X).

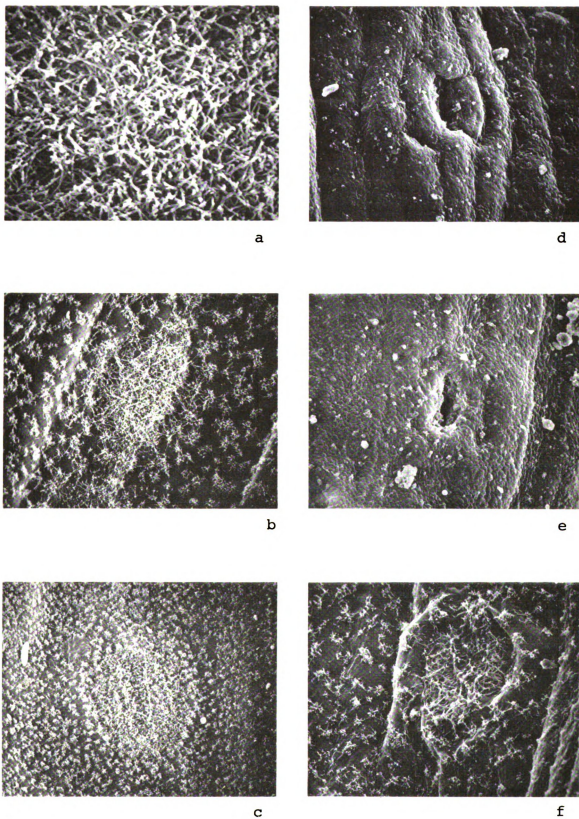
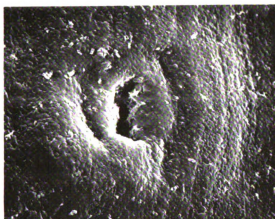
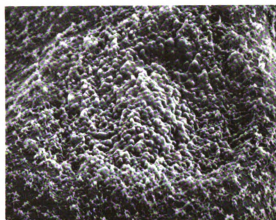


Figure 3

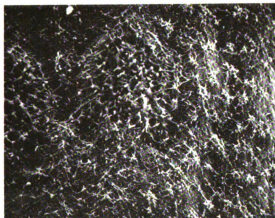
Figure 4.--Surface waxes of spruce foliage, Part II (a, pre-drought Sit-Ore 625X; b,c, pre-drought Wh-Alas 625X; d, pre-drought Red-Que 1250X; e,f, pre-drought Wh-Alas 625X).



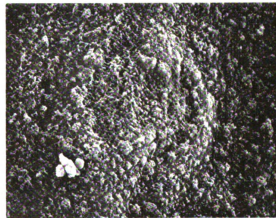
a



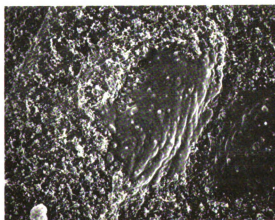
d



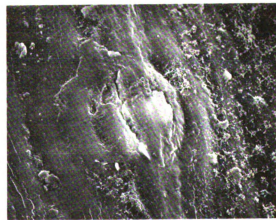
b



e



c



f

Figure 4

fibrous and more amorphous. This condition was also observed on some needles formed prior to the drought in seedlot Red-Que (Figure 4d).

Thus, the only distinctive and relatively consistent differences observed in this study occurred in needles prior to the drought period in seedlots Eng-Col and Wh-Alas. In the Eng-Col seedlot, the needles appeared to have little or no fibrous structured surface wax and the epistomatal chambers appeared to be free of wax. In seedlot Wh-Alas, the needles formed prior to the drought had stomates which for the most part appeared to be completely occluded with wax.

Discussion

The epicuticular waxes on needles formed prior to the drought differed considerably from the waxes on needles formed after the drought stress in seedlots Wh-Alas and Eng-Col. This would indicate that the extent of drought stress at the time of needle elongation is not, in itself, a sufficient explanation for surface wax differences.

The striking differences observed in seedlots Eng-Col and Wh-Alas could be explained in several ways. The waxes were either formed in the observed configurations or their configurations were altered after formation. If they were formed originally in the observed configurations, two explanations are offered: First, the differences could be due to developmental changes as the plants grew older.

This would necessitate the coincidence of a developmental change with the imposition of a drought stress, which is unlikely. A second possibility is that the imposition of a drought stress triggered a change in the subsequent formation of surface waxes that was irreversible, at least for the duration of the study. If the presence of wax is indeed a useful adaptation to drought, then it might be that drought would trigger increased wax formation on new needles. This explanation is supported by the response of seedlot Eng-Col. However, seedlot Wh-Alas seems to respond opposite to this pattern; pre-drought formed needles had occluded stomates and the needles formed during and after the drought had less completely occluded stomates.

Post-formation alteration of the surface waxes is another possible explanation of the observations. This might be the result of mere "weathering" (Reicosky, 1973) or it could be an active plant process.

It is possible that the undulations of the surface of the Eng-Col needles are a result of the breakdown of pre-existing fibrous wax clusters. In the case of the pre-drought formed needles in seedlot Wh-Alas, it is not difficult to imagine a progression from fine fibrous filaments in the epistomatal chambers to thickened filaments, to the "molten wax" stage.

Presuming post-formation alteration does occur, one advantage to the trees in seedlot Wh-Alas can readily

be seen. In times of severe drought, the sealing of the stomates would tend to prevent water loss which would be an adaptive advantage. There are two reasons why the pre-drought needles might be sealed whereas those needles formed during the drought would not be. Clark (1961) has shown that the photosynthetic rate of older needles is less than that of fully formed new needles. Thus, stomatal occlusion of the older needles by wax would be less disadvantageous to photosynthesis than if the younger needles were sealed off. Secondly, as the environment is known to affect plant anatomy, as in the case of sun and shade leaves, it is possible that the needles formed during the drought are anatomicly adapted to the dry conditions while the needles formed during the moist period are so poorly adjusted to drought that adjustments are made by wax occlusion of the epistomatal chamber.

It should be noted that seedlot Wh-Alas had, in other studies, an unusual tendency to set buds and halt height growth in response to drought. This would certainly be compatible with the sealing of stomatal openings, with the attendant lowering of the photosynthetic rate of the seedlings.

In summation, there appeared to be little difference between the surface waxes of any of the species examined when they were grown under similar conditions. It appeared

that conditions of drought stress influenced the needle surface waxes in only two of the twelve seedlots examined. These differences were of an opposite nature in the two seedlots, but both were of possible importance in improving the water status of the plant during droughty periods.

CHAPTER IV

CONCLUSIONS AND RECOMMENDATIONS

The responses of the six species and seedlots to drought, as indicated in Figure 1 are highly variable and not in the expected pattern based on the habitat from which the seed was collected. From the statistical analysis it must be concluded that a northern Michigan black spruce seedlot behaved in a manner similar to blue spruce. This is a somewhat surprising result in view of the fact that the black spruce in question were growing in a swamp, an area of apparently adequate moisture, while blue spruce grow in regions of apparent aridity.

The finding that drought stress can cause changes in the relative size of the organs of seedlings is without precedent, and may be an adaptive feature allowing for growth under a variety of conditions. However, the rather large number of studies that have shown that drought stress is not able to change the relative size of plant organs would seem to indicate that this adaptive mechanism is used only under extreme drought conditions.

The results of the photosynthesis study fit well with the expected pattern. Species adapted to dry areas

are less affected by drought than species adapted to wet areas. In addition, this study indicates that more than one aspect of the response of a plant to photosynthesis must be investigated to obtain an adequate picture of plant adaptation.

The differences between seedlots for both rate of transpiration under conditions of no soil water stress and rate of change of the transpiration rate with changes of soil water potential do not consistently form an interpretable pattern. Further experiments appear necessary before conclusions about the adaptive role of transpiration in the genus Picea can be made.

The differences between surface waxes of the spruces are slight or non-existent. The conditions of this experiment may not have been the best for observing differences between species, but it is evident that drought alone is not a sufficient stimulus to the immediate change of surface wax characteristics.

Further research in certain areas touched by this study that might prove fruitful are:

1. An investigation of the root development of young seedlings. It is quite probable that early root development is an important determiner of drought resistance. Casual observations made during this study indicate that large differences exist between species.

2. An investigation of the rates of growth of these species using higher moisture levels. Several seedlots were obviously stunted at all water levels used in this study. What might occur at wetter treatment levels is hard to say, but of great interest.

3. An investigation of the water used per gram of dry matter produced (water efficiency) between water levels and seedlots might be interesting. Data was collected for this purpose in this experiment, but the variation within treatments was too high to allow interpretation.

4. The effect of drought stress on surface wax development should be followed over a long period of time. Perhaps a drought stress occurring during bud growth in the fall would result in waxier needles during the following growing season.

5. A study of the anatomy of the needles, stems and roots of the species might be interesting in that structural differences might suggest functional changes within the plant with regards to water relations.

6. A study designed to determine if some of the differences found here are in fact of adaptive significance. This might well be carried out in the natural ranges of several of the species.

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