EFFECTS OF WATER STRESS ON *PICEA* SEEDLINGS

By

Robert Edward Schutzki

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Forestry

1988

ABSTRACT

EFFECTS OF WATER STRESS ON PICEA SEEDLINGS

By

Robert Edward Schutzki

The effects of desiccation on container-grown white spruce (*Picea glauca* (Moench) Voss) and blue spruce (*Picea pungens* Engelm.) were studied in relation to: changes in seedling moisture content; changes in respiration and water vapor loss; and root growth capacity following a 20 day growth period.

Blue spruce exhibited higher initial moisture contents than white spruce. Shoot and root moisture contents following desiccation tended to be higher in blue spruce. Seedling moisture loss increased with an increase in VPG from 0.5 to 1.5 kPa. The 1.5 kPa VPG caused a 41% reduction in seedling moisture content. Total seedling exposure resulted in a 46.6% reduction in moisture content, followed by root exposure at 42.8%, and shoot exposure at 21.2%. The duration of exposure increased moisture loss from 28% to 44.9% between the 1 and 3 hour exposure treatments.

Desiccation treatment of 1.5 kPa VPG was used to determine seedling ability to rehydrate and commence root growth. Seedling rehydration, expressed as percent gain in

fresh weight, increased with an increase from 1 to 3 hours of exposure. One hour exposure resulted in 46% reduction in white root production.

Root respiration was higher when compared to shoot or total seedling. Water vapor loss increased with increasing VPG within the duration of exposure treatments. A linear relationship between water vapor loss and respiration was found in both white and blue spruce during the 3 hour exposure treatment. Respiration declined with a decrease in water vapor loss.

Fall acclimation decreased seedling sensitivity to desiccation. Initial seedling moisture content decreased from August through November in the overwintering structure. Seedling moisture loss decreased between sampling dates, suggesting that seasonal modifications were occurring in the shoot. Root growth capacity in both the nonexposed and exposed seedlings increased from August to October. Respiration rates increased from August to September and then returned to the August levels. Respiration rates between total seedling and root exposure treatments coincided with a shift from shoot to root activity.

Daylength caused an increase in dry weight and a decrease in seedling moisture content over six weeks. Shortening daylength caused a decrease in respiration with each sampling period. Short daylength altered seedling sensitivity to desiccation, however, six weeks did not produce an appreciable difference in performance.

ACKNOWLEDGEMENT

I am sincerely grateful to Dr. James W. Hanover (committee chairman) for his guidance, encouragement and support during the course of my graduate studies. I thank Dr. J.A. Flore for his friendship, valued critiques, and the unrestricted use of his equipment; Drs. D.I. Dickmann, R.L. Perry and E. Young for their critical reviews and participation on my guidance committee. I am indebted to my friends for their encouragement and especially to R. Prentice for his willing assistance in the greenhouse and L. Gloden for her assistance in preparation of this manuscript. Finally, I extend my deepest appreciation to my family; Norma, Scott and Sarah, for without their love and understanding this undertaking would not have been possible.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 3

Chapter 4

LIST OF FIGURES

INTRODUCTION

Planting stock quality has been defined as "Fitness for purpose, with fitness being measured by performance" (Sutton, 1980). Understanding the relationship between morphological and physiological characteristics which make up quality, and factors that influence their change, is critical to predicting outplant success. Physiological status of planting stock can be adversely affected by the stresses imposed during the transition from production to field planting. Seedling susceptibility to desiccation during this transitional period, and its subsequent effect on growth, has been, and continues to be, a major concern in plantation establishment.

Research investigating the effects of desiccation on planting stock quality and subsequent field performance has been focused on field-grown nursery stock. The extent of desiccation injury on nursery stock is influenced by lift date, length of storage (Hermann, 1964), and exposure to dry conditions during processing (Mullin, 1974; Coutts, 1981; Ritchie et al., 1985). The use of container seedlings has practically eliminated the stress associated with lifting, processing, and storage of bare-root nursery stock. Container production systems have hastened production time and broadened planting windows. However, the production system that has afforded these opportunities may also increase susceptibility to other forms of planting shock.

Water stress has been identified as a major contributor to planting shock of container-grown seedlings. Water stress is primarily due to the changes in environmental conditions that occur between production and outplanting. The physiological active state of both shoots and roots in container planting stock predisposes the seedlings to injury from desiccation during the planting process or through soil moisture deficits during initial establishment. Field-grown nursery stock has experienced a variety of environmental stress through its production cycle. These stresses, in many cases, have enhanced the resistance of the plants to subsequent stress. Container seedlings may not have had adequate environmental conditioning prior to planting, rendering them more susceptible to planting and/or site related stress.

Environmental preconditioning or hardening off is extremely important in developing stress resistance in container seedlings. Traditional methods of hardening-off include moderate moisture stress, shortened photoperiod, and/or transfer from greenhouse to natural environmental conditions. Understanding the relationship between hardening-off and stress resistance becomes critical in the development of production and planting schedules. The objectives of this study were to characterize the response of container-grown spruce to desiccation; to examine the influence of environmental preconditioning on seedling sensitivity to desiccation; and to increase the understanding of the interrelationship between seedling physiological quality, post-harvest stress, and seedling recovery.

CHAPTER I

EFFECTS OF WATER STRESS ON *PICEA* SEEDLINGS: I. INFLUENCE OF PLANT-AIR VAPOR PRESSURE GRADIENT, PLANT PART EXPOSURE, AND DURATION OF EXPOSURE ON *PICEA GLAUCA* (MOENCH) VOSS AND *PICEA PUNGENS* ENGELM.

ABSTRACT

The effects of desiccation on seedling moisture content, rehydration capability, and root growth capacity were studied on container-grown white spruce (*Picea glauca* (Moench) Voss) and blue spruce (*Picea pungens*, Engelm.). Initial seedling moisture contents ranged from 1.99-2.32 grams H_2O gram dry weight^{-1}. Blue spruce exhibited higher shoot and root moisture contents than in white spruce.

Seedling moisture loss increased with an increase in plant-air vapor pressure gradient (VPG). An increase in VPG from 0.5 kPa to 1.5 kPa resulted in a 24% increase in moisture loss. A 1.5 kPa VPG caused a 41% reduction in moisture content when averaged over species, plant part exposure and duration of exposure. Seedling moisture content was least effected by shoot exposure. Moisture loss from the root exposure treatment was double that recorded for shoot exposure. An increase in duration of exposure caused an increase in moisture loss.

Seedling rehydration, expressed as percent gain in fresh weight, increased with an increase in duration of exposure. The rehydration of treated seedlings resulted in uniform shoot moisture contents across duration treatment levels. Root moisture content was similar between the 1, 2

and 3 hour exposure treatments. Desiccation had a negative influence on root growth capacity. One hour exposure resulted in a 46% reduction in the number of white roots greater than 1 mm in length compared to the control seedlings. A further reduction of 59% was found between the 1 and 3 hour treatments.

INTRODUCTION

Root growth potential (RGP) (Stone, 1955) has been widely used as a method for assessing planting stock quality in terms of the ability to continue or initiate root growth under optimum environmental conditions. Hermann and Lavender (1979) developed a vigor evaluation test estimating physiological vigor as an expression of percent survival and budbreak activity. Ritchie, Roden and Kleyn (1985) modified the previous methods and evaluated seedlings based on the measurement of Dormancy Release Index (DRI), RGP, stress resistance and frost hardiness. McCreary and Duryea (1987) compared the methods of root growth potential, vigor evaluation and plant moisture status following exposure to varying quality reducing treatments as predictors of field performance. A common denominator in these methods was to monitor seedling performance following exposure to environmental stress.

Studies of desiccation effects on planting stock quality and subsequent field performance have focused on field-grown stock because of the potential drying associated with lifting, handling and planting. However, with the increased use of container-grown stock and the advantages of extended planting season, the potential effects of desiccation on this stock type during planting warrants attention. Morphological or physiological differences between container and field-grown seedlings could contribute to differences in response to stress experienced during the planting process.

The objectives of this study were (1) to characterize the effects of different levels of desiccation on seedling moisture content in container-grown *Picea glauca* (Moench) Voss and *Picea pungens* Engelm, (2) to determine the interrelationship between shoot and root moisture loss and its subsequent effect on seedling internal water balance, and (3) to determine the sensitivity of seedlings to degree and duration of stress exposure on their ability to rehydrate and commence root growth.

MATERIALS AND METHODS

White spruce (*Picea glauca* [Moench] Voss) and blue spruce (*Picea pungens* Engelm.) were used in these experiments. White spruce seeds were obtained from a southern Ontario seed source and blue spruce from bulk seed of a half-sib family from the San Juan mountain region of Colorado. Seeds were sown in polyethylene-coated paper plant-bands, 5 x 5 x 27 cm (36/case) filled with a 3:1:1 (V:V:V) sphagnum peat:perlite:vermiculite mixture and placed in standard milk cases. Following sowing, the plant-bands were watered and subsequently drenched with Benlate (DuPont) and Subdue (Ciba-Geigy). Fertilization was initiated two weeks after sowing and continued at 2 week intervals with soluble fertilizer (Peter's) 15-16-17 (NPK). Water was applied as necessary to maintain uniform soil moisture. Four weeks after sowing, germinants were thinned to one germinant per plant-band.

Cases of plant-bands were arranged on a growth frame in a controlled environment room. Temperatures within the growth frame ranged from 22-27°C. Irradiation was supplied by high output cool-white fluorescent fixtures. Photosynthetic photon flux density (PPFD) at plant heights averaged 165 $\mu m\ m^{-2} sec^{-1}$. Plants were exposed to continuous light for 5 months after which daylength was reduced to 8 hours per 24 hour period. Seedlings were maintained at an 8 hour daylength for 2 months prior to the experiment.

Experiment 1 was designed as a split plot factorial replicated four times. Vapor pressure gradient, species, plant part exposure, and duration of exposure (3x2x3x3) were factors within the experiment. Table 1 presents the sources of variation and degrees of freedom used in the analysis of variance. An analysis of variance was also performed on a separate control seedling group representing vapor pressure gradient, species, and plant part exposure (3x2x3) replicated four times. Means were separated using Duncan's multiple range test.

The two groups of seedlings were randomly selected from the growth frame the night prior to conducting the desiccation treatments. Seedlings were thoroughly watered, sealed in clear polyethylene bags and covered with a black polyethylene sheet a minimum of 14 hours until preparation for the desiccation treatments to minimize differences in hydration level between seedlings. Seedlings were removed from the polyethylene bag, and planting media was gently washed from the roots with water (room temperature). Seedlings were blotted dry with absorbent tissue to remove any surface moisture on shoots and roots, fresh weights were recorded, and individual seedlings were placed into a controlled environmental chamber. Chambers were covered with black cloth throughout the desiccation treatment. Upon completion of the treatment, the exposed plant part was removed and severed at the root collar. Treated fresh weights were recorded for both the roots and shoots. Shoot and root dry weights were determined after oven drying at 100°C for 72 hours. Plant part moisture content was calculated gravimetrically and percent weight loss was based on fresh weight using the following equations:

$$\text{Moisture Content} = \frac{\text{Fresh wgt (gm)} - \text{Dry wgt (gm)}}{\text{Dry wgt (gm)}}$$

$$\text{\% Weight Loss} = \frac{\text{Fresh wgt (gm)} - \text{Dry wgt (gm)}}{\text{Fresh wgt (gm)}} \times 100$$

The control seedlings were handled using the same procedure with the exception of the desiccation treatment.

Plant part treatments consisted of total seedling exposure (1), roots only (2), and shoots only (3). In treatment 1, the total seedling was placed into the chamber. In the root and shoot only treatments, the respective plant part not subjected to the treatment was wrapped in a double layer of saran and a layer of aluminum foil. The exposed plant part was sealed into the chamber. Both plant parts were covered with black cloth during the treatment.

The desiccation treatments were conducted in an open gas analysis system described by Sams and Flore (1982). The system measures changes in CO_2 and water vapor within 4 individual plant chambers (11 x 21 x 9.5 cm). Interior sensors monitor plant temperature, chamber temperature, and photon flux density.

Air flow entering the chamber was monitored at 1.0 liter min^{-1} ±2% using Aalborg FM102-05 flow meters. Chamber temperatures were controlled using a refrigerated water bath and circulation system into each chamber. A variable speed fan, located in the bottom of the chamber, forced adequate air mixing around the entire sample. Plant temperature was determined with chromel-constantan thermocouples (0.03 mm) pressed against the underside of the sample (Omega 250 EQ Digital Temperature Indicator) and chamber air temperature was recorded with thermistors (YSI 47 Scanning Telethermometer). Air vapor pressure was controlled by saturating incoming air with water at a set temperature. Dew points of incoming and outgoing chamber air were monitored with a chilled mirror dew point hygrometer (General Eastern System 1100AP).

Plant temperatures were maintained at 24-25°C. Dew point of incoming air varied according to the desired plant to air vapor pressure gradient (VPG) entering the chamber. Vapor pressure gradients of 0.5, 1.0, 1.5 kPa were used. Seedlings were exposed to the respective VPGs for 1, 2, and 3 hours.

A second experiment was conducted on seedlings of the same population to determine the effects of duration of desiccation (0, 1, 2, 3 hours) at a vapor pressure gradient of 1.5 kPa on their ability to rehydrate and commence root growth. Seedlings were randomly selected from the growth frame and handled as in the previous experiment. White and blue spruce were divided into 2 groups representing a destructive sample to determine degree of plant moisture loss, and a potted sample for monitoring plant moisture contents and number of white roots following a 15 and 30 day growth period. Prior to potting both treated and control seedlings were dipped (3 sec) into water. Seedlings were potted into 26-liter containers of the non-fertilized 3:1:1 planting mixture and placed into the original growth frame under 8-hour photoperiod. Soil moisture was maintained during the growth period. At the conclusion of the growth period, pots were removed from the frame, watered, sealed into clear polyethylene bags and stored overnight under a black polyethylene sheet (14 hours). The following day seedlings were gently removed from the pots for determination of plant part moisture content and root production. Plant part moisture contents were determined as in the previous experiment, and the number of white roots above 1 mm in length were recorded.

The data in Experiment 2 were analyzed as a 3 factor completely randomized design replicated four times. Species, duration of exposure and growth period were factors within the analysis (2 x 3 x 2). Duncan's multiple range test was used to separate means.

Table 1. Sources of variation and degrees of freedom for split plot factorial in Experiment 1.

Source	dF
Replication	3
Vapor Pressure Gradient (VPG)	2
Error (a)	6
Species (S)	1
VPG x S	2
Plant Part Exposure (PPE)	2
VPG x PPE	4
S x PPE	2
VPG x S x PPE	4
Duration of Exposure (H)	2
H x VPG	4
H x S	2
H x VPG x S	4
H x PPE	4
H x VPG x PPE	8
H x S x PPE	4
H x VPG x S x PPE	8
Error (b)	153

RESULTS

Seedling moisture characteristics of the control sample are presented in Table 2. Blue spruce exhibited a higher moisture content than white spruce in both the shoot and root. The root system maintained an approximate moisture increase of 0.63-0.81 grams over that of the shoot (root-shoot MC). Blue spruce had a lower shoot/root ratio than white spruce.

Vapor pressure gradient, species, plant part exposure and duration of exposure influenced the loss of moisture content in treated seedlings (Table 3). A significant increase in moisture loss occurred between the 0.5 and 1.5 kPa vapor pressure gradient. The difference of 1.0 kPa resulted in a 24% increase in moisture loss. Moisture loss calculated as percent of fresh weight was increased by a VPG of 1.5 kPa. Blue spruce experienced a greater loss in moisture content than white spruce. Significant decreases in moisture content and increases in percent loss were observed within the plant part exposure treatments. Twice as much moisture was lost from the root or total seedling exposure treatments than from the shoot treatment. Smaller, yet significant, differences were found between total seedling and root exposure. A significant interaction was observed between species and plant part exposure in moisture content loss (Fig. 1). Blue spruce total seedling and root exposure treatments lost the greatest amount of moisture.

Table 2. Seedling characteristics for the control sample representing vapor pressure gradient, species and plant part exposure.[z,y]

Factor	Total Seedling		Shoot		Root		Shoot Root Relationship	
	Dry wgt (gm)	MC	Dry wgt (gm)	MC	Dry wgt (gm)	MC	Root-Shoot MC	Shoot/Root Ratio
Vapor Pressure Gradient (kPa)								
0.5	3.14	2.13	2.58	2.00	0.54	2.78	0.78	5.0
1.0	3.46	2.15	2.83	2.03	0.63	2.66	0.63	4.8
1.5	2.81	1.91	2.32	1.96	0.49	2.71	0.75	5.5
Species								
White Spruce	3.18	2.04b	2.69	1.95b	0.49	2.58b	0.63	5.9b
Blue Spruce	3.09	2.20a	2.46	2.05a	0.62	2.86a	0.81	4.2a
Plant Part Exposure								
Total Seedling	2.56	2.12	2.13	2.01	0.42b	2.76	0.76	5.4
Root	3.48	2.16	2.85	2.02	0.63a	2.78	0.76	4.9
Shoot	3.36	2.08	2.75	1.97	0.61a	2.61	0.64	4.8

[z]Means within main effect vertical column followed by same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test. Means not followed by letters are not significant.

[y]MC = moisture content gm/gm oven dry weight.

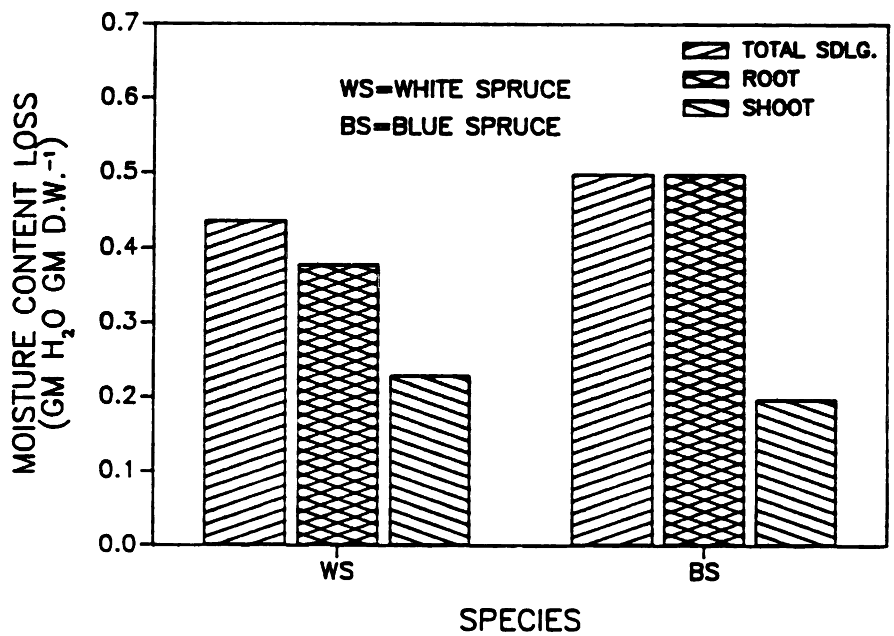
Table 3. The effects of VPG, species, plant part exposure and duration of exposure on seedling moisture content.[z,y]

	Initial Total Seedling		Moisture Loss Treated Total Seedling		Treated Shoot		Treated Root	
	Dry wgt (gm)	MC	Loss MC	Loss % fresh wgt	Dry wgt (gm)	MC	Dry wgt (gm)	MC
Vapor Pressure Gradient (kPa)								
0.5	2.76	2.23	0.33b	10.3b	2.28	1.92	0.48	1.77a
1.0	3.01	2.21	0.36ab	11.2b	2.50	1.90	0.52	1.58b
1.5	2.77	2.20	0.41a	12.8a	2.30	1.85	0.49	1.46b
Species								
White Spruce	2.82	2.11	0.35b	11.1	2.40	1.81b	0.42b	1.44b
Blue Spruce	2.88	2.32	0.39a	11.7	2.31	1.96a	0.57a	1.76a
Plant Part Exposure								
Total Seedling	2.71b	2.22	0.47a	14.4a	2.23b	1.85b	0.48	1.29b
Root	3.09a	2.21	0.43b	13.3b	2.57a	1.88b	0.53	1.30b
Shoot	2.75b	2.21	0.21c	6.62c	2.27b	1.94a	0.48	2.22a
Duration of Exposure (hrs)								
1	2.72	2.21	0.28c	8.8c	2.25	1.94a	0.48	1.79a
2	2.90	2.20	0.37b	11.6b	2.39	1.88b	0.51	1.54b
3	2.93	2.23	0.45a	13.8a	2.42	1.85b	0.51	1.48b

[z]Means within main effect vertical column followed by same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

[y]MC = moisture content gm/gm oven dry weight.

Figure 1. Moisture content loss for species and plant part exposure when averaged over vapor pressure gradient and duration of exposure within Experiment 1. Standard error equals ± 0.014.



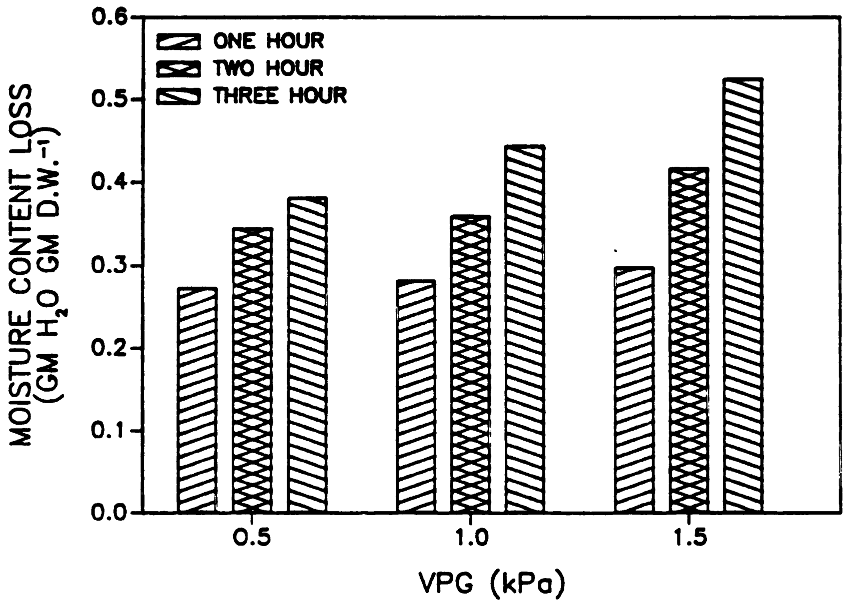
MOISTURE CONTENT LOSS
(GM H_2O GM D.W.$^{-1}$)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
TOTAL SDLG.
ROOT
SHOOT
WS=WHITE SPRUCE
BS=BLUE SPRUCE
WS
BS
SPECIES

White spruce total seedling exposure treatment lost more moisture than the root exposure treatment. Shoot exposure of either blue or white spruce loss significantly less than the other two exposure treatments. Within the VPG and duration of exposure interaction (Fig. 2), the 1.5 kPa VPG 3 hour treatment caused the greatest loss in moisture content. The 1.5 kPa 2 hour treatment was similar to both the 1.0 kPa 3 hour and the 0.5 kPa 3 hour treatments. The 1.0 kPa 2 hour treatment was similar to the 0.5 kPa 2 and 3 hour treatments. The 1 hour treatment caused the same moisture loss regardless of vapor pressure gradient.

The effects of VPG, species, plant part exposure and duration of exposure on shoot and root moisture contents are presented in Table 3. Root moisture levels were decreased between the 0.5 kPa VPG and the 1.0 and 1.5 kPa treatments. Blue spruce maintained higher shoot and root moisture levels following desiccation. Shoot and root moisture content in the total seedling and root exposure treatments were significantly lower than levels recorded for shoot exposure. Duration of exposure also influenced shoot and root moisture levels. Higher levels were found in the 1 hour treatment.

The desiccation treatment caused a dramatic change in the internal water balance of the seedling (Table 4). With the exception of the shoot exposure treatment, desiccation caused a shift in the balance toward the shoots. The 0.5 kPa VPG did not influence the shift as greatly as the 1.0 or 1.5 kPa VPG. Blue spruce was not effected as severely as

Figure 2. Moisture content loss for vapor pressure gradient and duration of exposure when averaged over species and plant part exposure. Standard error equals ± 0.017.



ONE HOUR
TWO HOUR
THREE HOUR
MOISTURE CONTENT LOSS
(GM H_2O GM D.W.$^{-1}$)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.5
1.0
1.5
VPG (kPa)

Table 4. The effects of VPG, species, plant part exposure and duration of exposure on root-shoot moisture content difference and on seedling shoot/root ratio.[z,y]

	Treated Shoot-Root Relationship	
	Root-Shoot MC	Shoot/Root Ratio
Vapor Pressure Gradient (kPa)		
0.5	-0.15a	5.2
1.0	-0.32b	5.2
1.5	-0.39b	5.0
Species		
White Spruce	-0.37b	6.0a
Blue Spruce	-0.20a	4.3b
Plant Part Exposure		
Total Seedling	-0.56b	5.1
Root	-0.57b	5.1
Shoot	0.28a	5.2
Duration of Exposure (hrs)		
1	-0.15a	5.1
2	-0.34b	5.1
3	-0.37b	5.2

[z]Means within main effect vertical column followed by same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

[y]MC = moisture content gm/gm oven dry weight.

Table 5. Experiment 2: The effects of species and duration of exposure on seedling moisture content following exposure to 1.5 kPa vapor pressure gradient.[z,y]

Factor	Initial Total Seedling Dry wgt (gm)	Initial Total Seedling MC	Treated Total Seedling Loss MC	Treated Total Seedling Loss % fresh wgt	Treated Shoot MC	Treated Root MC	Treated Shoot-Root Relationship Root-Shoot MC	Treated Shoot-Root Relationship Shoot/Root Ratio
Species								
White Spruce	3.28	2.02	0.37	12.1	1.68	1.55b	-0.12b	4.8a
Blue Spruce	3.80	2.03	0.35	11.4	1.65	1.82a	0.17a	3.6b
Duration of Exposure (hrs)								
0	3.61	1.99	0.00c	0.0d	1.81a	2.74a	0.93a	4.3
1	3.31	2.04	0.35b	11.6c	1.70a	1.59b	-0.12b	3.6
2	3.41	2.07	0.50a	16.1b	1.66a	1.22c	-0.44b	4.5
3	3.83	1.99	0.58a	19.5a	1.49b	1.21c	-0.28b	4.3

[z]Means within main effect vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

[y]MC = moisture content gm/gm oven dry weight.

white spruce. Shoot exposure maintained a positive balance in favor of the root, however, it was drastically reduced from control group (Table 2). The 1 hour exposure treatment showed less of an effect on the balance shift than the 2 or 3 hour treatments.

Experiment 2 examined the effects of species, duration of exposure and growth period on seedlings subjected to a 1.5 kPa VPG. The effect of desiccation on seedling moisture contents of the destructive sample are presented in Table 5. Duration of exposure influenced seedling moisture loss. The 2 and 3 hour exposure resulted in a 39 and 64 percent increase in moisture loss over the 1 hour treatment. Moisture loss calculated as percent fresh weight significantly increased with each hour of exposure. Shoot moisture content decreased after 3 hours of exposure. Blue spruce root moisture content was greater than white spruce. Root moisture content decreased within the first 2 hours of exposure. Blue spruce maintained a positive root-shoot moisture content relationship when averaged over duration of exposure. Duration of exposure increased the shift toward higher shoot moisture content.

The effects of species, duration of exposure and growth period on percent weight gain or loss in the potted sampling group is presented in Table 6. Desiccation loss in percent fresh weight was influenced by duration of exposure. The treatments resulted in a significant increase in loss with each treatment level. The difference in fresh weight

Table 6. Experiment 2: The effects of species, duration of exposure and growth period on percentage weight gain/loss between initial, treated and potted fresh weights.[z,y]

Factor	Initial fresh wgt (gm) IFW	Treated fresh wgt (gm) TRFW	Potted fresh wgt (gm) PFW	% wgt loss IFW-TRFW	% wgt loss IFW-PFW	% wgt gain PFW-TRFW
Species						
White Spruce	8.83b	7.77b	8.10b	12.7	8.5	5.3
Blue Spruce	10.38a	9.14a	9.56a	12.3	7.9	5.4
Duration of Exposure (hrs)						
0	10.72	10.71a	10.32a	0.0d	3.7c	-3.7d
1	8.68	7.66b	8.06b	11.8c	7.4b	5.1c
2	9.44	7.90b	8.54b	16.4b	9.7b	8.0b
3	9.58	7.55b	8.39b	21.6a	12.2a	12.2a
Growth Period (days)						
15	9.55	8.44	8.77	12.4	8.7	4.8
30	9.55	8.47	8.90	12.5	7.8	6.0

[z]IFW = Initial fresh weight; TRFW = Treated fresh weight; PFW = Potted fresh weight.

[y]Means within vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

Table 7. The effects of species, duration of exposure and growth period on potted seedling moisture content and white root production following exposure to a 1.5 kPa vapor pressure gradient.[z,y]

Factor	Potted total seedling Dry wgt (gm)	Potted total seedling MC	Potted Shoot Dry wgt (gm)	Potted Shoot MC	Potted Root Dry wgt (gm)	Potted Root MC	Shoot Root Relationship Root-Shoot MC	No. of white roots >1 mm
Species								
White Spruce	2.74b	1.97	2.26	1.92a	0.47b	2.18	0.26b	64
Blue Spruce	3.27a	1.93	2.50	1.82b	0.77a	2.27	0.45a	50
Duration of Exposure (hrs)								
0	3.51a	1.96	2.73	1.83	0.78	2.47a	0.64a	104a
1	2.75b	1.94	2.17	1.85	0.58	2.22ab	0.38ab	56b
2	2.89b	1.94	2.34	1.89	0.56	2.10b	0.21b	42bc
3	2.86b	1.95	2.28	1.90	0.58	2.10b	0.20b	23c
Growth Period (days)								
15	3.00	1.93	2.36	1.86	0.64	2.17	0.31	40b
30	3.01	1.96	2.40	1.88	0.61	2.28	0.40	73a

[z]Means within main effect vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

[y]MC = moisture content gm/gm oven dry weight.

between initial fresh weight (IFW) and potted fresh weight (PFW) represents the weight loss not regained through the potted growth period. Duration of exposure increased the PFW deficit. The percent weight gain from treated fresh weight (PFW-TRFW) is a measure of increased weight following treatment. An increased percent weight gain was observed with increased duration of exposure.

Seedling moisture contents and white root production as influenced by growth period are recorded in Table 7. White spruce shoot moisture content was greater than blue spruce. Duration of exposure influenced seedling root moisture content averaged over species and growth period. Root moisture content in the control (0 hrs) was similar to 1 hour treatment and significantly higher than the 2 and 3 hour treatments. Blue spruce achieved a higher moisture content level in favor of the root when compared to white spruce (root-shoot MC). The control duration treatment maintained statistically higher levels, when compared to the 2 and 3 hour treatments.

Desiccation effects on root growth capacity, as indicated by the number of white roots are evident in Table 7. There was a 46% reduction in the number of white roots greater than 1 mm in length between the control and the 1 hour exposure treatment. A 59% reduction was observed between the 1 and 3 hour treatments.

DISCUSSION

The basic intent underlying experiments 1 and 2 was to characterize the effects of different levels of desiccation on Picea seedlings. Seedlings used in these studies were maintained under short photoperiod prior to their selection. Shoot growth had ceased, a terminal bud was present and foliage showed signs of maturity. Root systems were light brown and white roots were present. Initial seedling moisture contents ranged from 1.99 to 2.31 gram H_2O gram dry weight^{-1} and were generally similar across main effects with the exception of species. Blue spruce exhibited higher shoot and root moisture contents than white spruce. The higher moisture content of blue spruce is presumed to be a tissue moisture holding characteristic. Differences in shoot/root ratio were also found between species. Blue spruce had a lower shoot/root ratio, indicating a greater initial tendency for root development. These basic differences are similar to results found by Heckman (1985) and are attributed to specific growth characteristics of these species in accelerated production systems.

Desiccation of planting stock reduces internal moisture content. The extent of the disruption is dependent on plant part exposure and the intensity of exposure, in terms of both VPG and its duration. Hermann and Lavender (1979) developed a vigor evaluation test based on percent survival and days to bud break following a 15-minute exposure to 90°F and 30% relative humidity. Survival below 85% in the growth room indicated poor field survival. Coutts (1981a) observed reductions in fine root water content from 349 to 97% when the root system of Sitka spruce was exposed for 4.5 hours in a growth room at 115°C, 85% relative humidity, 42 wm^{-2}, and 0.3 ms^{-1} air movement. Ritchie et al. (1985) suspended seedlings in a growth chamber for 60 minutes at 30°C, 2.1 kPa vapor pressure deficit (VPD) and light intensity of 200 $\mu mol\ m^{-2}s^{-1}$ PPFD in evaluating stress resistance as influenced by lift date and duration of freezer storage. Sucoff et al. (1985) varied the vapor pressure deficit for 1 hour exposure treatments and monitored changes in water potentials in roots, leaves and shoots of white spruce and red pine. Results indicated that root water potential may be the preferred predictor of postplanting success.

Seedling moisture loss was increased with an increase in VPG. Losses increased by 24% when PVG was increased from 0.5 kPa to 1.5 kPa. The 1.5 kPa VPG caused a reduction of 41% when averaged over species, plant part exposure and duration. The desiccation treatment in Experiment 2 consisted of 1.5 kPa VPG over 1, 2 and 3 hours. Losses in moisture content ranged from 0.35 to 0.58 gram gram $D.W.^{-1}$. Due to the variations in desiccating conditions in the literature, it seems important to include moisture content and the extent of moisture loss with performance data. The results outlined in Fig. 2 provide a closer look at the VPG and duration of exposure interaction. A change in VPG did not significantly influence moisture loss across the 1 hour exposure treatment. It required 3 hours exposure before there was a significant difference in moisture loss between the VPG levels. Consequently, without recording loss data, comparisons between experiments are limited.

Blue spruce was effected by desiccation more than white spruce (Table 3, Fig. 1), with the increased loss associated with the roots. The increased initial moisture contents of blue spruce could contribute to the higher losses, i.e. blue spruce may have less tissue resistance to loss or simply provides more available water.

Moisture loss is greatly influenced by the plant part exposed. Shoot exposure has the least effect on moisture loss. In the absence of light, shoot exposure caused a 0.21 gm H_2O gm d.w.$^{-1}$ loss in moisture content, corresponding to a 6% loss in fresh weight. Moisture loss in the root exposure treatment doubled that of the shoot. These results are similar to results of Coutts (1981a) and Sucoff et al. (1985) indicating the increased sensitivity of roots to exposure. The effect of moisture loss on shoot and root water potential was not investigated. Sucoff et al. (1985) showed that root water potential closely followed decreases in root moisture content. Shoot response varied in that there was a greater reduction in moisture content before shoot water potential was effected. Coutts (1981a) provided evidence that the root exposure caused an importation of moisture from the shoot. In one study, he found that water loss from the roots exceeded the amount originally present in the entire root system. Similarities in shoot moisture content between the root and total seedling exposure treatments in the present experiment tends to support the supposition that root exposure causes an importation of moisture from the shoot.

The extent of desiccation on seedling moisture relations can be seen in the root-shoot moisture balance. Data for the root-shoot moisture balance (Table 2) indicate the priority of root moisture content. The root system maintained a 62-77% higher level than the shoot in the container-grown stock. The relationship is different than levels found in bare root plants following storage. Sucoff et al. (1985), using red pine and white spruce from storage, began a desiccation experiment with shoots and roots at approximately the same level. A study on cold storage of scotch pine and blue spruce (LeFevre, 1988) indicated moisture contents in shoots and roots were similar following seven months of storage. The drastic shift in the gradient, as effected by desiccation of container stock in the present experiment (Table 4), could be a predominate factor in the alteration of seedling performance.

Understanding seedling response to desiccation and its effect on internal moisture status is important in determining planting stock quality. However, quality in terms of "fitness for purpose" (Sutton, 1980) is determined by plant performance. The second experiment evaluated seedling response to desiccation. Evaluation was based on an ability to rehydrate and commence root growth. Percent weight loss and gain relationships between IFW, TRFW and PFW provided a basis to assess rehydration capabilities of the seedlings. The percent weight loss between IFW and PFW (Table 6) represents the reduction in fresh weight attributed to the desiccation treatment. The percent weight loss deficit from IFW increased with duration of exposure. The 3.7% reduction in fresh weight of the control (0 hr) treatment is a reflection of transplant shock (Coutts, 1980). Mechanical damage, desiccation or poor-soil contact can reduce water uptake by plants (Grossnickle, 1988).

The percent weight loss differences in the duration treatments could be attributed to a combination of transplant shock and irreversible root damage from desiccation. PFW-TRFW is also measure of the plants response to the growth period following desiccation. The -3.7% reflects the transplant reduction in the control (0 hr) treatment. Weight gain increased with the severity of the treatment. The overall results on shoot and root moisture content support this assumption. The rehydration of the treated seedlings resulted in uniform shoot moisture levels across the 4 duration treatments and similarly in root moisture between the 1, 2 and 3 hour treatments. The increased rehydration with duration of exposure could be an example of the elastic properties of the plant tissue

(Kandiko et al., 1980; Sucoff et al., 1985) or an uptake response by both living and dead tissue (Kramer, 1933).

If water uptake is one of the prerequisites of root growth (Stone, 1955), then root growth capacity (RGC) acts as a measure of treated stock quality. RGC as an expression of physiological status of the seedlings offers an estimate of potential survival (Burdett, 1987). The increases in water uptake by the exposed plants in these experiments and the seemingly similar moisture contents in the plant parts did not outweigh the injury due to desiccation. The plants not exposed to drying conditions produced almost twice as many white roots as the 1 hour treatment. Subsequent duration of exposure resulted in further decreases in white roots. The thirty day growth period showed the importance of root growth capacity and provided an indication of the time necessary for seedlings to rebound under optimum conditions following severe desiccation.

REFERENCES

Barnett, J.P. 1983. Relating seedling morphology and physiology of container-grown southern pines to field success. Proc. of Soc. Am. For., Portland, Oregon. pg 405-409.

Boyer, J.N. and D.B. South. 1984. A morphological comparison of greenhouse-grown loblolly pine seedlings with seedlings grown outdoors. Tree Planters Notes. Summer 1984, pg. 15-18.

Brix, H. 1960. Determination of viability of Loblolly pine seedlings after wilting. Bot. Gaz. 121:220-223.

Burdett, A.N. 1987. Understanding root growth capacity: Theoretical considerations in assessing planting stock quality by means of root growth tests. Can. J. For. Res. 17:768-775.

Coutts, M.P. 1980. Control of water loss by actively growing sitka spruce seedlings after transplanting. J. Exp. Bot. 31:1587-1597.

Coutts, M.P. 1981a. Effects of root or shoot exposure before planting on the water relations, growth, and survival of sitka spruce. Can. J. For. Res. 11:703-709.

Coutts, M.P. 1981b. Leaf water potential and control of water loss in droughted sitka spruce seedlings. J. Exp. Bot. 32:1193-1201.

Cummings, W.W. 1942. Exposure of roots of shortleaf pine stock. J. For. 40:490-492.

DeWald, L.E. and P.P. Feret. 1987. Change in loblolly pine root growth potential from September to April. Can. J. For. Res. 17:635-643.

Duryea, M.L. and D.P. Lavender. 1982. Water relations, growth and survival of root-wrenched Douglas-fir seedlings. Can. J. For. Res. 12:545-555.

Farmer, R.E. 1979. Dormancy and root growth capacity of white and sawtooth oaks. For. Sci. 25:491-494.

Farmer, R.E., R.W. Reinholt and F. Schmekenburger. 1986. Environmental preconditioning and variance in early growth of balsam poplar. Silvae Genetica 35:129-131.

Grossnickle, S.C. 1988. Planting stress in newly planted jack pine and white spruce. 1. Factors influencing water uptake. Tree Physiol. 4:71-83.

Heckman, J.W. 1985. Environmental control of spruce seedling growth and shoot development. Ph.D. Thesis, Michigan State University.

Hermann, R.K. 1964. Effects of prolonged exposure of roots on survival of 2-0 Douglas-Fir seedlings. J. For. 62:401-403.

Hermann, R.K. 1967. Seasonal variation in sensitivity of Douglas-Fir seedling to exposure of roots. For. Sci. 13:140-149.

Hermann, R.K. and D.P. Lavender. 1979. Testing the vigor of coniferous planting stock. Forest Research Laboratory, Oregon State University, Corvallis, Res. Note 63.

Johnson-Flanagan, A.M. and J.N. Owens. 1985. Root growth and root growth capacity of white spruce (Picea glauca (Moench) Voss) seedlings. Can. J. For. Res. 15:625-630.

Johnson-Flanagan, A.M. and J.N. Owens. 1985. Development of white spruce (Picea glauca) seedling roots. Can. J. Bot. 63:456-462.

Kandiko, R.A., R. Timmis and J. Worrall. 1980. Pressure-volume curves of shoots and roots of normal and drought conditioned western hemlock seedlings. Can. J. For. Res. 10:10-16.

Kaufmann, M.R. 1968. Water relations of pine seedlings in relation to root and shoot growth. Plant Physiol. 43:281-288.

Kramer, P.J. 1933. The intake of water through dead root systems and its relation to the problem of absorption by transpiring plants. Am. J. Bot. 20:481-492.

Kramer, P.J. 1950. Effects of wilting on the subsequent intake of water by plants. Am. J. Bot. 37:280-284.

LeFevre, R.E. 1988. Moisture loss during storage and new growth of bare-root conifer seedlings. M.S. Thesis, Michigan State University.

McCreary, D.D. and M.L. Duryea. 1987. Predicting field performance of Douglas-Fir seedlings: Comparison of root growth potential, vigor and plant moisture stress. New Forests 3:153-169.

Moon, J.W. and J.A. Flore. 1986. A basic computer program for calculation of photosynthesis, stomatal conductance and related parameters in an open gas exchange system. Photosynthesis Research 7:269-279.

Mullin, R.E. 1963. Growth of white spruce in the nursery. For. Sci. 9:68-72.

Mullin, R.E. 1971. Some effects of root clipping, root exposure and extended planting dates with white spruce. For. Chron. 47:90-93.

Mullin, R.E. 1974. Effects of root exposure on establishment and growth of outplanted trees. Proc. Int. Sym. Ecol. and Phys. of Root Growth. pg. 229-242.

Mullin, R.E. and T.R. Myland. 1982. Tests of time of lifting, shipping and containers for overwinter storage at Dryden Nursery. Ont. Min. Nat. Resources Nursery Notes No. 77.

Nichols, T.J. and A.A. Alm. 1983. Root development of container-reared, nursery grown and naturally regenerated pine seedlings. Can. J. For. Res. 13:239-245.

Pharis, R.P. 1966. Comparative drought resistance of five conifers and foliage moisture content as a viability index. Ecology 47:211-221.

Ritchie, G.A. and R.G. Shula. 1984. Seasonal changes of tissue water relations in shoots and root systems of Douglas-fir seedlings. For. Sci. 30:538-548.

Ritchie, G.A., J.R. Roden and N. Kleyn. 1985. Physiological quality of lodgepole pine and interior spruce seedling: Effect of lift date and duration of freezer storage. Can. J. For. Res. 15:636-645.

Sams, C.E. and J.A. Flore. 1982. The influence of age, position and environmental variables on net photosynthetic rate of sour cherry leaves. J. Amer. Soc. Hort. Sci. 107:339-344.

Spomer, L.A. 1985. Techniques for measuring plant water. HortSci. 20:1021-1028.

Stone, E.C. 1955. Poor survival and the physiological condition of planting stock. For. Sci. 1:89-94.

Stransky, J.J. 1963. Needle moisture as a mortality index for southern pine seedlings. Bot. Gaz. 124:178-179.

Sucoff, E., C. Buschena and P. Tamte. 1985. Desiccation and water potential in the roots, leaves and shoots of bareroot red pine and white spruce. Can. J. For. Res. 15:989-992.

Sutton, R.F. 1980. Techniques for evaluating planting stock quality. For. Chron. 56:116-120.

Switzer, G.L. 1960. Exposure and planting depth effects on loblolly pine planting stock on poorly drained sites. J. For. 58:390-391.

Tear, E.C., K.O. Higginbotham and J.M. Mayo. 1982. Effects of drying soils on survival of young Picea glauca seedlings. Can. J. For. Res. 12:1005-1009.

Timmis, R. 1980. Stress resistance and quality criteria for tree seedlings: Analysis, measurement and use. N. Z. J. For. Sci. 10:21-53.

Ursic, S.J. 1961. Tolerance of loblolly pine seedlings to soil moisture stress. Ecology 42:823-825.

Ziegler, E.A. 1914. Loss due to exposure in the transplanting of white pine seedlings. For. Quarterly 12:31-33.

Ziegler, E.A. 1915. Further notes on the effect of exposure on white pine seedlings. For. Quarterly 13:163-170.

CHAPTER II

EFFECTS OF WATER STRESS ON *PICEA* SEEDLINGS: II. WATER VAPOR LOSS AND RESPIRATION.

ABSTRACT

Respiration and water vapor loss were characterized during desiccation of white spruce (Picea glauca (Moench) Voss) and blue spruce (Picea pungens, Engelm.). Respiration for white and blue spruce ranged from 1.01-1.13 mg CO_2 gm $D.W.^{-1}hr^{-1}$. Increases in vapor pressure gradient (VPG) did not influence respiration rate. Root exposure generated a higher respiration rate than shoot or total seedling exposure. The VPG and plant part exposure interaction revealed a significant reduction in root respiration rate with each increment of exposure. White spruce exhibited a 25 and 23% reduction in respiration within the 2 and 3 hour exposure treatments. Blue spruce reductions were 12% in the 2 hour and 37% in the 3 hour exposures.

Rate of vapor loss increased with an increase in VPG within each duration treatment. Root exposure was more sensitive to water vapor loss when compared to either the shoot or total seedling exposure treatments. A linear relationship between water vapor loss and respiration was found in both white and blue spruce following 3 hours of exposure. Respiration decreased as the rate of water vapor loss decreased.

INTRODUCTION

Planting shock (PS) is the reduction in seedling performance attributed to stress which occurs when plants are transferred from the nursery to the field (Hallman et al., 1978; Coutts, 1980). A variety of mechanical and physiological stresses accompany the seedlings through lifting, processing, storage and subsequent planting (Sutton, 1980). These stresses have an adverse effect on the physiological status of the seedling.

Water stress can effect both physiological and metabolic changes in tissues, depending upon the duration and severity of the stress (Hsiao, 1974) and has been identified as a major cause of planting shock. Mechanical damage to the root system may also effect planting stock quality (Hermann, 1964; Lavender and Wareing, 1972; Coutts, 1980). In a sitka spruce study, Coutts (1980) found that mechanical and physiological injury to the root system terminated root extension and reduced subsequent transpiration. Hallman et al. (1978) found that exposure and planting caused a significant reduction in transpiration and photosynthesis in Scotch pine seedlings as long as five weeks after planting. In studies using conifer seedlings, respiration rates were found to decrease with increased water stress (Zavitkovski and Ferrell, 1968, 1970; Puritch, 1973). Water deficit initially caused a decrease, followed by an increase, then a sudden drop in respiration rate in loblolly pine (Brix, 1962). McCreary and Zaerr (1987) found that root damage was the principle cause of poor seedling quality and investigated the relationship between root respiration and growth performance. They suggested that root respiration could indicate prior physiological damage and predict field performance. McCreary and Zaerr (1987) showed that significantly lower respiration rates occurred in the 30 and 60 minute desiccation treatments and concluded that root respiration may be useful in assessing root damage by desiccation.

The present study was conducted to characterize the effects of desiccation on water vapor loss and respiration rate. Results from this experiment should be useful in furthering our understanding of plant responses during transition handling. The objectives of this study were: 1) to characterize evaporation rate as influenced by desiccation , and 2) to examine plant part respiration in response to desiccation.

MATERIALS AND METHODS

White spruce [*Picea glauca* (Moench) Voss] from a southern Ontario seed source and blue spruce (*Picea pungens*, Engelm.) from bulk seed of a half-sib family from the San Juan Mountain region of Colorado were used in the experiment. Seedlings were grown in polyethylene coated plant bands (5x5x27 cm) with 3:1:1 (v:v:v) mixture of sphagnum peat:perlite:vermiculite. Fertilization was initiated two weeks after sowing and continued on 2-week intervals with a soluble 15-16-17 (NPK) formulation. Water was applied as necessary to maintain optimum soil moisture. Seedlings were grown on a laboratory grown frame, under the following environmental conditions: temperatures, 22-27°C; PPFD, 165 $\mu mm^{-2} sec^{-1}$. Plants were grown for 5 months under continuous light and 2 months under 8 hours photoperiod per 24 hours prior to the experiment.

The experimental design in the desiccation experiment consisted of a split plot factorial replicated four times. Vapor pressure gradient, species, plant part exposure and time (3x2x3x3) were factors within the experiment. The 3 levels within the time factor represent 15 minute intervals within the 1, 2 and 3 hour exposure treatments discussed in the previous chapter. The total time of exposure was analyzed separately, using interval time as the factor levels within each analysis of variance. Four, eight and twelve time intervals corresponded respectively to the 1, 2 and 3 hour exposures. Duncan's multiple range test was used to separate means.

Seedlings were randomly selected from the growth frame the night prior to treatment. A detailed description of seedling preparation and handling was given in Chapter I. Preparation for the desiccation treatment consisted of removing seedlings from the polyethylene bag, gently washing the planting media from the roots, and blotting the seedlings dry with absorbent tissue to remove any surface moisture on shoots and roots. Seedling fresh weights were recorded and individual seedlings were placed into controlled environmental plant chambers. Chambers were covered with black cloth throughout the desiccation treatment. Upon completion of the treatment, the plant part exposed was removed and severed at the root collar. Dry weights of the shoot and root were determined after oven drying at 100°C for 72 hours.

Plant part exposure treatments consisted of total seedling (TS), roots only (R) and shoots only (S). In the TS treatment, the total seedling was placed into the chamber. In the root and shoot only treatments, the respective plant part not subjected to the treatment was wrapped in a double layer of saran and a layer of aluminum foil. The exposed plant part was sealed into the chamber. Both plant parts were covered in a black cloth during the treatment.

Desiccation treatments were conducted in an open gas analysis system described by Sams and Flore (1982). The system measures changes in CO_2 and water vapor within 4 individual plant chambers (11x21x9.5 cm). Interior sensors monitor sample temperature, chamber temperature and PPFD. Carbon dioxide exchange was measured with a Beckman 865 infrared gas analyzer equipped with an optical filter to eliminate water vapor interference. Respiration was calculated as CO_2 (mg CO_2 gram dry weight^{-1} hour^{-1}) evolution using equations and a computer program described by Moon and Flore (1986).

Air flow entering the chamber was monitored at 1.0 liters min^{-1} ±2% using Aalborg FM102-05 flow meters. Chamber temperatures were controlled using a refrigerated water bath and circulation system into each chamber. A variable speed fan located in the bottom of the chamber forced adequate air mixing around the entire sample. Plant temperature was determined by chromel-constantan thermocouples (0.03 mm) pressed against the underside of the sample (Omega 250 EQ Digital Temperature Indicator) and chamber air temperature was recorded with thermistors (YSI 47 Scanning Telethermometer). Seedling temperature was maintained at 24-25°C. Air vapor pressure was controlled by saturating incoming air with water at a set temperature. Dew points of incoming and outgoing chamber air were monitored with a chilled mirror dew point hygrometer (General Eastern System 1100AP). Dew points of incoming air varied according to the desired vapor pressure gradient (VPG) within the chamber. VPGs of 0.5, 1.0 and 1.5 kPa were used. Water vapor loss rates were based on flow rate, mole fraction of water vapor of the incoming and outgoing air streams and plant part dry weight. A conversion factor was used to express the results in terms of mg H_2O gram D.W.$^{-1}$hr^{-1} using same computer program (Moon and Flore, 1986). Carbon dioxide and water vapor concentrations were recorded on 15-minute intervals.

Table 1. Initial seedling fresh weight and seedling, shoot and root dry weights as effected by VPG, species, and plant part exposure.[z]

Factor	Initial fresh weight (gms)	Seedling dry weight (gms)	Shoot dry weight (gms)	Root dry weight (gms)
<u>VPG (kPa)</u>				
0.5	8.92	2.76	2.28	0.48
1.0	9.66	3.01	2.50	0.52
1.5	8.86	2.78	2.29	0.49
<u>Species</u>				
White spruce	8.75b	2.82	2.40	0.42b
Blue spruce	9.54a	2.88	2.31	0.58a
<u>Plant Part Exposure</u>				
Total seedling	8.73b	2.71b	2.23b	0.48
Root	9.85a	3.09a	2.57a	0.53
Shoot	8.85b	2.75b	2.26b	0.48

[z]Means within main effect vertical column followed by same letter are not significantly different at $P=0.05$ using Duncan's Multiple Range Test.

RESULTS

The mean data for seedling dry weight are presented in Table 1. Root system dry weight was approximately 17% of the total seedling dry weight.

Mean interval respiration rates for the main effects are outlined in Table 2. The respiration and water vapor loss rates are expressed on the basis of plant part dry weight. Vapor pressure gradient had no influence on the overall respiration rates. White spruce exhibited a higher respiration rate than blue spruce after two hours of exposure. However, rates were similar after 1 and 3 hour treatments. Roots exhibited a higher respiration rate than shoot or total seedling at all exposure times.

There was a significant VPG x plant part exposure interaction for exposed roots within the 1, 2 and 3 hour exposure treatments (Fig. 1). Respiration rate decreased between the 0.5 kPa and the two higher VPG treatments. Total seedling and shoot respiration were not affected by vapor pressure gradient after two or three hours of exposure.

There were no recorded differences in respiration rates between species. Species respiration rates for plant part exposure x time interaction, are presented separately (Fig. 2 and Fig. 3). The white spruce root exposure treatment showed an increased reduction in respiration when compared

Figure 1. Respiration rates for vapor pressure gradient and plant part exposure interaction when averaged over species and time interval. Rates are the means of the 15 minute interval measurements within the 1, 2 and 3 hour exposure treatments. Standard errors equal: 1 hour ± 0.099; 2 hour ± 0.071; 3 hour ± 0.055.

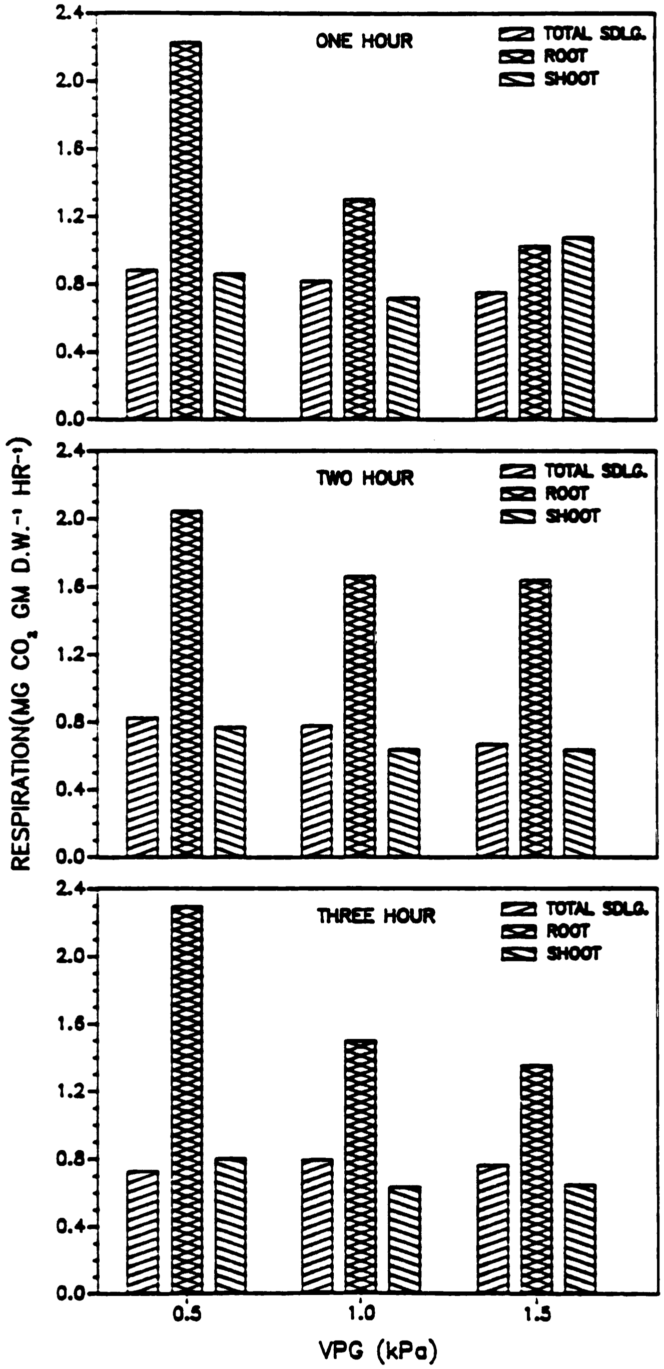
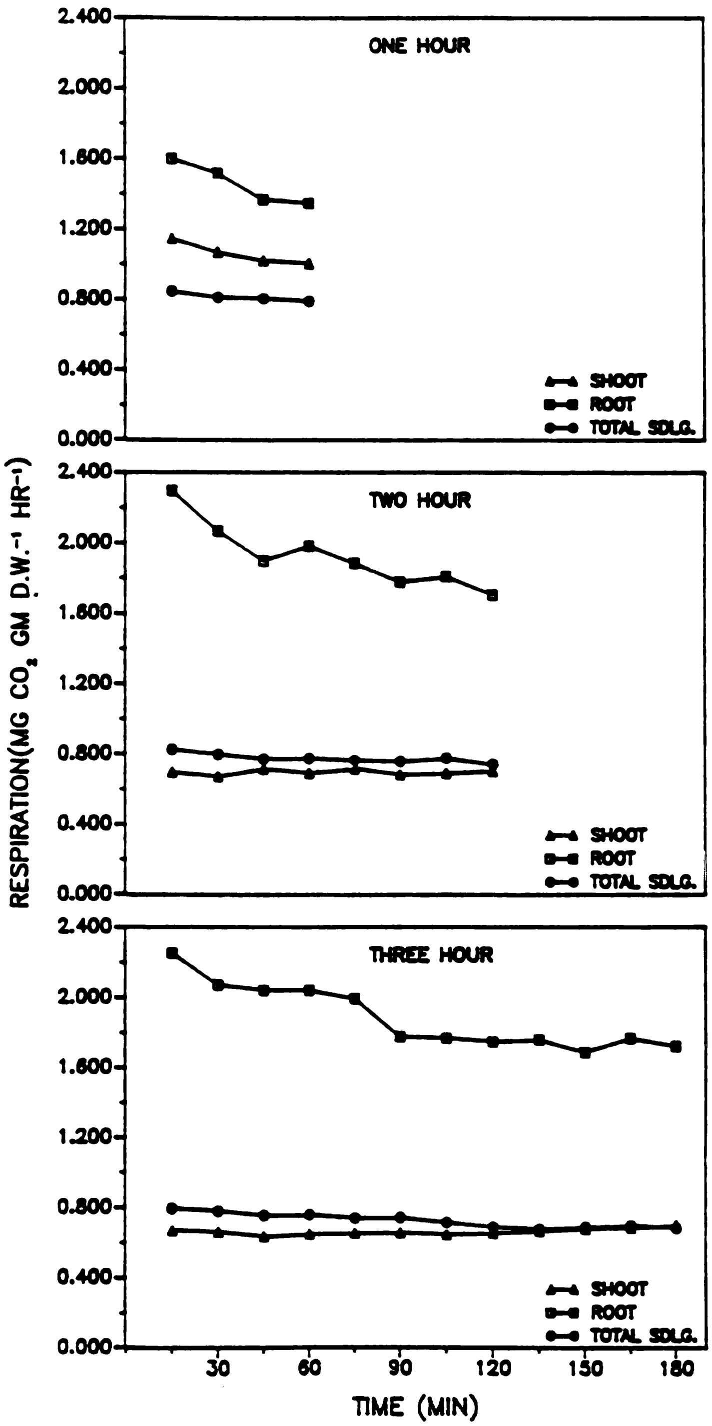

ONE HOUR
TWO HOUR
THREE HOUR
TOTAL SDLG.
ROOT
SHOOT
RESPIRATION(MG CO_2 GM D.W.$^{-1}$ HR^{-1})
VPG (kPa)
0.0
0.4
0.8
1.2
1.6
2.0
2.4
0.5
1.0
1.5

Table 2. Respiration and water-vapor loss for 1, 2 and 3 hour exposure time. Rates are the means of 15-minute interval measurements.[z]

Factor	Respiration ($mg\ CO_2\ gm\ D.W.^{-1}hr^{-1}$) Exposure 1 hr	2 hr	3 hr	Water vapor loss ($mg\ H_2O\ gm\ D.W.^{-1}hr^{-1}$) Exposure 1 hr	2 hr	3 hr
<u>VPG (kPa)</u>						
0.5	1.32	1.21	1.27	0.01b	0.01c	0.01c
1.0	0.94	1.02	0.97	0.03b	0.03b	0.02b
1.5	0.95	0.98	0.92	0.05a	0.04a	0.04a
<u>Species</u>						
White Spruce	1.11	1.13a	1.09	0.03	0.02	0.02
Blue Spruce	1.04	1.01b	1.02	0.03	0.03	0.02
<u>Plant Part Exposure</u>						
Total Seedling	0.82b	0.75b	0.76b	0.01b	0.01b	0.01b
Root	1.52a	1.78a	1.72a	0.06a	0.06a	0.05a
Shoot	0.88b	0.68b	0.69b	0.01b	0.01c	0.01c

[z]Means within main effect vertical column followed by same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

Figure 2. Respiration rates for white spruce total seedling, root and shoot taken at 15 minute intervals during the 1, 2 and 3 hour exposure treatments. Standard errors equal: 1 hour ± 0.162; 2 hour ± 0.164; 3 hour ± 0.155.


ONE HOUR
TWO HOUR
THREE HOUR
SHOOT
ROOT
TOTAL SDLG.
RESPIRATION(MG CO_2 GM D.W.$^{-1}$ HR^{-1})
TIME (MIN)
2.400
2.000
1.600
1.200
0.800
0.400
0.000
30
60
90
120
150
180

to the total seedling and shoot treatments after 2 and 3 hours of exposure.

Blue spruce maintained a relatively consistent respiration rate in the one and two hour exposure treatments (Fig. 3). Basic differences between the root exposure treatment and the total seedling and shoot treatments were found. Respiration in the three hour treatment significantly decreased between the initial rate and that recorded after 180 minutes.

Main effects on water-vapor loss are presented in Table 2. As VPG increased, rate of vapor loss increased at all exposure times. Root exposure treatment consistently exhibited a higher rate of water vapor loss than the shoot or total seedling treatments. After 2 and 3 hour exposure, water loss increased from shoot to total seedling to root exposure treatments.

The interaction between VPG and plant part exposure for 1, 2 and 3 hour exposure are presented in Fig. 4. Total seedling and root exposure resulted in an increased rate of water vapor loss with increased vapor pressure gradient for all exposure times. The same trend was observed in the two and three hour exposure treatment for the shoots. After 2 hours, significant differences between total seedling and shoot exposure were observed within the 0.5 and the 1.5 kPa treatments. The three hour exposure treatment resulted in total seedling and shoot exposure differences at the 1.0 and 1.5 kPa VPG levels.

Figure 3. Respiration rates for blue spruce total seedling, root and shoot taken at 15 minute intervals during the 1, 2 and 3 hour exposure treatments. Standard errors equal: 1 hour ± 0.162; 2 hour ± 0.164; 3 hour ± 0.155.

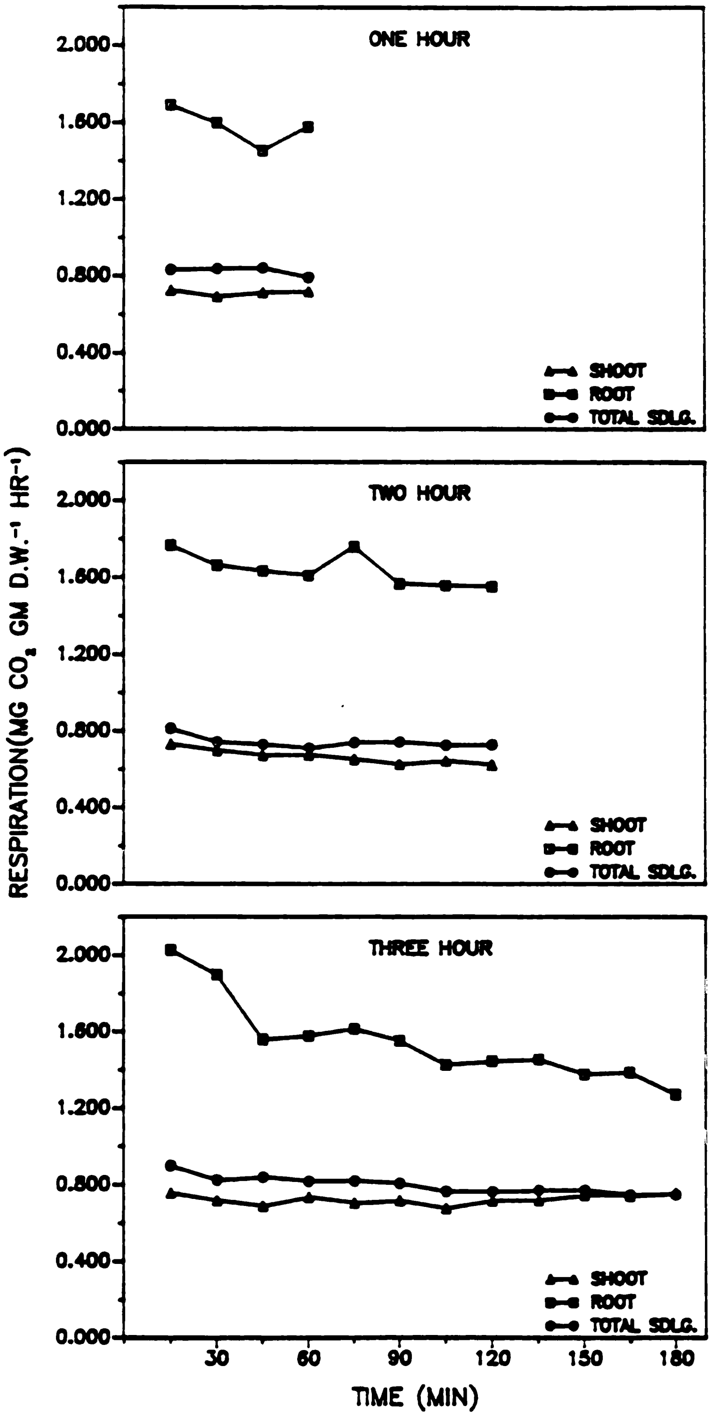

ONE HOUR
TWO HOUR
THREE HOUR
SHOOT
ROOT
TOTAL SDLG.
RESPIRATION(MG CO_2 GM D.W.$^{-1}$ HR^{-1})
TIME (MIN)
2.000
1.600
1.200
0.800
0.400
0.000
30
60
90
120
150
180

Figure 4. Water vapor loss for vapor pressure gradient and plant part exposure interaction when averaged over species and time interval. Rates are the means of the 15 minute interval measurements within the 1, 2 and 3 hour exposure treatments. Standard errors equal: 1 hour ± 0.003; 2 hour ± 0.002; 3 hour ± 0.001.

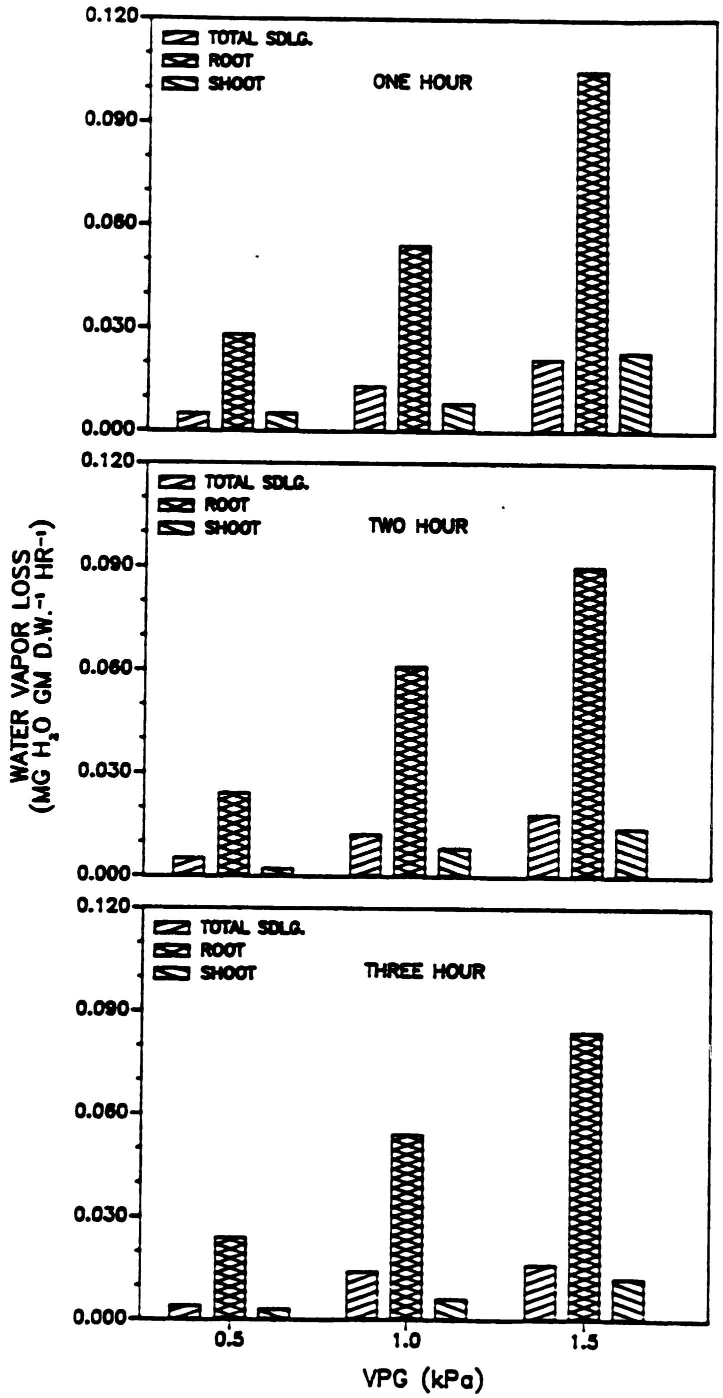
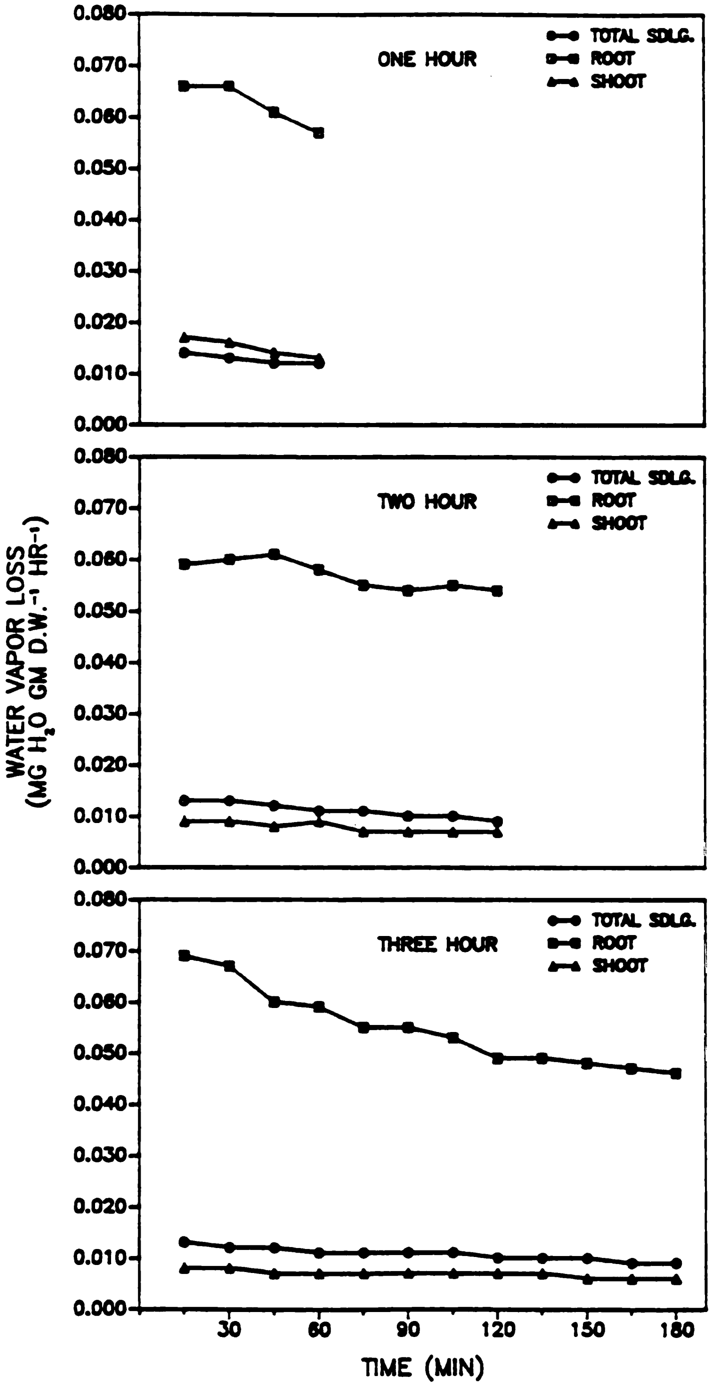
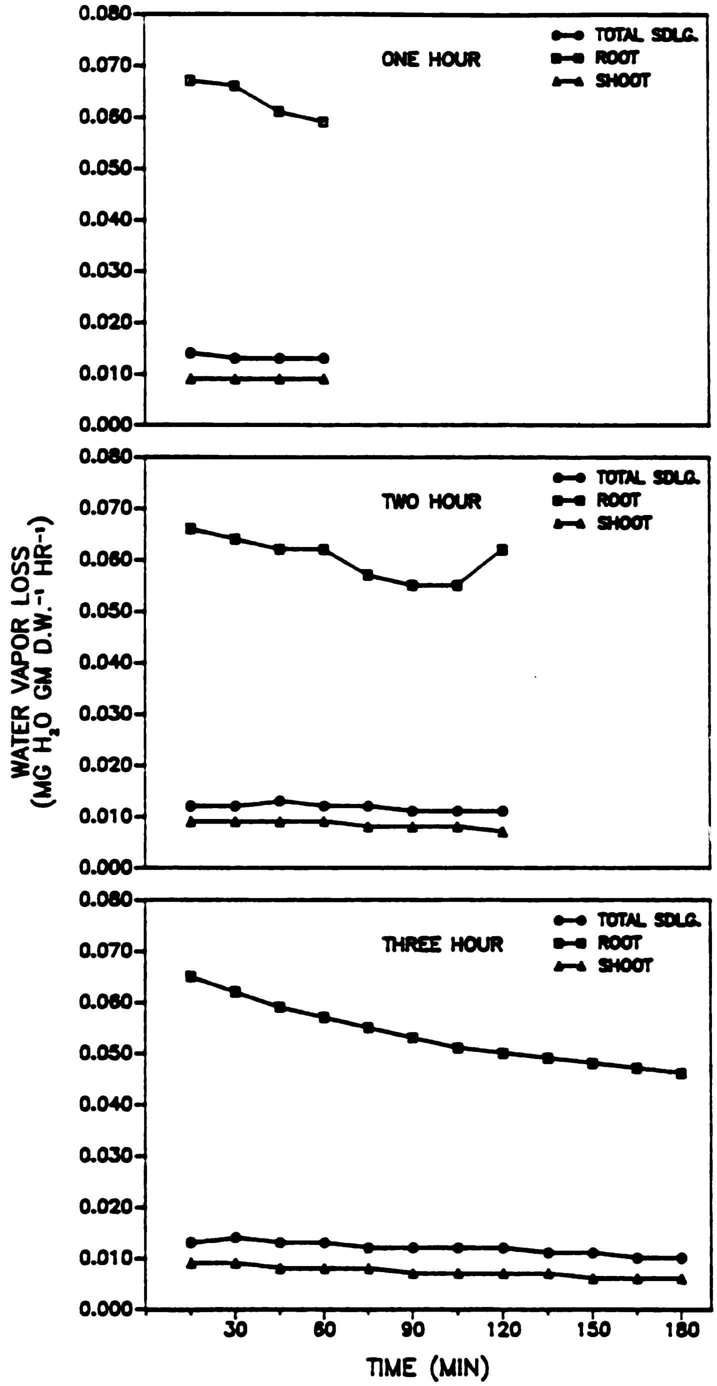

TOTAL SDLG.
ROOT
SHOOT
ONE HOUR
TWO HOUR
THREE HOUR
WATER VAPOR LOSS
(MG H2O GM D.W.-1 HR-1)
0.000
0.030
0.060
0.090
0.120
0.5
1.0
1.5
VPG (kPa)

Figure 5. Water vapor loss for white spruce total seedling, root and shoot taken at 15 minute intervals during the 1, 2 and 3 hour exposure treatments. Standard errors equal: 1 hour ± 0.004; 2 hour ± 0.004; 3 hour ± 0.002.



ONE HOUR
TWO HOUR
THREE HOUR
TOTAL SDLG.
ROOT
SHOOT
WATER VAPOR LOSS (MG H_2O GM D.W.$^{-1}$ HR^{-1})
0.080
0.070
0.060
0.050
0.040
0.030
0.020
0.010
0.000
30
60
90
120
150
180
TIME (MIN)

Figure 6. Water vapor loss for blue spruce total seedling, root and shoot taken at 15 minute intervals during the 1, 2 and 3 hour exposure treatments. Standard errors equal: 1 hour ± 0.004; 2 hour ± 0.004; 3 hour ± 0.002.



ONE HOUR
TWO HOUR
THREE HOUR
TOTAL SDLG.
ROOT
SHOOT
WATER VAPOR LOSS
(MG H_2O GM D.W.$^{-1}$ HR^{-1})
0.000
0.010
0.020
0.030
0.040
0.050
0.060
0.070
0.080
30
60
90
120
150
180
TIME (MIN)

Figure 7. Relationship between rate of water vapor loss and respiration for white spruce total seedling exposure during the 3 hour treatment at 1.5 kPa VPG. Correlation coefficient (R^2) ($P \leq 0.05$) equals .87.

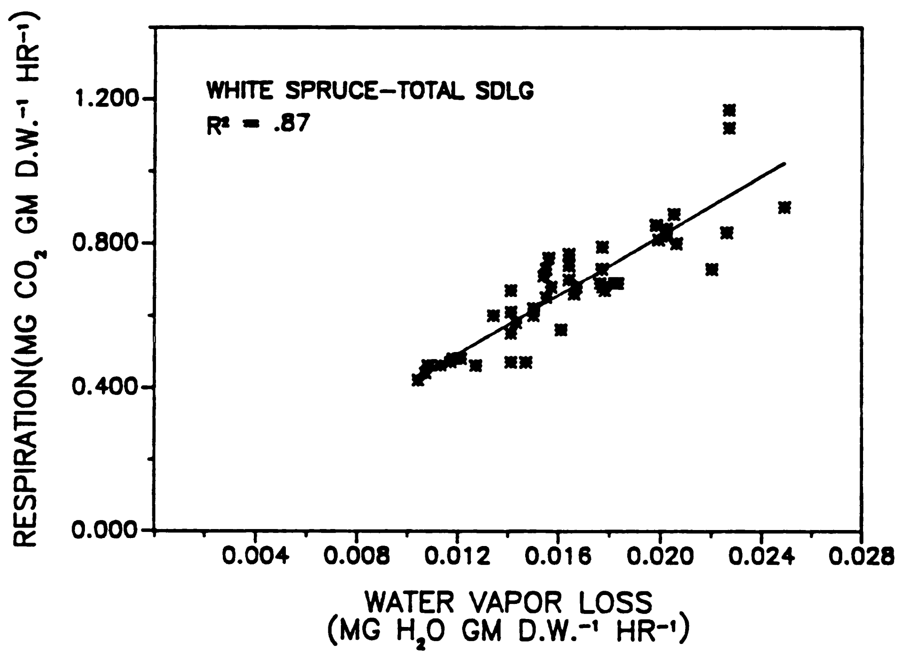
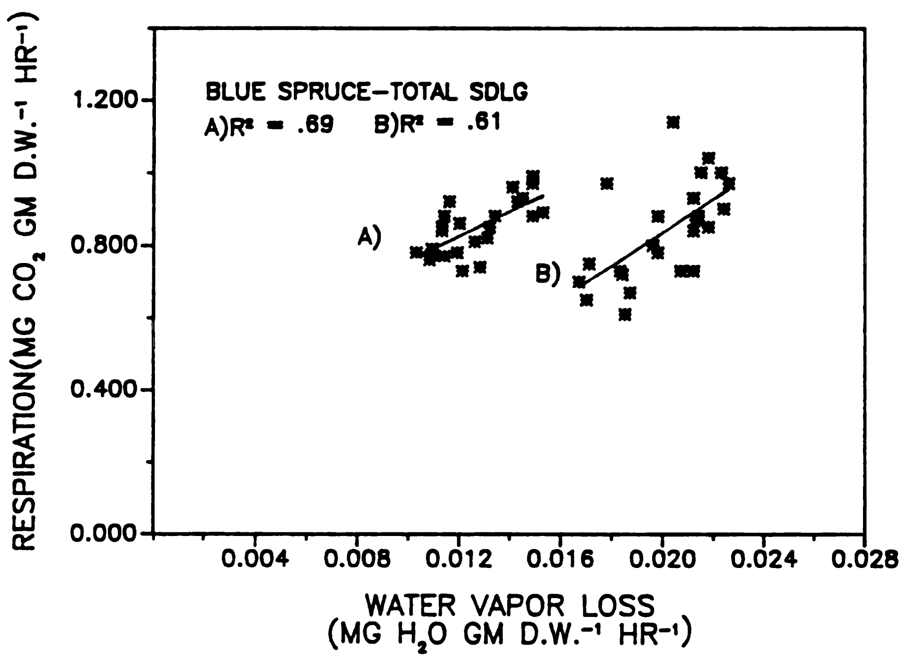

WHITE SPRUCE-TOTAL SDLG
R^2 = .87
RESPIRATION(MG CO_2 GM D.W.$^{-1}$ HR^{-1})
1.200
0.800
0.400
0.000
0.004
0.008
0.012
0.016
0.020
0.024
0.028
WATER VAPOR LOSS
(MG H_2O GM D.W.$^{-1}$ HR^{-1})

Figure 8. Relationship between rate of water vapor loss and respiration for blue spruce total seedling exposure during 3 hour treatment at 1.5 kPa VPG. Correlation coefficient (R^2) ($P \leq 0.05$) for: A) .69; B) .61.



BLUE SPRUCE-TOTAL SDLG
A)R² = .69 B)R² = .61
A)
B)
RESPIRATION(MG CO₂ GM D.W.⁻¹ HR⁻¹)
1.200
0.800
0.400
0.000
0.004
0.008
0.012
0.016
0.020
0.024
0.028
WATER VAPOR LOSS
(MG H₂O GM D.W.⁻¹ HR⁻¹)

The white spruce x plant part exposure x time interaction is presented in Fig. 5. The 3 hour treatment had a significant effect on the rate of water vapor loss in both white and blue spruce (Fig. 5 and Fig. 6). Exposure resulted in a significant decrease in overall rate with time.

The relationship between rate of water vapor loss and respiration was examined for white and blue spruce total seedling exposure treatment during 3 hours of exposure at 1.5 kPa VPG. Respiration in white spruce was linearly related to water loss (Fig. 7). Respiration rate decreased as the rate of water vapor decreased. Segregation of the replicates produced a similar trend in blue spruce (Fig. 8). Regressions were performed on the data based on the pattern observed in the scatter. Regression line A represents replicates 1 and 2. Line B represents replicates 3 and 4. A significant relationship was observed between water loss and respiration.

DISCUSSION

Respiratory rates observed in these experiments are comparable to values recorded by other researchers (Ledig, Drew and Clark, 1976; Zavitkovski and Ferrell, 1970; Puritch, 1973). Respiration for white and blue spruce ranged from 1.01-1.13 (mg CO_2 gm D.W.$^{-1}$hr^{-1}). There were significant differences depending on the plant part exposed: total seedling, shoot or root.

Seasonal patterns of CO_2 exchange in loblolly pine (Drew and Ledig, 1981) and pitch pine (Ledig, Drew and Clark, 1976) have been correlated to changes in shoot and root growth. Drew and Ledig (1981) observed a decrease in rate of CO_2 exchange per unit needle dry weight at the time of secondary needle formation. Johnson-Flanagan and Owens (1986) reported higher total respiration rates in elongating roots when compared to absorbing and brown roots. Environmental conditions also influence seedling CO_2 exchange. Soil temperature can have an effect on photosynthesis and respiration through its influence on nutrient and water uptake (Lawrence and Oechel, 1983). Drought causes reductions in photosynthesis and respiration with increasing stress. Recovery from stress is linked to recovery of root function (Zavitkovski and Ferrell, 1968).

The characterization of respiration is highly dependent on the developmental stage of the seedling and environmental conditioning. The seedlings used in our experiment were maintained under eight hour photoperiod for 2 months prior to the treatment. Shoot growth had ceased, a terminal bud was present, and foliage showed signs of maturity. The root systems were light brown in color and white roots were present.

Root respiration rate was significantly higher than rates recorded for the shoot or total seedling treatment. The relationship between root and shoot respiration corresponds to the relationship found in pitch pine (Ledig et al., 1976). Ledig et al. (1976) found that respiratory demands of the roots increased with the cessation of shoot growth. The shift in rates occurred on seedlings approximately 1300 days old. In the present study, root respiration averaged over exposure time was 1.67 mg CO_2 gm D.W.$^{-1}$hr^{-1}. These results were comparable to root respiration rates observed by the CO_2 efflux method in several conifer seedlings (Ledig et al., 1976). Older woody roots respire less for their mass than do younger roots (Ledig et al., 1976). The younger and relatively higher portion of white roots in a container seedling root system can explain the higher rates. Similarities in rates between the total seedling and the shoot exposure treatment could be explained by the fact that root dry weight accounts for only 17% of the seedling dry weight.

The severity of the desiccation by the vapor pressure gradient x duration of exposure interaction did not have any effect on shoot or total seedling respiration rate (Fig. 1).

Significance in the VPG x plant part exposure interaction was limited to root exposure. The recorded decrease in respiration rate between the 0.5 kPa and the latter two levels was consistent between the time of exposure. Evidence supporting the negative effect of desiccation on root respiration was reported by McCreary and Zaerr (1987). They observed an increased mortality and reduced growth and respiration rate in surviving Douglas-fir seedlings when exposed to a 60 minute desiccation prior to planting. Puritch (1973) found that needle and stem respiration rates of Abies decreased when water potential reached -7 to -10 bars, at which time rates dropped to 45-75% of the original levels. Desiccation causes a more pronounced effect on the root water status than that of the shoot (Chapter I). Brix (1962) suggests that a decrease in respiration in response to water stress could be caused by the reduction in respiratory substrates. The combination of increased water stress with a reduced concentration of substrates could have contributed to the decrease between the 0.5 and 1.0 kPa treatments.

The species x plant part exposure x time interaction provides additional information concerning the respiratory response to desiccation. There was no statistical evidence for a decrease in respiratory rate within the one hour treatment. The effects of desiccation on root respiration were observed after 2 and 3 hour exposure treatments for both white and blue spruce (Fig. 2 and Fig. 3). White spruce exhibited a 25 and 23% reduction in respiration rates within the 2 and 3 hour exposure treatments, respectively, while blue spruce had a 12% and 37% reduction. The reduction in respiration rate could be attributed to cessation of growth and root injury.

Root respiration has been suggested as a potential indicator of seedling quality (Johnson-Flanagan and Owen, 1986). McCreary and Zaerr (1987) found that root respiration during growth room recovery could be correlated with desiccation injury and subsequent performance. In the present experiment, the decrease in respiration was monitored during the imposed stress. To better understand the links between root respiration and subsequent performance, the respiratory response should be monitored from the imposition of the stress through the recovery period. However, its use as a predictor of field performance may be questionable due to variation in field conditions.

Planting shock has a pronounced effect on transpiration rates following planting (Hallman et al., 1978; Coutts, 1980). Hallman et al. (1978) monitored the effects of transplanting and exposure on the control of transpiration. Transplanting caused a fifty-percent reduction in transpiration level when compared to an undisturbed sample. Additional exposure for 20 minutes in full sun resulted in an 18% reduction in fresh weight and a corresponding decrease in transpiration to 25% of the potential value.

Reduced values persisted throughout the five weeks of the experiment. Coutts (1980) monitored reductions in transpiration in response to varying degrees of root damage. The negative effects on transpiration could be detected after 2-4 hours and continued to decrease for a few days depending on the extent of the damage. It was concluded that root damage could induce partial closure of the stomata independent of a decrease in leaf water potential. The water loss monitored in the present experiment could not be classified as transpiration. Although stomatal conductance may be involved, the parameter monitored was considered evaporation. The intent was to characterize the water vapor loss and to determine through subsequent research whether this rate could be modified.

Increase in vapor pressure gradient increased the rate of loss. This result was anticipated, but, the extent of the difference caused by an 0.5 kPa increase was not known. Rate of water vapor loss within the one hour exposure treatment increased by 92 and 100% with each 0.5 kPa increase in VPG. The change in VPG from 0.5 to 1.0 kPa generated a 145% and 138% increase in rate of vapor loss after 2 and 3 hours of exposure. The subsequent increases from 1.0 to 1.5 kPa were significant but not as dramatic, 51 and 48% respectively. The decrease in rate, with subsequent increased exposure could be due to a combination of decreased moisture levels (Chapter I) and an increased resistance to water movement in dehydrated tissue. Plant part exposure treatment effects were expected due to differences found in Chapter I. The increased sensitivity of roots to exposure (Coutts, 1981; Sucoff et al., 1985) is apparent in the rate at which water vapor was lost into the system.

The water vapor loss data presented in this experiment is difficult to interpret. Water vapor loss was a measure of evaporation rate from the exposed tissue. Plant characteristics as well as environmental conditions within the plant chamber could have influenced the rate of vapor released from the tissue. In this experiment, the intent was to investigate the response as it related to varying degrees of desiccation. The trends observed were more or less expected, however, more importantly the data becomes a baseline for future research. Physiological status of the initial seedling stock was relatively similar, however, variations in morphological characteristics such as needle surface area and portion of white to woody root were not monitored. These morphological characteristics could have influenced the recorded rates. The uncertainty of the morphological variables limits the interpretation to relative terms within this experiment.

The relationship between water vapor loss and respiration was evident for both white and blue spruce. Respiration rate follows the decrease in rate of water vapor loss. The results from our experiments compliment the work performed by McCreary and Zaerr (1987). They correlated a decrease in root respiration to desiccation during a growth room recovery period. The results suggest that the reduction in respiration during the course of desiccation is linearly related to the rate of water loss.

In examining research on the effect of exposure on plant processes, the ability of the plant to resist stress conditions is referred to tolerance or avoidance. The rates of water vapor loss and respiration measured in this experiment will be basic to subsequent research aimed at understanding the relationship among water loss, sensitivity and recovery of spruce.

REFERENCES

Anderson, J.E. and S.J. McNaughton. 1973. Effects of low soil temperature on transpiration, photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. Ecol. 54:1220-1223.

Baldwin, V.C. and C.W. Barney. 1976. Leaf water potential in planted ponderosa and lodgepole pines. For. Sci. 22:344-350.

Barnard, E.L. and J.R. Jorgenson. 1977. Respiration of field-grown loblolly pine roots as influenced by temperature and root type. Can. J. Bot. 55:740-743.

Boyer, W.D., R.M. Romancier and C.W. Ralston. 1971. Root respiration rates of four tree species grown in the field. For. Sci. 17:492-493.

Brix, H. 1962. The effect of water stress on the rate of photosynthesis and respiration in tomato plants and loblolly pine seedlings. Physiol. Plant. 15:10-20.

Brix, H. 1979. Effects of plant water stress on photosynthesis and survival of four conifers. Can. J. For. Res. 9:160-165.

Coutts, M.P. 1980. Control of water loss by actively growing sitka spruce seedlings after transplanting. J. Exp. Bot. 31:1587-1597.

Drew, A.P. and F.T. Ledig. 1981. Seasonal patterns of CO_2 exchange in the shoot and root of Loblolly pine seedlings. Bot. Gaz. 142:200-205.

Grossnickle, S.C. 1988. Planting stress in newly planted jack pine and white spruce. 1. Factors influencing water uptake. Tree Physiology 4:71-83.

Hallman, E., P. Hari, P.K. Rasanen and H. Smolander. 1978. Effect of planting shock on the transpiration, photosynthesis and height increment of scotch pine seedlings. Acta For. Fenn. 161:1-25.

Hermann, R.K. 1964. Effects of prolonged exposure of roots on survival of 2-0 Douglas-fir seedlings. J. For. 62:401-403.

Hsiao, T.C. and E. Acevedo. 1974. Plant responses to water deficits, water-use efficiency and drought resistance. Agric. Meteorol. 14:59-84.

Johnson-Flanagan, A.M. and J.N. Owens. 1986. Root respiration in white spruce [Picea glauca (Moench) Voss] seedlings in relation to morphology and environment. Plant Physiol. 81:21-25.

Krueger, K.W. and W.F. Ferrell. 1965. Comparative photosynthetic and respiratory responses to temperature and light by Pseudotsuga menziesii var menziesii and var glauca seedlings. Ecol. 46:794-801.

Lavender, D.P. and P.F. Wareing. 1972. Effects of daylength and chilling on the responses of Douglas-fir seedlings to root damage and storage. New Phytol. 71:1055-1067.

Lawrence, W.T. and W.C. Oechel. 1983. Effects of soil temperature on the carbon exchange of targa seedlings. 1. Root respiration. Can. J. For. Res. 13:840-849.

Lawrence, W.T. and W.C. Oechel. 1983. Effects of soil temperature on carbon exchange of taiga seedlings. II. Photosynthesis, respiration and conductance. Can. J. For. Res. 13:850-859.

Ledig, F.T., A.P. Drew and J.G. Clark. 1976. Maintenance and constructive respiration, photosynthesis and net assimilation rate in seedlings of pitch pine (Pinus rigida Mill.). Ann. Bot. 40:289-300.

McCreary, D.O. and J.B. Zaerr. 1987. Root respiration has limited value for assessing Douglas-fir seedling quality. Can. J. For. Res. 17:1144-1147.

McGregor, W.H.D. and P.J. Kramer. 1963. Seasonal trends in rates of photosynthesis and respiration of loblolly pine and white pine seedlings. Amer. J. Bot. 50:760-765.

Moon, J.W. and J.A. Flore. 1985. A basic computer program for calculation of photosynthesis, stomatal conductance and related parameters in an open gas exchange system. Photosynthesis Res. 7:269-279.

Parker, J. 1956. Drought resistance in woody plants. Bot. Rev. 22:241-289.

Puritch, G.S. 1973. Effect of water stress on photosynthesis respiration and transpiration of four Abies species. Can. J. For. Res. 3:293-298.

Sams, C.E. and J.A. Flore. 1982. The influence of age, position and environmental variables on net photosynthetic rate of sour cherry leaves. J. Amer. Soc. Hort. Sci. 107:339-344.

Seiler, J.R. and J.D. Johnson. 1985. Photosynthesis and transpiration of loblolly pine seedlings as influenced by moisture-stress conditioning. For. Sci. 31:742-749.

Sucoff, E., C. Buschena and P. Tamte. 1985. Desiccation and water potential in the roots, leaves and shoots of bare-root red pine and white spruce. Can. J. For. Res. 15:989-992.

Sutton, R.F. 1980. Techniques for evaluating planting stock quality. For. Chron. 56:116-120.

Timmis, R. 1980. Stress resistance and quality criteria for tree seedlings: Analysis, measurement and use. N. Z. J. For. Sci. 10:21-53.

Unterscheutz, P., W.F. Ruetz, R.R. Geppert and W.K. Ferrell. 1974. The effect of age, pre-conditioning and water stress on the transpiration rates of Douglas-fir (Pseudotsuga menziesii) seedlings of several ecotypes. Physiol. Plant. 32:214-221.

Zavitkovski, J. and W.K. Ferrell. 1968. Effect of drought upon rates of photosynthesis, respiration and transpiration of seedlings of two ecotypes of Douglas-fir. Bot. Gaz. 129:346-350.

Zavitkovski, J. and W.K. Ferrell. 1970. Effect of drought upon rates of photosynthesis, respiration and transpiration of seedlings of two ecotypes of Douglas-fir. II. Two-year-old seedlings. Photosynthetica 4:58-67.

CHAPTER III

EFFECTS OF WATER STRESS ON *PICEA* SEEDLINGS: III. DESICCATION IN FALL ACCLIMATED WHITE SPRUCE (*PICEA GLAUCA* (MOENCH) VOSS) AND BLUE SPRUCE (*PICEA PUNGENS* ENGELM.)

ABSTRACT

The effects of fall acclimation on seedling moisture content and sensitivity to desiccation were investigated on white spruce (*Picea glauca* (Moench) Voss) and blue spruce (*Picea pungens*, Engelm.). Initial seedling characteristics were modified by acclimation. Seedling dry weight increased and moisture content decreased from August through November.

Seedling moisture loss decreased between sampling dates. Differences in moisture content loss between the total seedling and the root exposure treatments suggested that seasonal modification was occurring in the shoot. Desiccation caused a shift in the root-shoot moisture balance in favor of the shoot. The severity of the shift lessened from August through November, indicating a change in seedling response to desiccation.

The original seedling fresh weight following desiccation and the 20 day growth period was markedly decreased. However, the deficit was lessened in October and November. Root growth capacity (RGC) in both the nonexposed and exposed seedlings increased from August to October, although the number of roots in the exposed group was significantly less. The increase in RGC indicated the

positive influence fall acclimation has on seedling desiccation tolerance.

Respiration rates increased from August to September and then returned to August level. Increased respiration coincided with the shift from shoot to root activity. The decrease in respiration rate between the total seedling and root exposure treatment indicated root sensitivity to desiccation. The rate of water vapor loss decreased from August through November.

INTRODUCTION

Physiological dormancy has been linked with the ability to tolerate desiccation injury associated with lifting, processing and storage of bare-root conifer seedlings (Mullin, 1967; Hermann, 1967). Hermann (1967) found that lifted Douglas-fir seedlings increased their tolerance of desiccation from fall to winter. Chilling and short day pretreatments decreased the adverse effects of root damage and dark storage on Douglas-fir seedling vigor upon planting (Lavender and Wareing, 1972). Lavender and Wareing (1972) also found that chilling increased root growth capacity in root damaged treatments. Ritchie et al. (1985), evaluating physiological quality, found that lodgepole pine and interior spruce were most resistant to desiccation stress when lifted after mid-October. Sixty minute exposure of the root system had no effect on survival of seedlings lifted between November 1 and February 28. In an attempt to link dormancy and stress resistance, a Stress Injury Index was plotted against the dormancy release index (DRI), indicating that the lowest injury occurred at DRI values between 0.2 and 0.4 (Ritchie et al., 1985). This was similar to values found by Hermann (1967).

Dormancy is one of several physiological parameters which, when measured, can be used in qualifying planting stock status as well as predicting performance after outplanting. Ritchie et al. (1985), demonstrated that physiological quality is reflected in root growth potential, frost hardiness and resistance to desiccation stress. The importance of scheduling nursery harvesting practices with optimum physiological quality is critical in bare-root seedling operations (DeWald and Feret, 1987; Ritchie et al., 1985).

Container nursery production has lessened the problems associated with restrictive harvest windows and, for the most part, reduced stresses occurring during lifting and processing. The controlled root environment has eliminated concerns with root damage. Root systems of container seedlings, however, may not be subjected to the environmental conditioning experienced by field grown stock prior to planting. The natural resistances developed through photoperiod and temperature changes in fall may be the basis for developing preconditioning treatments to increase tolerance of greenhouse grown seedlings to planting and site related stress. The objective of this study was to examine seedling response to desiccation as influenced by natural acclimation between August and November. Parameters measured included seedling moisture content, respiration and root growth capacity.

MATERIALS AND METHODS

White spruce (*Picea glauca* (Moench) Voss.) from a southern Ontario seed source and Blue spruce (*Picea pungens* Engelm.) from bulk seed of a half-sib family from the San Juan mountain region of Colorado were used in the experiment. Seedlings were grown in polyethylene coated plant bands (5x5x27 cm) with 3:1:1 (V:V:V) mixture of sphagnum peat:perlite:vermiculite. Slow release fertilizer (Osmocote, 18-6-12) and micronutrients (Micromax, Sierra Co.) were incorporated into the planting mixture. Water was applied as necessary to maintain optimum soil moisture. Seedlings were grown in a double layer poly greenhouse at the Tree Research Center, Department of Forestry, Michigan State University. Photoperiod in the polystructure was extended using high output cool-white fluorescent fixtures. Plants were grown for 22 weeks under 20 hour photoperiod. On August 24, 1987 a selection of actively growing seedlings was transferred to an overwintering structure. The overwintering structure was initially covered with shade cloth and in November with white polyethylene. Seedlings were sampled for treatment when placed into the structure (August 24) and on monthly intervals until November 24.

The experiment design consisted of a split plot replicated four times. Sample date, species and plant part exposure (4x2x3) were factors. Sample dates were August 24, September 24, October 24 and November 24. Plant part exposure treatment levels varied with analysis. A moisture content study was done with 3 levels: a non-exposed control; total seedling; and root only exposure. In the root exposure treatment, the shoot was wrapped in a double layer of saran and a layer of aluminum foil. The root system was sealed into the chamber and both plant parts were covered with a black cloth during treatment. The root growth capacity study consisted of a non-exposed and exposed total seedling. An analysis of respiration and water vapor loss in the moisture content study was done on the total seedling and root exposure treatments at 6-20 minute intervals within the 2-hour exposure treatment. Analysis of variance was performed on each study and Duncan's Multiple Range Test was used to separate means.

Seedlings were randomly selected from the overwintering structure the night prior to treatment. Seedlings were thoroughly watered, sealed in clear polyethylene bags and covered with a black polyethylene sheet a minimum of 14 hours. Seedlings remained covered with a black polyethylene sheet until preparation for the desiccation treatment. Preparation for the desiccation treatment consisted of removing seedlings from the polyethylene bag. Plant bands were removed, planting media was gently washed from the roots and seedlings were blotted dry with absorbent tissue to remove any surface moisture on shoots and roots. Seedling fresh weights were recorded and individual seedlings were placed into a controlled environmental chamber described in Chapter 2. Chambers were covered with a black cloth throughout the desiccation treatment. Upon completion of the treatment, the seedling was removed and severed at the root collar. Post-treatment fresh weights were recorded for both the roots and shoots. Dry weights of the shoot and root tissue were determined after oven drying at 100°C for 72 hours. Plant part moisture contents were calculated gravimetrically and percent weight loss was based on fresh weight. The following equations were used in calculations:

$$\text{Moisture Content} = \frac{\text{Fresh wgt (gm)} - \text{Dry wgt (gm)}}{\text{Dry wgt (gm)}}$$

$$\%\ \text{Weight Loss} = \frac{\text{Fresh wgt (gm)} - \text{Dry wgt (gm)}}{\text{Fresh wgt (gm)}} \times 100$$

Control seedlings were handled similarly with the exception of desiccation.

Desiccation treatments were conducted in an open gas analysis system described by Sams and Flore (1982) and modified by Gucci (1988). Differential CO_2 concentrations at the inlet and outlet of plant chamber were measured with an ADC 225 MK3 Infrared Gas Analyzer (Analyztical Development Company, Hoddesdon, U.K.). Air flow was regulated with Matheson 8100 series mass flow meters and Matheson 8200 series mass flow controllers connected to a Matheson multichannel Dyna-blender 8219 (Matheson Instruments, Horsham, Pennsylvania).

Respiration was measured as CO_2 (mg CO_2 gram dry weight^{-1}hour^{-1}) efflux and calculated using procedures described by Moon and Flore (1986). Plant temperatures within the chambers were maintained at 24-25°C. Air flow entering the chamber was set at 2.0 liter per minute in the total seedling exposure treatment and 1.5 liters per minute in the root exposure treatment. Dew point of incoming air was set to maintain a vapor pressure gradient of 1.5 kPa entering the chamber. Water vapor loss rates were based on flow rate, mole fraction of water vapor of incoming and outgoing air streams, and plant part dry weight. Data was expressed as mg H_2O gram D.W.$^{-1}$hr^{-1}. Seedlings were exposed for 2 hours with CO_2 and water vapor concentrations recorded on 20-minute intervals.

Seedlings used in the root growth capacity study were prepared for treatment using procedures mentioned above. Upon completion of the desiccation treatments, treated seedling weights were recorded. Prior to potting, both treated and control seedlings were dipped (3 sec) into water. Seedlings were potted into 26-liter containers of non-fertilized 3:1:1 planting mixture and placed into the original greenhouse under 20-hour photoperiod where they remained for 20 days. Optimum soil moisture was maintained during the growth period. At the conclusion, pots were removed, watered, sealed into clear polyethylene bags, and stored overnight under a black polyethylene sheet (14 hours). The following day seedlings were gently removed from the pots for determination of plant part moisture content and root production. Plant part moisture contents were determined as in the previous experiment, and the number of white roots above 1 mm in length were recorded.

RESULTS

Moisture Content

The means for the main effect of sampling date, species and plant part exposure on seedling dry weight and moisture content are presented in Table 1. Seedling dry weight increased between August and November, both in the shoot and root. Blue spruce had a significantly higher shoot and root dry weight than white spruce. Initial moisture content of seedlings decreased from August to November.

Sampling date had a significant influence on seedling moisture loss. Loss in moisture content was similar in August and September, followed by a significant decrease in both October and November. Plant part exposure also influenced moisture loss. The total seedling exposure treatment lost more than the root exposure treatment. Data for the interaction between sampling date and plant part exposure when averaged over species are presented in Table 2. Moisture loss from the total seedling exposure treatment decreased from August to November whereas loss from the root exposure treatment was similar between August and October. A significant decrease in moisture loss from the roots occured in November. The decrease in the initial seedling moisture content from August to November was observed in shoot and root moisture content following desiccation (Table 1). The decreases in moisture content reflect a seasonal reduction and the loss through desiccation. Blue spruce

Table 1. The effects of sampling date, species, and plant part exposure on seedling dry weight and moisture content following 2 hour exposure at 1.5 kPa VPG.[z,y]

	Initial Total Seedling		Treated Total Seedling		Treated Shoot		Treated Root	
	Dry wgt (gm)	MC	Loss MC	Loss % fresh wgt	Dry wgt (gm)	MC	Dry wgt (gm)	MC
<u>Sampling Date</u>								
August 24	1.99c	3.48a	0.53a	11.9	1.66c	3.05a	0.33c	2.35a
September 24	3.01bc	2.99ab	0.50ab	12.8	2.42bc	2.53b	0.58b	2.33a
October 24	3.87ab	2.21c	0.43b	13.4	2.95ab	1.78c	0.91a	1.78b
November 24	4.39a	1.75d	0.35c	12.5	3.42a	1.41d	0.97a	1.37c
<u>Species</u>								
White Spruce	2.97b	2.60	0.43	12.2b	2.42b	2.23	0.55b	1.89b
Blue Spruce	3.66a	2.61	0.47	13.1a	2.81a	2.16	0.85a	2.02a
<u>Plant Part Exposure</u>								
Nonexposed Control	3.19	2.64	0.00c	0.0c	2.53	2.41a	0.66b	3.53a
Total Seedling	3.13	2.59	0.76a	21.2a	2.48	1.99c	0.64b	1.13b
Root	3.62	2.59	0.60b	16.7b	2.83	2.19b	0.79a	1.20b

[z]Means within vertical column followed by same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

[y]MC = moisture content gm/gm oven dry weight.

Table 2. Moisture content loss and loss as percent initial fresh weight for the sampling date x plant part exposure interaction averaged over species following exposure to 1.5 kPa VPG for 2 hours.[z]

Sampling Date	Loss Moisture Content (gm H_2O gm $D.W.^{-1}$)		Loss % Initial Fresh Weight	
	Total Seedling Exposure	Root Exposure	Total Seedling Exposure	Root Exposure
August 24	0.95	0.65	20.95ab	14.65c
September 24	0.83	0.66	21.80a	16.46c
October 24	0.67	0.62	20.81ab	19.46b
November 24	0.59	0.45	21.16ab	16.39c
SE±	0.02	0.02	0.68	0.68

[z]SE± = standard error of the mean.

root moisture content was higher than white spruce. Plant part exposure influenced the shoot and root moisture contents. Shoot moisture content in the total seedling exposure treatment was significantly less than the root or nonexposed treatments. Root moisture content was similar between the total seedling and root exposure treatments, yet significantly less than the control. Total seedling loss, expressed as percent of fresh weight, was not influenced by sample date.

The internal water balance between the root and shoot was influenced by all main effects within the experiment (Table 3). Desiccation caused a shift in the root-shoot moisture balance from root to the shoot. The severity of the shift was lessened from August to November. Blue spruce was less affected than white spruce. Total seedling and root exposure treatments caused a pronounced shift in favor of the shoot when compared to the nonexposed seedling. The shift in root-shoot moisture balance was also observed in sampling date x plant part exposure interaction (Fig. 1). The moisture content advantage of the root in the nonexposed seedling increased through September and October and dropped to its original level in November. The shift toward higher shoot moisture content became less pronounced in the total seedling and root exposure treatment as the seedlings approached November. Shoot/root ratio decreased with sampling date. Blue spruce appeared to maintain an overall lower shoot/root ratio than white spruce seedlings.

Figure 1. Difference in moisture content between root and shoot (root MC - shoot MC) for the sampling date and plant part exposure interaction when averaged over species following desiccation at 1.5 kPa VPG for 2 hours. Standard error equals ± 0.078.

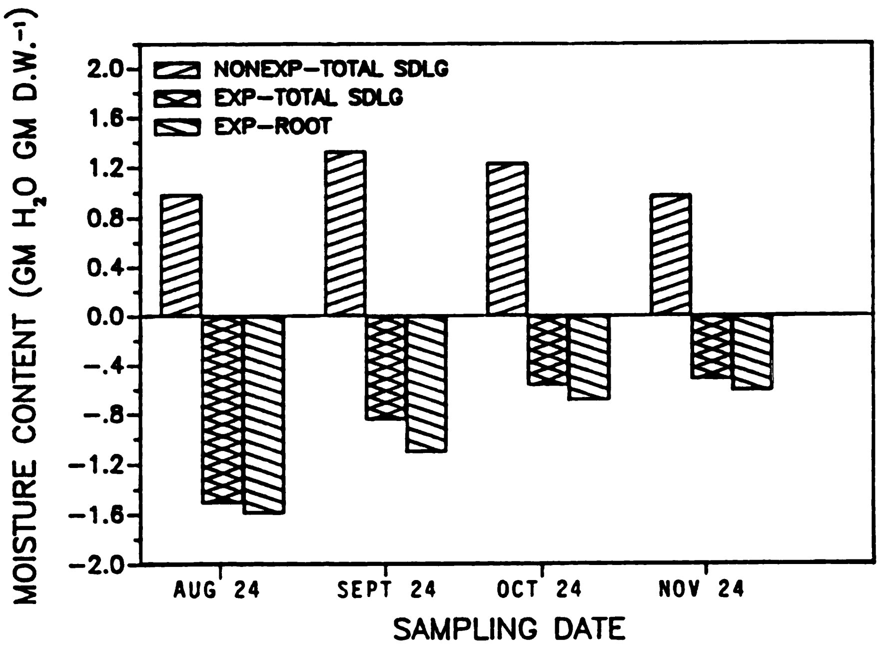

NONEXP-TOTAL SDLG
EXP-TOTAL SDLG
EXP-ROOT
MOISTURE CONTENT (GM H_2O GM D.W.$^{-1}$)
2.0
1.6
1.2
0.8
0.4
0.0
-.4
-.8
-1.2
-1.6
-2.0
AUG 24
SEPT 24
OCT 24
NOV 24
SAMPLING DATE

Table 3. The effects of sampling date, species and plant part exposure on root-shoot moisture content balance and on seedling shoot/root ratio following 2 hour exposure at 1.5 kPa VPG.[z,y]

	Treated Shoot-Root Relationship	
	Root-Shoot MC	Shoot/Root Ratio
<u>Sampling Date</u>		
August 24	-0.70c	5.2a
September 24	-0.21b	4.3b
October 24	-0.01a	3.4d
November 24	-0.05a	4.0c
<u>Species</u>		
White Spruce	-0.34b	4.8a
Blue Spruce	-0.14a	3.6b
<u>Plant part Exposure</u>		
Nonexposed Control	1.12a	4.3
Total Seedling	-0.85b	4.3
Root	-0.99c	4.1

[z]Means within vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

[y]MC = moisture content gm H_2O/gm oven dry weight.

Seedling Rehydration and Root Growth Capacity

The effect of sampling date, species and plant part exposure on percent weight gain or loss in the root growth capacity study is presented in Table 4. Blue spruce had a higher initial fresh weight than white spruce which was also observed in treated and potted fresh weights. Desiccation loss in percent fresh weight was influenced by plant part exposure. The 20.9% loss in the exposed seedling treatment was representative of the loss that occurred across sampling dates. The difference in fresh weight between initial fresh weight (IFW) and potted fresh weight (PFW) represents the weight gain or loss from initial fresh weight following the 20 day growth period (IFW-PFW). Weight gain over the IFW in the potted seedlings was recorded as a minus value. Weight loss from IFW was recorded as a positive value. The influence of the nonexposed seedling was observed in the sampling date main effect. A gain was recorded in August, October and November.

Blue spruce gained in fresh weight compared to the loss observed in the white spruce seedlings. IFW-PFW values for sampling date and plant part exposure can be evaluated easier from the interaction (Fig. 2). Negative values on the bar graph represent the weight gain over the initial fresh weight in the nonexposed seedlings. Weight gain was at its peak in August and subsequently, leveled off from September to November. Losses due to exposure were similar in August and September, and then significantly dropped in

Figure 2. Percent weight gain (-) or loss (+) of initial fresh weight following exposure to 1.5 kPa VPG for 2 hours and 20 day growth period. Means presented are the sampling date and plant part exposure interaction averaged over species. Standard error equals ± 2.44.

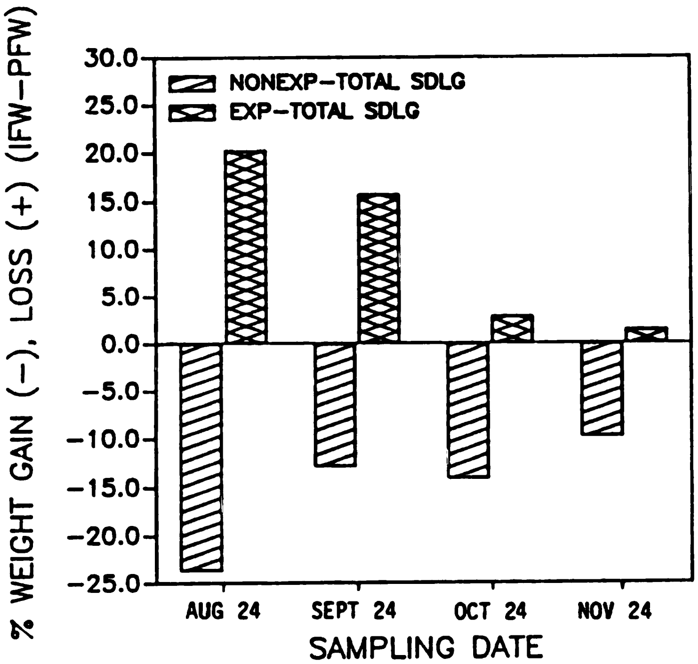

% WEIGHT GAIN (−), LOSS (+) (IFW−PFW)
30.0
25.0
20.0
15.0
10.0
5.0
0.0
−5.0
−10.0
−15.0
−20.0
−25.0
NONEXP−TOTAL SDLG
EXP−TOTAL SDLG
AUG 24
SEPT 24
OCT 24
NOV 24
SAMPLING DATE

Table 4. The effects of sampling date, species and plant part exposure on percentage weight loss relationship between initial, treated and potted fresh weights following 2 hour exposure to 1.5 kPa VPG and a 20 day growth period.[z,y]

Factor	Initial fresh wgt (gm) IFW	Treated fresh wgt (gm) TRFW	Potted fresh wgt (gm) PFW	% wgt loss IFW-TRFW	% wgt (-)gain, (+)loss IFW-PFW	% wgt gain PFW-TRFW
Sampling Date						
August 24	8.04	7.24	8.21	10.1	-1.7b	8.2c
September 24	10.20	9.12	10.08	10.9	1.4a	8.7bc
October 24	11.17	9.94	11.70	10.5	-5.6b	15.4a
November 24	10.07	9.02	10.49	10.4	-4.2b	14.2ab
Species						
White Spruce	9.26b	8.31b	9.19b	10.1	0.2b	8.4b
Blue Spruce	10.48a	9.34a	11.04a	10.9	-5.3a	14.9a
Plant Part Exposure						
Control (nonexposed)	9.59	9.59a	10.96b	0.0	-15.0b	12.7
Total Seedling	10.15	8.07b	9.27a	21.0	9.9a	10.6

[z]IFW = Initial fresh weight; TRFW = Treated fresh weight; PFW = Potted fresh weight.

[y]Means within vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

October and November. PFW minus TrFw represents the weight gain after the 20 day growth period. The sampling date and plant part exposure interaction is shown in Fig. 3. Percent weight gain in the exposed seedlings significantly increased between August and October. Increases observed in September and October were statistically similar between the exposed and nonexposed seedlings. The exposed seedlings in November out-performed the nonexposed seedlings in percent weight gain, however, potted fresh weights in the October and November sampling were similar.

Data for potted moisture content parameters are found in Table 5. Potted total seedling moisture content decreased from August to October. Blue spruce exhibited a higher moisture level than white spruce. Seedling exposure caused an overall decrease in potted moisture content. A significant sampling date x plant part exposure interaction was found in both potted shoot and root moisture contents (Fig. 4). Seedling exposure caused a decrease in shoot moisture from September to November. Differences within sampling date between exposed and nonexposed seedlings were found in August and November. Potted root moisture content in the nonexposed seedlings decreased from August to November. The exposed seedlings exhibited a relatively uniform root moisture level regardless of sampling date.

Sampling date main effects for root-shoot moisture content balance indicate a relatively uniform positive value between the September and November seedlings (Table 5). The

Figure 3. Percent potted weight gain (+) or loss (-) over treated fresh weight following desiccation and a 20 day growth period. Means presented are the sampling date and plant part exposure interaction average over species. Standard error equals ± 2.93.

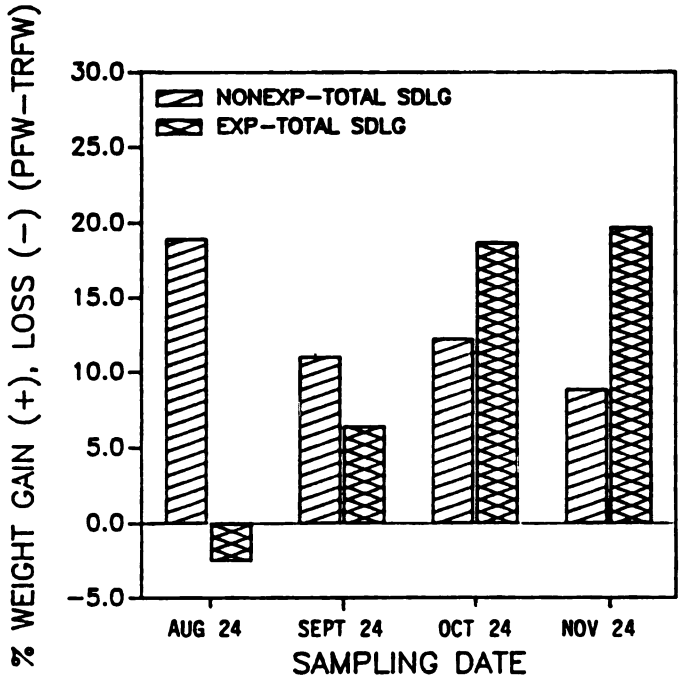
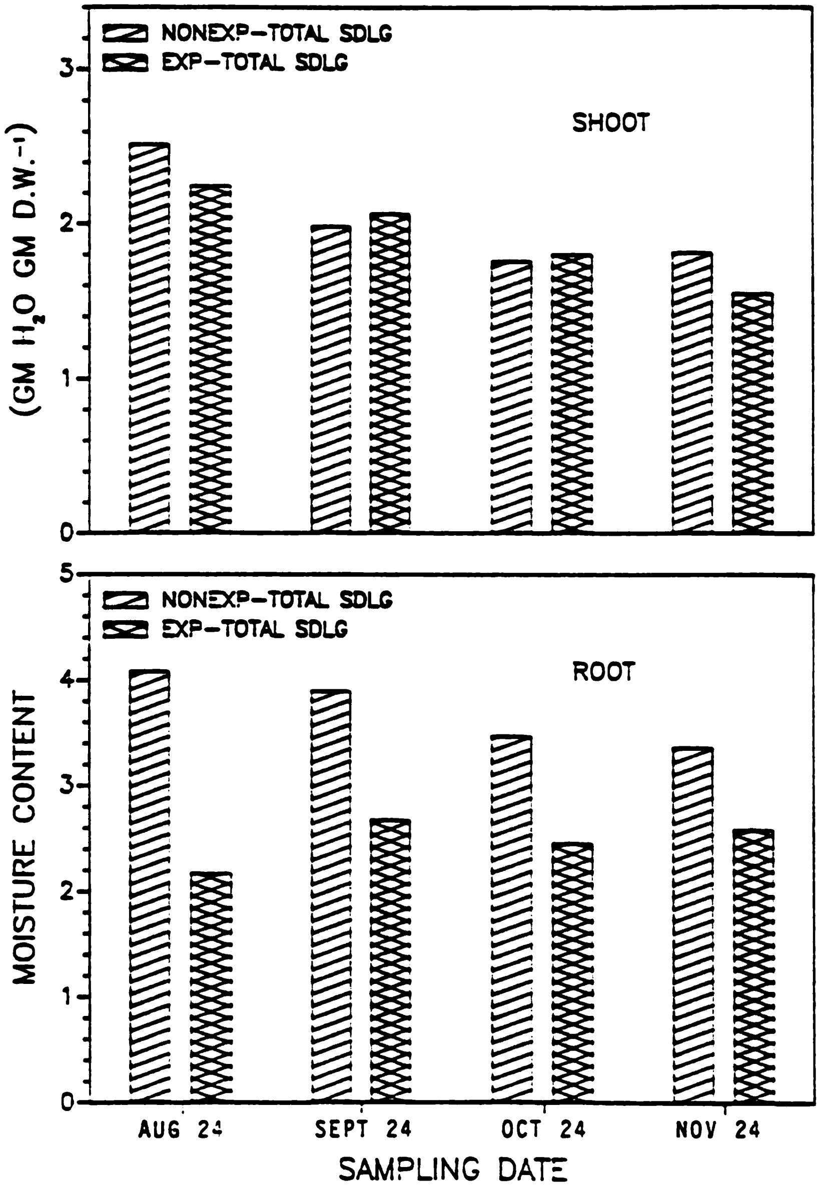

% WEIGHT GAIN (+), LOSS (−) (PFW−TRFW)
30.0
25.0
20.0
15.0
10.0
5.0
0.0
−5.0
NONEXP−TOTAL SDLG
EXP−TOTAL SDLG
AUG 24
SEPT 24
OCT 24
NOV 24
SAMPLING DATE

Figure 4. Shoot and root moisture content of potted seedlings following desiccation and 20 day growth period. Means presented are the sampling date and plant part exposure interaction averaged over species. Standard errors equal: shoot, ± 0.066; root, ± 0.152.



NONEXP–TOTAL SDLG
EXP–TOTAL SDLG
SHOOT
ROOT
MOISTURE CONTENT (GM H_2O GM D.W.$^{-1}$)
0
1
2
3
4
5
AUG 24
SEPT 24
OCT 24
NOV 24
SAMPLING DATE

Table 5. Effects of sampling date, species and plant part exposure on seedling moisture content and white root production following 2 hour exposure to a 1.5 kPa vapor pressure gradient and a 20 day growth period.[z,y]

Factor	Potted total seedling Dry wgt (gm)	Potted total seedling MC	Potted Shoot Dry wgt (gm)	Potted Shoot MC	Potted Root Dry wgt (gm)	Potted Root MC	Shoot Root Relationship Root-Shoot MC	No. of white roots >1 mm
Sampling Date								
August 24	2.32b	2.50a	1.96b	2.38a	0.35b	3.12	0.77b	81c
September 24	3.03ab	2.30b	2.43ab	2.02b	0.60ab	3.29	1.27a	144b
October 24	3.84a	2.05c	2.98a	1.78c	0.86a	2.96	1.19a	178a
November 24	3.59a	1.92c	2.91a	1.68c	0.68a	2.97	1.29a	133b
Species								
White Spruce	2.95	2.14b	2.46	1.96	0.49b	2.99	1.03	134
Blue Spruce	3.44	2.25a	2.68	1.96	0.76a	3.18	1.22	133
Tissue Exposure								
Control (nonexposed)	3.29	2.37a	2.60	2.01a	0.69a	3.70a	1.68a	185a
Total Seedling	3.10	2.02b	2.54	1.91b	0.56b	2.47b	0.56b	82b

[z]Means within vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

[y]MC = moisture content gm/gm oven dry weight.

Figure 5. Number of white roots greater than 1 mm in length following desiccation and a 20 day growth period. Means presented are the sampling date and plant part exposure interaction averaged over species. Standard error equals ± 15.95.

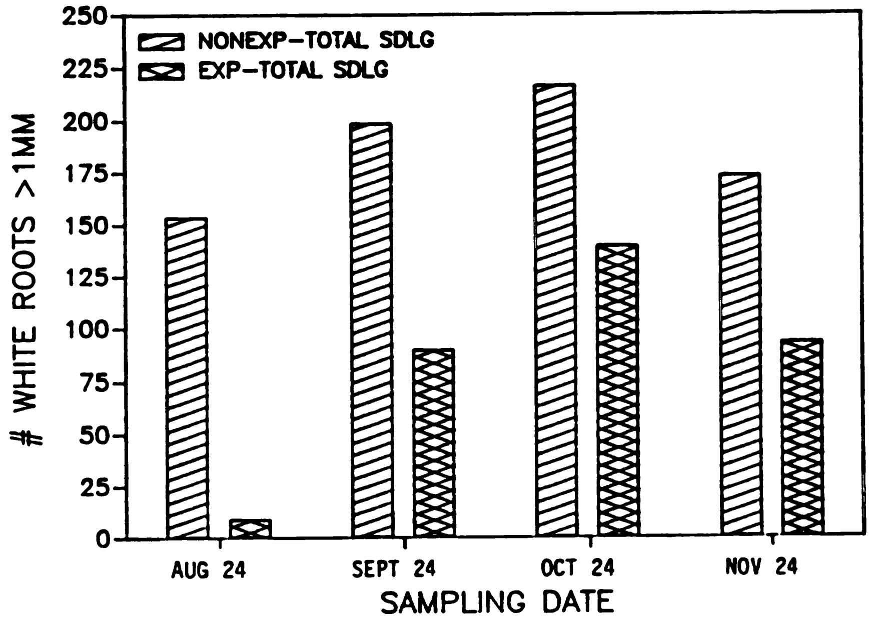
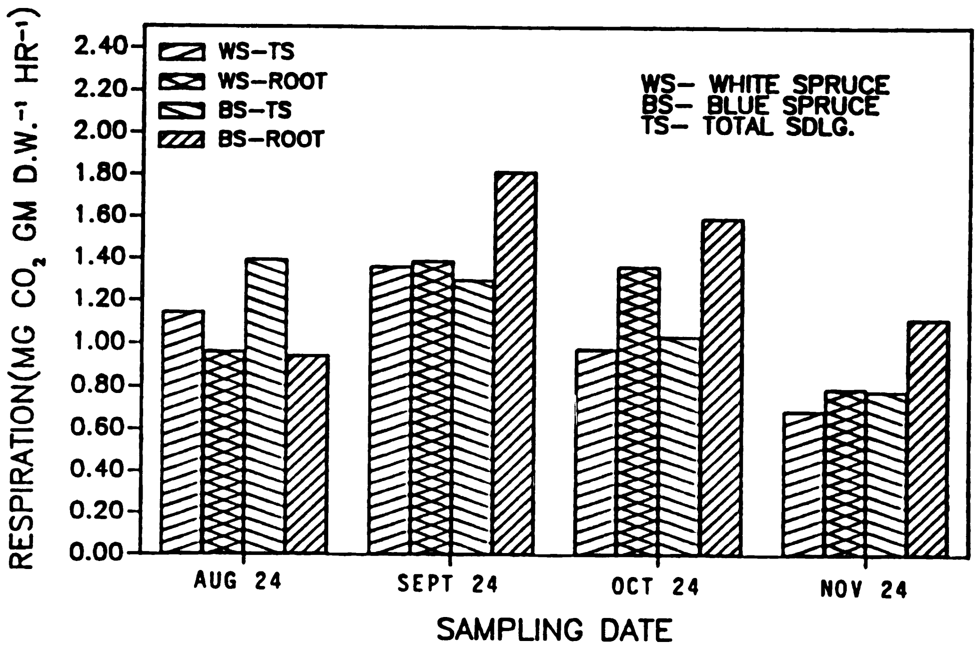

NONEXP-TOTAL SDLG
EXP-TOTAL SDLG
WHITE ROOTS >1MM
250
225
200
175
150
125
100
75
50
25
0
AUG 24
SEPT 24
OCT 24
NOV 24
SAMPLING DATE

Figure 6. Respiration for sampling date, species and plant part exposure interaction averaged over time interval during 2 hour exposure at 1.5 kPa VPG. Standard error equals ± 0.056.


RESPIRATION(MG CO_2 GM D.W.$^{-1}$ HR^{-1})
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
WS-TS
WS-ROOT
BS-TS
BS-ROOT
WS- WHITE SPRUCE
BS- BLUE SPRUCE
TS- TOTAL SDLG.
AUG 24
SEPT 24
OCT 24
NOV 24
SAMPLING DATE

number of white roots recorded above 1 mm long is presented in Fig. 5. Nonexposed seedling root growth significantly exceeded the exposed seedling production within each sampling date. Nonexposed seedling root growth increased from August to October. The exposed seedling root production also peaked in October, but, at a significantly lower amount.

Respiration and Water Vapor Loss

The influence of the main effects on respiration is presented in Table 6. Respiration appeared to increase from August to September then returned to the August level in both October and November. Blue spruce has an overall higher respiration rate than white spruce. Respiration was higher in the root exposure treatment than in the total seedling exposure treatment. A significant 3-way interaction between sampling date, species, and plant part exposure is presented in Fig. 6. Total seedling respiration from the August sampling date exceeded that of the root.

In September, blue spruce root respiration had increased substantially. In October root respiration exceeded that of the total seedling. November measurements showed a decrease in respiration rates in both total seedling and roots, however, blue spruce root respiration still was significantly higher. Data for the plant part exposure response to the 2 hour desiccation treatment are shown in Fig. 7. The obvious difference between the slopes

Table 6. The effects of sampling date, species, plant part exposure and time on respiration and water vapor loss following 2 hour exposure at 1.5 kPa VPG.[z]

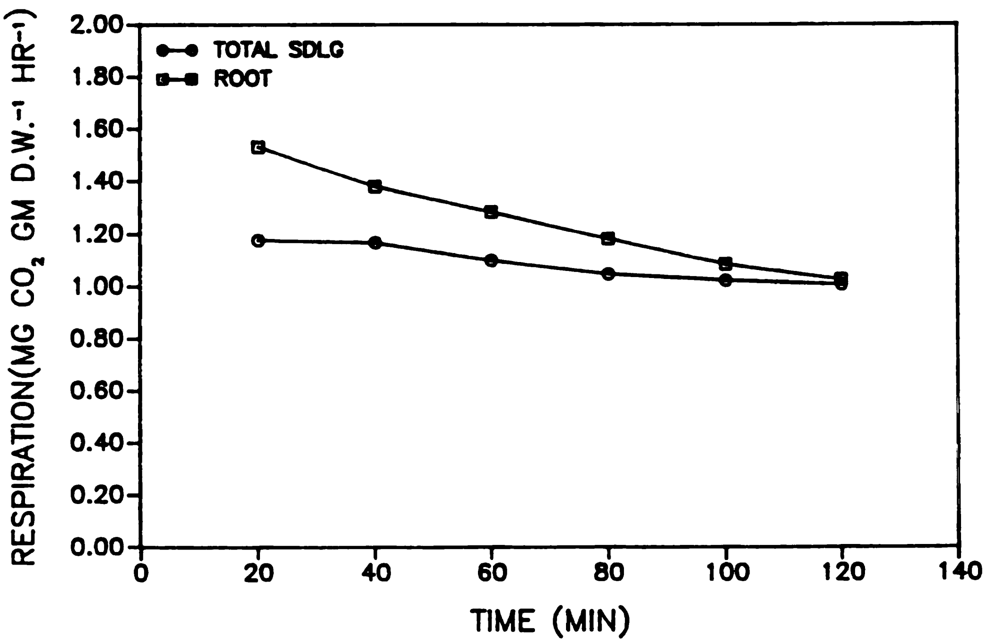
Factor	Respiration (mg CO_2 gm $D.W.^{-1}hr^{-1}$)	Water vapor loss (mg H_2O gram $D.W.^{-1}hr^{-1}$)
<u>Sampling Date</u>		
August 24	1.11bc	0.09a
September 24	1.46a	0.07b
October 24	1.24ab	0.05c
November 24	0.84c	0.04c
<u>Species</u>		
White spruce	1.08b	0.07a
Blue spruce	1.25a	0.06b
<u>Plant Part Exposure</u>		
Total seedling	1.08b	0.03b
Root	1.25a	0.10a
<u>Time (min)</u>		
20	1.35a	0.08a
40	1.27ab	0.07a
60	1.19bc	0.07b
80	1.11cd	0.06c
100	1.05d	0.05d
120	1.01d	0.05d

[z]Means within vertical column followed by same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

of the line indicates that desiccation has a more pronounced effect on root respiration rates than that of the total seedling.

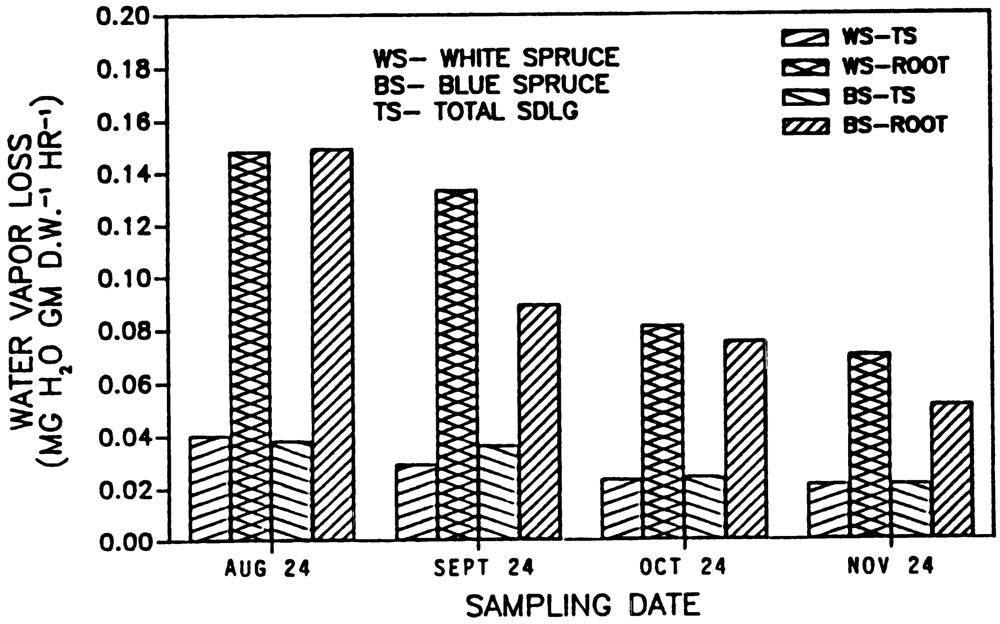
Rates of water vapor loss are presented in Table 6. A decrease in rate occured from August through November. White spruce lost water vapor at a higher rate than blue spruce. A significant interaction was found between sampling date, species, and plant part exposure (Fig. 8). Water vapor loss from the roots decreased from August to November. The higher rate of water loss in white spruce was attributed to the root exposure treatment on the September and November sampling. Sampling date influenced the rate of water vapor loss during the 2 hour treatment (Fig. 9). The rate of loss when averaged across species and plant part exposure indicated that initial rates of loss decreased from August to October. The decrease in rate across the 2 hour exposure treatment was more pronounced in the August sampling, and lessened with subsequent sampling date.

Figure 7. Respiration for plant part exposure and time interval interaction averaged over sampling date and species during 2 hour exposure at 1.5 kPa VPG. Standard error equals ± 0.049.



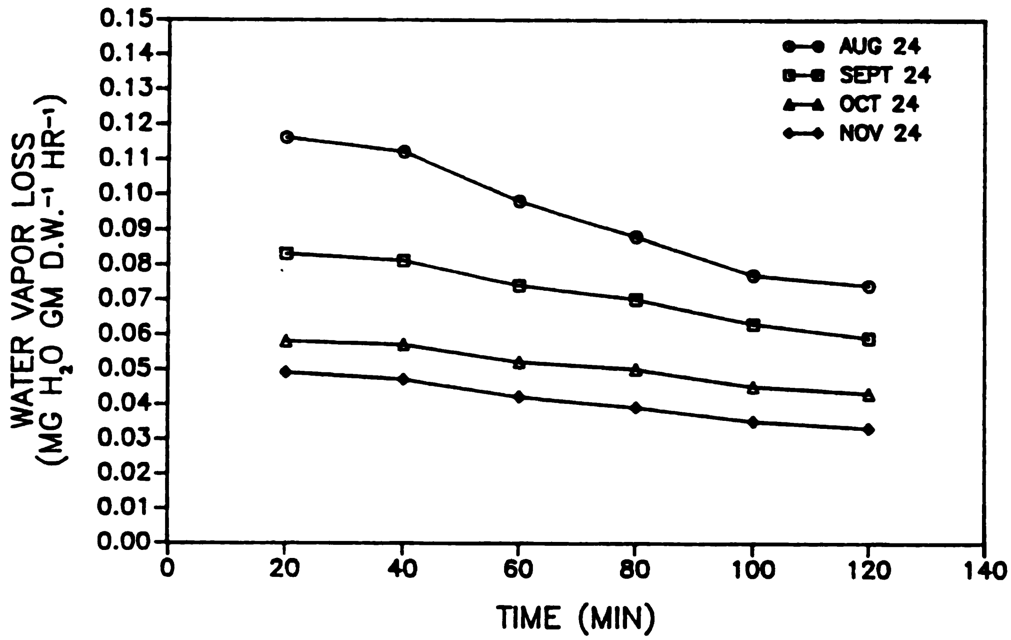
RESPIRATION(MG CO2 GM D.W.-1 HR-1)
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
TOTAL SDLG
ROOT
0
20
40
60
80
100
120
140
TIME (MIN)

Figure 8. Water vapor loss for sampling date, species and plant part exposure interaction averaged over time interval measurements during 2 hour exposure at 1.5 kPa VPG. Standard error equals ± 0.003.



0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
WATER VAPOR LOSS
(MG H_2O GM D.W.$^{-1}$ HR^{-1})
WS- WHITE SPRUCE
BS- BLUE SPRUCE
TS- TOTAL SDLG
WS-TS
WS-ROOT
BS-TS
BS-ROOT
AUG 24
SEPT 24
OCT 24
NOV 24
SAMPLING DATE

Figure 9. Water vapor loss for sampling date and time interval interaction averaged over species and plant part exposure during 2 hour exposure at 1.5 kPa VPG. Standard error equals ± 0.003.


0.15
0.14
0.13
0.12
0.11
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
WATER VAPOR LOSS
(MG H_2O GM D.W.$^{-1}$ HR^{-1})
AUG 24
SEPT 24
OCT 24
NOV 24
0
20
40
60
80
100
120
140
TIME (MIN)

DISCUSSION

Resistance to desiccation injury has been related to the dormancy status of planting stock (Hermann, 1967; Ritchie et al., 1985). Seedling sensitivity to moisture loss is modified as it descends into physiological rest. Placement of the greenhouse-grown seedlings outside into an overwintering structure influenced their response to desiccation between August and November. Natural photoperiodic and temperature conditions caused a cessation of shoot growth, and the formation of a terminal bud. Similarities in height data (not shown) between sampling dates indicated that shoot growth ceased upon placement into the structure. However, increased seedling dry weights from August to September suggest secondary development along with root growth continued throughout the sampling period. Similar results were found on European and Japanese larch (Ledig and Botkin, 1974). They reported increases in both shoot and root dry weight from August to October.

Fall acclimation had a significant influence on initial seedling moisture content. Total moisture in the seedlings decreased between sampling dates. Seasonal changes in tissue water relations have been documented by previous researchers. Meyer (1928) identified the importance of seasonal fluctuations in water and temperature relations in developing cold resistance in plants. He found that decreases in pitch pine needle moisture content occured from summer through April of the following year in recently developed needles. No differences were found once the needles had matured.

Pellett and White (1969) found that the root and shoot moisture content in _Juniperus_ _chinensis_ decreased in fall with a concurrent increase in cold hardiness. Levitt (1980) stated that water content was frequently inversely related to cold hardiness. Tyree et al. (1978) found decreases in symplast water volume as plants progressed into winter. These decreases were attributed to increases in cell dry weights following the cessation of growth. The increased seedling dry weights with a concurrent decrease in plant part moisture content (Table 1) tend to agree with the work by Tyree et al. (1978).

Another possible explanation for the decrease in plant part moisture content may be due to temperature influence on water uptake (Grossnickle and Blake, 1985). Low soil temperatures can influence root water uptake by increasing the viscosity of water while decreasing root permeability (Kramer, 1983). The increased dry weight suggested that photosynthesis and respiration continued throughout the sampling period. Transpirational increases during a time of decreased uptake could have resulted in the decreased moisture levels.

Seedling moisture loss reported for the 1.5 kPa VPG in chapter one was 0.41 gm H_2O gm D.W.$^{-1}$ when averaged over species, plant part exposure, and duration. This level was similar to moisture loss values recorded in October. Similarities in moisture loss could be based on the similarities between initial seedling moisture contents. Species moisture loss recorded in chapter one was slightly lower (0.38 and 0.39 g g D.W.$^{-1}$) than found in the present study (0.44 and 0.47 g g D.W.$^{-1}$). The influence of seedling moisture characteristics in August and September could have elevated the species loss. The loss pattern between total seedling and root exposure was similar between the two experiments. Total seedling moisture loss was greater than loss in the root exposure treatment. Shoot moisture loss based on the difference between total seedling and root moisture loss was approximately 21% of total seedling loss in the present study compared to 8% in Chapter I. The increased contribution of the shoot to loss could be a reflection of August and September shoot characteristics. The relatively active state of shoot growth could have been more susceptible to desiccation.

Seedling moisture loss decreased within the sampling date and plant part exposure treatments. Interaction between the two factors (Table 2) indicates that the loss in moisture content from the total seedling decreased with sampling date, yet the loss from the roots remained the same until a significant drop occurred in November. The data suggested that a modification was occurring in shoot moisture loss. Decreases in root temperatures from 15-0.25°C have been linked to reductions in stomatal conductance

(Teskey et al., 1984). Preconditioning Abies seedlings at 3°C for 3 months produced the same reductions in conductance. Reductions in transpiration were due to stomatal activity not lower water potentials (Teskey et al., 1984). Differences in moisture loss between the root exposure treatment and total seedling exposure in the present study suggest partial stomatal activity. Reductions could be due to temperature preconditioning; however, if this was true, differences would be restricted to the October or November treatment. Reductions between August and September could be a response to changes in tissue water relations at the cessation of growth or in response to mild moisture stress. Loss based on percent fresh weight does not appear to be valid in determining changes that occurred between sampling dates. The difference between initial fresh weight and treated fresh weight increased proportionally with increases in fresh weight resulting in the uniformity of the data. The comparison between plant part exposure treatments is somewhat indicative of the response; however, once again fluctuations cast doubt on the data. Moisture loss based on seedling dry weight provides a clearer picture.

Coutts (1981) and Sucoff et al. (1985) indicated that the root system was more sensitive to desiccation than the shoot. They suggested that root water status would be a desirable indicator of performance after outplanting. Root moisture contents were similar between the total seedling or root exposure treatments. In the total seedling exposure treatment, the root contributed to approximately 78% of the moisture loss.

The relationship between root-shoot internal water balance is an indication of the influence of container production on water relations. The presence of a moist planting media encompassing the root system contributed to the higher root-shoot balance when compared to bare root plants (Sucoff et al., 1985). Within the nonexposed sampling, the advantage of the root over that of the shoot is obvious. Data presented for the exposed group indicated a decrease in severity of the shift as the seedlings progressed from August through November. Although the relationship was relatively the same between exposure types, desiccation had less of an effect on the shift with sampling date. The increases in dry weight coupled with decreases in moisture content aided in minimizing the effects.

Seedling response following a 20 day growth period was evaluated on percent fresh weight data. Due to the nature of the experiment, moisture losses could not be calculated on a dry weight basis. Comparison of potted moisture contents was possible at the end of the experiment. This study was run in conjunction with the moisture content study in an effort to draw parallels in treatment effects. Total seedling exposure resulted in loss of 20.9% fresh weight (Table 4), which was similar to loss encountered in Table 1. IFW-PFW represents the weight gain or loss as result of the desiccation treatment. Nonexposed plants exceeded the original fresh weight on an average of 14.5% across sampling dates. Desiccation resulted in substantial losses from original fresh weight; however, it was lessened in the October and November treatment. Hermann (1967) showed a decrease in sensitivity to exposure between a November 5 and January 28 lift date, although effects of exposure could still be seen on fresh weight at the end of the season. The decrease in sensitivity in this study was indicated by the lessened deficit from the initial fresh weight in the October and November samplings. This study did not evaluate seedling response beyond the 20 day growth period, so the extent of damage on field performance is not known.

The response capability of seedlings can also be evaluated as percent weight gain over treated fresh weight. Negative values on the August sampling date indicate that the actively growing seedlings did not recover from their treated state. Although the plants were not classified as dead, evaluations beyond 20 days may have shown some mortality. The responses in the latter three sampling dates were fairly positive. Increased fresh weights in the September and October sampling were equal to that of the nonexposed plants. In the November seedling sample, exposure actually enhanced the % weight gain of the seedling. Potted shoot and root moisture contents (Fig. 4) provide a comparison for evaluating seedling moisture status as influenced by sampling date and plant part exposure.

Potted shoot moisture contents were different between the nonexposed and exposed seedlings in August and November. Potted root moisture content decreased in the control similar to the results in the moisture content study. Rehydration levels in the roots as a result of the 20 day growth period were essentially the same with the exception of the August and September sample.

Root growth capacity (Fig. 5) results coincided with data reported by Ritchie et al. (1985). He reported peaks of RGP during October and November. RGP dropped off in December and January. The drop in RGP was attributed to the decline associated with true physiological dormancy. The high levels prior to December were indications that rest had not been reached. Root growth in both the exposed and nonexposed seedlings peaked in late October. There was an obvious difference in the number of roots. The peak in October was expected due to the fall shift to root production following the cessation of shoot growth. The effects of exposure on root growth capacity were still obvious in the exposed seedlings, however, the degree of difference lessened in the November sample. Based on the effects of dormancy on RGP (Ritchie et al., 1985; Carlson, 1985, DeWald and Feret, 1987), further sampling may have resulted in uniform numbers between the nonexposed and exposed treatments.

Root growth capacity for 2 hour exposure at 1.5 kPa VPG in Chapter 1 was 42 roots greater than 1 mm in length. The two-fold increase in roots in the present study between September and November could be reflective of the temperature effect on seedling conditioning (Lavender and Wareing, 1972).

Seasonal patterns in CO_2 exchange have identified a shift in shoot and root respiration as seedlings approach fall (McGregor and Kramer, 1963; Drew and Ledig, 1981). Total seedling respiration in both blue and white spruce exceeded that of the root in August. The levels were similar in white spruce but blue spruce root activity had significantly increased in September. Root activity for both species peaked in October (Fig. 5) and was associated with an increase in root respiration. As root growth dropped in November so did the respiration rate. The plant part exposure and time interaction (Fig. 7) gives an indication of plant part response during the desiccation treatment. The differences in the slope between total seedling and root respiration show the effects of drying on root function. The decrease in rate was in agreement with results reported in Chapter I and with research studying the effect of water stress on respiration (Puritch, 1973; Zavitkovski and Ferrell, 1968).

Water vapor loss was effected by sampling date, species and plant part exposure (Fig. 8). Sampling date influenced the rate of water vapor loss during desiccation. The trend in data supports the results found in moisture loss on a dry weight basis. Differences in moisture content of the tissue as well as available free water could effect the rate of vapor loss into the system. The drastic effect of exposure on root tissue is evident. Change in sensitivity of the plant part to loss as shown by moisture content and root growth capacity studies was reflected in the vapor loss rates. Total seedling exposure resulted in a slight reduction in rate across sampling dates; however, as indicated in Chapter II, difference in seedling morphological characteristics could have lessened the significance. The slight decrease in apparent slope of the line in Fig. 9 from the August through November indicates the increased sensitivity of actively growing tissue to desiccation.

Fall acclimation influences the sensitivity of container-grown seedlings to desiccation injury. Decreased sensitivity may be linked to dormancy or a concurrent increase in cold hardiness. In any event, investigations of preconditioning treatments which enhance these physiological changes may result in increased predictability of outplant performance of container-grown planting stock.

REFERENCES

Carlson, W.C. 1985. Effects of natural chilling and cold storage on budbreak and root growth potential of loblolly pine (Pinus taeda L.). Can. J. For. Res. 15:651-656.

Coutts, M.P. 1981. Effects of root or shoot exposure before planting on the water relations, growth and survival of sitka spruce. Can. J. For. Res. 11:703-709.

DeWald, L.E. and P.P. Feret. 1987. Changes in loblolly pine root growth potential from September to April. Can. J. For. Res. 17:635-643.

Drew, A.P. and F.T. Ledig. 1981. Seasonal patterns of CO_2 exchange in the shoot and root of loblolly pine seedlings. Bot. Gaz. 142:200-205.

Garber, M.P. 1983. Effects of chilling and photoperiod on dormancy release of container-grown loblolly pine seedlings. Can. J. For. Res. 13:1265-1270.

Grossnickle, S.C. and T.J. Blake. 1985. Acclimation of cold-stored jack pine and white spruce seedlings: effect of soil temperature on water relations patterns. Can. J. For. Res. 15:544-550.

Gucci, R. 1988. The effect of fruit removed on leaf photosynthesis, water relations and carbohydrate partitioning in sour cherry and plum. Ph.D. Thesis, Michigan State University.

Hermann, R.K. 1967. Seasonal variation in sensitivity of Douglas Fir seedlings to exposure of roots. For. Sci. 13:140-149.

Kramer, P.J. 1983. Factors affecting the absorption of water. In: Water relation of plants. pp. 235-261. Academic Press, New York.

Lavender, D.P. and P.F. Wareing. 1972. Effects of daylength and chilling on the responses of Douglas Fir (<u>Pseudotsuga menziesii</u> (Mirs) Franco) seedlings to root damage and storage. New Phytol. 71:1055-1067.

Ledig, F.T. and D.B. Botkin. 1974. Photosynthetic CO_2-uptake and the distribution of photosynthate related to growth of larch and sycamore progenies. Silvae Genet. 23:188-192.

Levitt, J. 1980. Responses of plants to environmental stress. Vol. 1: Chilling, freezing and high temperature stresses. 497 pp. Academic Press, New York, N.Y.

Macey, D.E. and J.T. Arnott. 1986. The effect of moderate moisture and nutrient stress on bud formation and growth of container-grown white spruce seedlings. Can. J. For. Res. 16:949-954.

McGregor, W.H. and P.J. Kramer. 1963. Seasonal trends in rates of photosynthesis and respiration of loblolly pine and white pine seedlings. Amer. J. Bot. 50:760-765.

Meyer, B.S. 1928. Seasonal variations in the physical and chemical properties of the leaves of the pitch pine, with special reference to cold resistance. Amer. J. Bot. 15:449-472.

Moon, J.W. and J.A. Flore. 1985. A basic computer program for calculation of photosynthesis, stomatal conductance and related parameters in an open gas exchange system. Photosynthesis Res. 7:269-279.

Mullin, R.E. 1967. Root exposure of white spruce nursery stock. For. Chron. 43:155-160.

Pellett, N.E. and D.B. White. 1969. Relationship of seasonal tissue changes to cold acclimation of _Juniperus chinensis_ 'Hetzi'. J. Amer. Soc. Hort. Sci. 94:460-462.

Puritch, G.S. 1973. Effect of water stress on photosynthesis, respiration and transpiration of four _Abies_ species. Can. J. For. Res. 3:293-298.

Ritchie, G.A. and R.G. Shula. 1984. Seasonal changes of tissue-water relations in shoots and root systems of Douglas-fir seedlings. For. Sci. 30:538-548.

Ritchie, G.A., J.R. Roden and N. Kleyn. 1985. Physiological quality of lodgepole pine and interior spruce seedlings: Effects of lift date and duration of freezer storage. Can. J. For. Res. 15:636-645.

Roberts, S.W. 1979. Properties of internal water exchange in leaves of _Ilex opaca_ Ait. and Cornus florida L. J. Exp. Bot. 30:955-963.

Sams, C.E. and J.A. Flore. 1982. The influence of age, position and environmental variables on net photosynthetic rate of sour cherry leaves. J. Amer. Soc. Hort. Sci. 107:339-344.

Sucoff, E., C. Buschema and P. Tamte. 1985. Desiccation and water potential in the roots, leaves and shoots of bare-root red pine and white spruce. Can. J. For. Res. 15:989-992.

Sutton, R.F. 1980. Techniques for evaluating planting stock quality. For. Chron. 56:116-120.

Teskey, R.O., T.M. Hinckley and C.C. Grier. 1984. Temperature-induced change in the water relations of Abies cornabilis (Dougl.) Forbes. Plant Physiol. 74:77-80.

Tyree, M.T., Y.N.S. Cheung, M.E. MacGregor and A.J.B. Talbot. 1978. The characteristics of seasonal and ontogenetic changes in the tissue water relations of Acer, Populus, Tsuga and Picea. Can. J. Bot. 56:635-647.

Zavitkovski, J. and W.K. Ferrell. 1968. Effect of drought upon rates of photosynthesis, respiration and transpiration of seedling of two ecotypes of Douglas Fir. Bot. Gaz. 129:346-350.

CHAPTER IV

EFFECTS OF WATER STRESS ON *PICEA* SEEDLINGS. IV. PHOTOPERIOD AND TISSUE SENSITIVITY

ABSTRACT

The effects of daylength on the response of container-grown white spruce (*Picea glauca* (Moench) Voss) and blue spruce (*Picea pungens* Engelm.) to desiccation were examined. Accumulated dry weight increased 146% in the long day (LD) and 52% in the short day (SD) treatments. Initial seedling moisture content decreased over the six week period.

Daylength did not influence moisture loss. Blue spruce moisture loss was greater than white spruce. Moisture loss decreased with sampling period. The extent of desiccation on seedling regrowth was observed following a 20 day growth period. Nonexposed seedlings averaged a 12.4% weight gain compared to the 31.1% loss exhibited in the exposed seedlings. White root production was drastically reduced in the exposed seedlings. Nonexposed seedlings produced 116 roots compared to 21 in the exposed group after 6 weeks.

White spruce respiration (1.17 mg CO_2 gm D.W.$^{-1}$hr^{-1}) was significantly higher than blue spruce respiration (1.01 mg CO_2 gm D.W.$^{-1}$hr^{-1}). LD seedlings exhibited a peak in respiration during the third week. SD respiration steadily decreased with each successive sampling period. Decreased rates of water vapor loss coupled with reduction in moisture content reflect changes in tissue maturation and sensitivity

to desiccation. Short daylength decreases seedling sensitivity to desiccation; however, the six week duration did not seem to have a positive effect on performance.

INTRODUCTION

Photoperiod is an integral factor in the manipulation of growth and development of tree seedlings in container production systems. Extended daylength (shortened nights) promotes the development of both morphological and physiological characteristics. Long daylength (LD) promotes increases in shoot and root dry weight (Arnott and Mitchell, 1981; Smit-Spinks et al., 1985). Increased root/shoot ratio (Barney, 1950), delay of budset (Arnold, 1979) and acceleration of tissue maturity (Young and Hanover, 1976) have been attributed to extended photoperiod. Light in addition to optimal temperature and adequate levels of moisture and nutrients are the principles in accelerated-optimal-growth systems (Hanover et al., 1976).

Short daylength (SD) is as important as LD in the development of quality nursery stock. Short days initiate the first visible stage of dormancy in conifer seedlings (Owston and Kozlowski, 1981). Wheeler (1979) observed a reduction in seedling height in lodgepole pine within 2 weeks of removal of continuous light. SD stimulated the transition from needle primordia production to budscale initiation in blue spruce and continued mild temperatures insured adequate bud development for the subsequent seasons growth (Young and Hanover, 1977). Colombo et al. (1981), observed bud scale formation in white spruce within one week following a shift to 8 hour daylength at 20°C. Needle primordia development increased between 2-5 weeks and was complete within 8 weeks of the shift.

Short days have also been linked to the initial stages of cold hardiness (Van den Driesche, 1969; Timmis and Worrall, 1975; Colombo et al., 1981). Timmis and Worrall (1975) reported that SD was equally effective in inducing cold acclimation in actively growing or quiescent Douglas fir. Scotch pine shoot dormancy and cold acclimation regardless of shoot activity were attributed to short daylength (Smit-Spinks et al., 1985). Root hardiness has been suggested as being related to short day exposure (Johnson and Havis, 1977), although evidence supporting this finding is varied (Smit-Spinks et al., 1985).

The interrelationship between short daylength and chilling requirement has increased stress resistance in fall lifted nursery stock (Lavender and Wareing, 1972). Results suggested that a natural sequence of short days followed by chilling were favorable in developing maximum stress resistance of bare root seedlings. Lavender and Stafford (1985) suggest that stress resistance in Douglas fir seedlings requires mild temperatures and short days, followed by chilling during formation of a resting bud. A sequential progression into quiescent and rest is critical in achieving the highest level of cold and non-cold related stress resistance. The relationship of temperature and daylength coupled with our understanding of seedling physiological development becomes the basis for hardening of container-grown seedlings (Pollard and Logan, 1977).

The objective of this experiment was to evaluate the effects of daylength on the response of container-grown white and blue spruce to desiccation. Extended planting windows of container-grown nursery stock may subject seedlings to planting stress prior to development of physiological rest. The goal was to determine whether or not exposure to short daylength will enhance seedling resistance to moisture loss through desiccation.

MATERIALS AND METHODS

White spruce (*Picea glauca* (Moench) Voss.) from a southern Ontario seed source and Blue spruce (*Picea pungens* Engelm.) from bulk seed of a half-sib family from the San Juan mountain region of Colorado were used in the experiment. Seedlings were grown in polyethylene coated plant bands (5x5x27 cm) with 3:1:1 (V:V:V) mixture of sphagnum peat:perlite:vermiculite. Slow release fertilizer (Osmocote, Sierra Chemical Co., 18-6-12) and micronutrients (Micromax, Sierra Chemical Co.) were incorporated into the planting mixture. Water was applied to maintain uniform soil moisture. Seedlings were grown in a double layer poly greenhouse at the Tree Research Center, Department of Forestry, Michigan State University. Photoperiod in the polystructure was extended using high output cool-white fluorescent fixtures. Plants were grown for 20 weeks under 20 hour extended daylength.

Actively growing seedlings were transferred to a laboratory growth frame and allowed to acclimate for 2 weeks under 20 hour daylength prior to the commencement of the experiment. Light levels under both the long and short daylength treatments were approximately 130 $\mu m\ m^{-2} sec^{-1}$ photosynthetic photon flux density (PPFD). The long and short day treatments received 20 and 8 hours, respectively, of light per 24 hour period. Irradiation was supplied by T96 high output cool-white fluorescent fixtures.

Temperatures within the growth frame ranged from 22-27°C. The experiment was conducted for six weeks with samples taken at time zero, after 3 weeks and at the conclusion of the experiment.

The experiment was designed as a split plot factorial replicated four times. Daylength, species, plant part exposure and sampling interval (2x2x3x3) were factors. Plant part exposure treatment levels varied with analysis. A moisture content study was analyzed with 3 levels; a non-exposed total seedling, total seedling and root exposure. In the root exposure treatment, the shoot was wrapped in a double layer of saran and a layer of aluminum foil. The root system was sealed into the chamber. Both plant parts were covered with a black cloth during treatment. The root growth capacity study consisted of a nonexposed and exposed total seedling. A respiration and water vapor loss analysis of the moisture content study consisted of total seedling and root exposure with a fifth factor representing 6-20 minute intervals within the 2 hour exposure treatment. Analysis of variance was performed on each study and Duncan's Multiple Range Test was used to separate means.

Seedlings were randomly selected from the growth frame the night prior to treatment. Seedlings were thoroughly watered, sealed in clear polyethylene bags and covered with a black polyethylene sheet in the laboratory a minimum of 14 hours. In preparation for the desiccation treatment, seedlings were removed from the polyethylene bag and planting media was gently washed from the roots with water (room temperature). Seedlings were blotted dry with absorbent tissue to remove any surface moisture on shoots and roots, fresh weights were recorded and individual seedlings were placed into a controlled environmental plant chamber. The plant chamber is an 11 x 21 x 9.5 cm plexiglass box. Interior sensors monitor plant temperature, chamber temperature and light as described in Chapter II. Chambers were covered with a black cloth throughout the desiccation treatment. Upon completion of the treatment, the exposed plant part was removed and severed at the root collar. Treated fresh weights were recorded for both the roots and shoots. Dry weights of the shoot and root tissue were determined after oven drying at 100°C for 72 hours. Plant part moisture contents were calculated gravimetrically and percent weight loss was based on fresh weight according to the following equations:

$$\text{Moisture Content} = \frac{\text{Tissue fresh wgt (gm)} - \text{Tissue dry wgt (gm)}}{\text{Dry wgt (gm)}}$$

$$\text{\% Weight Loss} = \frac{\text{Fresh wgt (gm)} - \text{Dry wgt (gm)}}{\text{Fresh wgt (gm)}} \times 100$$

The control seedlings were handled using the same procedures with the exception of desiccation.

Desiccation treatments were conducted in an open gas analysis system described by Sams and Flore (1982) and modified by Gucci (1988). Differential CO_2 concentrations at the inlet and outlet of plant chamber were measured with an ADC 225 MK3 Infrared Gas Analyzer (Analytical Development Company, Hoddesdon, U.K.). Air flow was regulated with Matheson 8100 series mass flow meters and Matheson 8200 series mass flow controllers connected to a Matheson multichannel Dyna-blender 8219 (Matheson Instruments, Horsham, Pennsylvania).

Respiration was measured as CO_2 (mg CO_2 gram dry weight^{-1}hour^{-1}) efflux and calculated using equations and computer program described by Moon and Flore (1986). Plant temperatures within the chambers were maintained at 24-25°C. Air flow entering the chamber was monitored at 2.0 liter per minute in the total seedling exposure treatment and 1.5 liters per minute in the root exposure treatment. Dew point of incoming air maintained a vapor pressure gradient of 1.5 kPa entering the chamber. Water vapor loss was based on flow rate, mole fraction of water vapor of incoming and outgoing air streams and plant part dry weight. Water vapor loss was expressed in terms of mg H_2O gram D.W.$^{-1}$hr^{-1} using the same computer program (Moon and Flore, 1986). Seedlings were exposed for 2 hours, with water vapor and CO_2 concentrations recorded on 20 minute intervals.

Seedlings used in the root growth capacity study were prepared for treatment using procedures previously mentioned. Upon completion of the desiccation treatments, seedling treated weights were recorded. Prior to potting both treated and control seedlings were dipped (3 sec) into water. Seedlings were potted into 26-liter containers of the non-fertilized 3:1:1 planting mixture and placed into the growth frames under 20 hour photoperiod. Seedlings remained in the growth frame for 20 days. Optimum soil moisture was maintained during the growth period. At the conclusion, pots were removed, watered, sealed into clear polyethylene bags, and stored overnight under a black polyethylene sheet (14 hours). The following day seedlings were gently removed from the pots for determination of plant part moisture content and root production. Plant part moisture contents were determined as in the previous study, and the number of white roots above 1 mm in length were recorded.

Table 1. The interaction of daylength and treatment period (weeks) on total seedling, shoot and root dry weight of desiccated seedlings averaged over species and plant part exposure treatments.[z]

Daylength x Period	Total seedling dry wgt (gms)	Shoot dry wgt (gms)	Root dry wgt (gms)
Long Day			
0 wks	0.99	0.83	0.16
3 wks	1.68	1.41	0.27
6 wks	2.43	2.00	0.44
Short Day			
0 wks	1.01	0.83	0.18
3 wks	1.48	1.25	0.23
6 wks	2.12	1.78	0.34
SE±	0.09	0.08	0.02

[z]SE± = standard error of the mean.

RESULTS AND DISCUSSION

Seedling Dry Weight

Daylength and sampling period influenced seedling dry weight accumulation during the six week period (Table 1). There was a significant increase in seedling dry weight with each successive sampling period regardless of daylength. The accumulated increase resulted in 146% weight gain in the LD seedlings and a 52% increase in the SD plants. The differences between daylength treatment were only observed at the 6 week sampling. LD total seedling increase amounted to 15% over the SD plants. The proportional increases for each plant part were 12% in shoot and 23% in root dry weight accumulation. A similar trend in dry weight accumulation was reported for Scotch pine (Smit-Spinks et al., 1985). LD seedling dry weight was significantly greater than SD plants after 7 weeks. They observed a 57% increase in root dry weight followed by a 45% increase in the shoots. Similar to the data reported for Scotch pine, there was a greater increase in shoot dry weight (115%) than in root dry weight (89%) for short day plants within the six week period of the present experiment. Vance and Running (1985) found that reductions in light intensity effected root more than shoot biomass accumulations.

Moisture Content

Means for the main effects on initial total seedling moisture contents and moisture contents influenced by the

Table 2. Effects of daylength, species, plant part exposure and period on total seedling, treated total seedling, treated shoot and treated root moisture contents.[z]

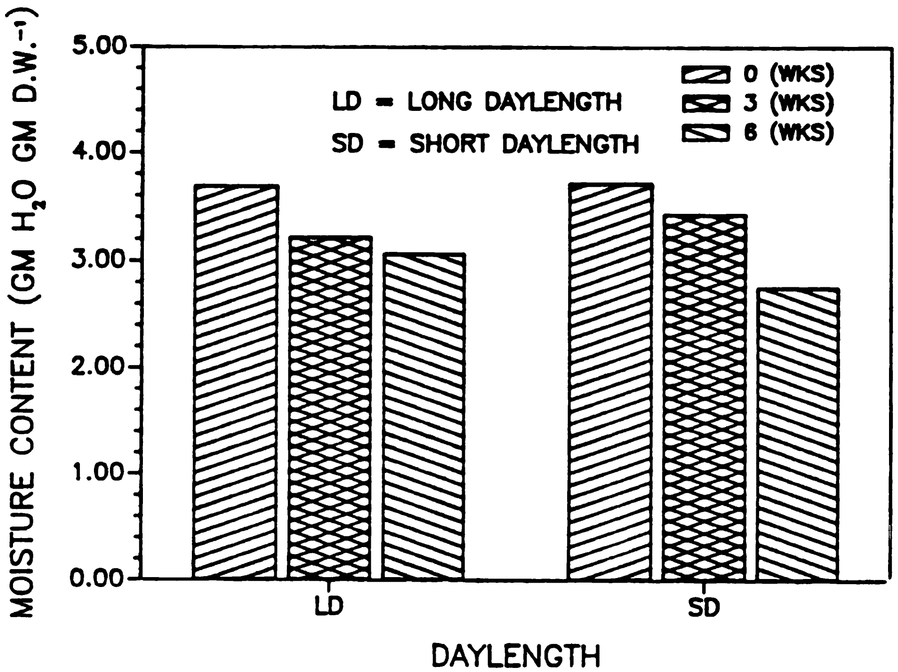
Factors	Initial total seedling	Treated total seedling	Treated shoot	Treated root
	gm H_2O gm $D.W.^{-1}$			
Daylength				
LD	3.31	2.77	2.84	2.39
SD	3.30	2.74	2.83	2.29
Species				
White spruce	3.17b	2.68b	2.75b	2.28b
Blue spruce	3.44a	2.83a	2.92a	2.41a
Plant Part Exposure				
Nonexposed total seedling	3.31	3.31a	3.08a	4.41a
Total seedling	3.34	2.41c	2.64c	1.22c
Root	3.27	2.55b	2.78b	1.40b
Period (weeks)				
0	3.69a	3.05a	3.16a	2.46a
3	3.32b	2.79b	2.87b	2.35ab
6	2.90c	2.43c	2.47c	2.22b

[z]Means within vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

desiccation treatment are presented in Table 2. Blue spruce exhibits higher seedling moisture. This increase was similar to the moisture content characteristics presented in Chapter I.

Initial seedling moisture contents decreased with time in the growth frame. The reduction in moisture content could be due to tissue maturation and the proportional increases in dry matter. As dry matter increases, there is a relative change in cell water volume (Tyree et al., 1978). The apparent decrease in light intensity from the greenhouse to growth frame could have influenced the relative growth rate and tissue water relations. A decrease in initial total seedling moisture content occurred in both the long and short day treatment, however, short daylength resulted in a greater reduction after 6 weeks (Fig. 1). The influence of sample period on moisture content appears to be more pronounced on the shoot as indicated by the difference within the treated shoot and treated root moisture contents. The maturation and increased shoot dry weights could have influenced tissue water relations. Reductions in shoot moisture content between August 24 and September 24 within Chapter III support the evidence suggesting a modification in tissue water relations. The reduction found in SD total seedling moisture (Fig. 1) could be the initial influence of daylength on cold acclimation (Pellett and White, 1969; Levitt, 1980).

Figure 1. Effects of daylength and sampling period on seedling moisture content. Standard error equals ± 0.052.



MOISTURE CONTENT (GM H_2O GM D.W.$^{-1}$)
5.00
4.00
3.00
2.00
1.00
0.00
LD = LONG DAYLENGTH
SD = SHORT DAYLENGTH
0 (WKS)
3 (WKS)
6 (WKS)
LD
SD
DAYLENGTH

Total seedling exposure resulted in a greater reduction in moisture content than root exposure (Table 2). These results are similar to the pattern of reduction in moisture content that occurred between total seedling and root exposure in Chapter I and III. Approximately 6% of the reduction was attributed to shoot loss supporting evidence (Chapter I; Coutts, 1981; Sucoff et al., 1985) that the root is more susceptible to desiccation loss.

Means for the influence of daylength, species, plant part exposure and sample period on loss due to desiccation are shown in Table 3. Blue spruce loss based on moisture content or percentage fresh weight was greater than white spruce. Plant part exposure treatment loss mimic trends found in moisture content. Moisture loss significantly decreased with sampling period. The decrease in moisture loss with time could be linked to tissue maturation and a decrease in available tissue water due to the reduction in total seedling moisture contents (Table 2). A significant 3-way interaction was found between species, plant part and sampling period for both loss in moisture content and percent fresh weight (Table 4). The data support the main effect result that blue spruce losses are greater than white spruce. White spruce total seedling moisture loss was relatively consistent over the six weeks. Root moisture loss declined between the first three weeks, then remained constant. Blue spruce total seedling moisture loss decreased with each sampling. Root loss followed the

Table 3. Effects of daylength, species, plant part exposure and sample period on moisture content loss and percent loss of fresh weight following desiccation.[z]

Factor	Loss MC	Loss % fresh wgt.
Daylength		
LD	0.54	12.5
SD	0.55	12.8
Species		
White spruce	0.49b	11.6b
Blue spruce	0.61a	13.7a
Plant Part Exposure		
Nonexposed total seedling	0.00a	0.00c
Total seedling	0.93a	21.2a
Root	0.72b	16.7b
Period (weeks)		
0	0.65a	13.7a
3	0.52b	12.1b
6	0.47c	12.1b

[z]Means within vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

Table 4. The interaction of species, plant part exposure and treatment period (weeks) on moisture content loss (gm gm D.W.$^{-1}$) and percent loss of fresh weight following desiccation.[z]

Treatment Combination		Loss MC	Loss % fresh wgt.
<u>White Spruce</u>			
Nonexposed total seedling	0 wks	0.00	0.0
	3 wks	0.00	0.0
	6 wks	0.00	0.0
Total seedling	0 wks	0.86	19.0
	3 wks	0.82	19.2
	6 wks	0.76	19.0
Root	0 wks	0.75	16.8
	3 wks	0.62	14.7
	6 wks	0.57	15.5
<u>Blue Spruce</u>			
Nonexposed total seedling	0 wks	0.00	0.0
	3 wks	0.00	0.0
	6 wks	0.00	0.0
Total seedling	0 wks	1.30	26.7
	3 wks	0.98	22.2
	6 wks	0.84	21.3
Roots	0 wks	0.97	20.0
	3 wks	0.73	16.6
	6 wks	0.66	16.9
SE±		0.04	0.7

[z]SE± = standard error of the mean.

Table 5. Effects of daylength, species, plant part exposure and sampling period on percentage weight loss relationship between initial, treated and potted fresh weights following 2 hour exposure to a 1.5 kPa VPG and 20 day growth period.[zy]

Factor	% wgt loss IFW-TRFW	% wgt (+)gain, (-)loss PFW-IFW
Daylength		
LD	10.5	-7.3
SD	11.2	-11.4
Species		
White spruce	9.8b	-10.9
Blue spruce	11.8a	-7.8
Plant Part Exposure		
Nonexposed	0.0b	12.4
Total seedling	21.7a	-13.1
Sampling Period (weeks)		
0	11.9	-16.4b
3	10.6	-12.1b
6	10.1	0.4a

[z]Means within vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

[y]IFW = Initial Fresh Weight.
TRFW = Treated Fresh Weight.
PFW = Potted Fresh Weight.

pattern of white spruce. The higher moisture loss from blue spruce occurred during the first 2 sampling periods for both the total seedling and root exposure treatment. This moisture loss by blue spruce was also observed in Chapter I and Chapter III. It appears that the higher initial moisture contents may contribute to greater loss although greater moisture contents were not coupled with the higher loss rate in Chapter III. Results reported in Chapter I show similarities between shoot moisture loss suggesting that the species difference may be due to the roots. The lack of consistent parallels between moisture content loss data and percent loss of fresh weight casts doubt on the use of the fresh weight parameter as a true indicator of plant response.

Seedling Rehydration and Root Growth

The seedling root growth study was conducted to examine seedling capability for regrowth following desiccation. Unfortunately, due to the nature of the study initial desiccation loss and seedling rehydration response was based on fresh weight. Initial loss (Table 5) due to desiccation was similar to the loss in percent fresh weight observed in the moisture content study (Table 3). Total seedling exposure resulted in a 21.7% loss in fresh weight compared to 21.4% in the moisture content study. The blue spruce response was also observed in this study (Table 6). Blue spruce lost 23.7% compared to 19.7% from white spruce.

Table 6. Percent weight loss from initial fresh weight following desiccation as influenced by species and plant part exposure.[z]

Species x Tissue Exposure	% wgt loss (IFW-TRFW)[1]
White Spruce	
Nonexposed Seedling	0.0
Exposed Seedling	19.7
Blue Spruce	
Nonexposed Seedling	0.0
Exposed Seedling	23.7
SE±	0.3

[1]IFW = Initial Fresh Weight.
TRFW = Treated Fresh Weight.

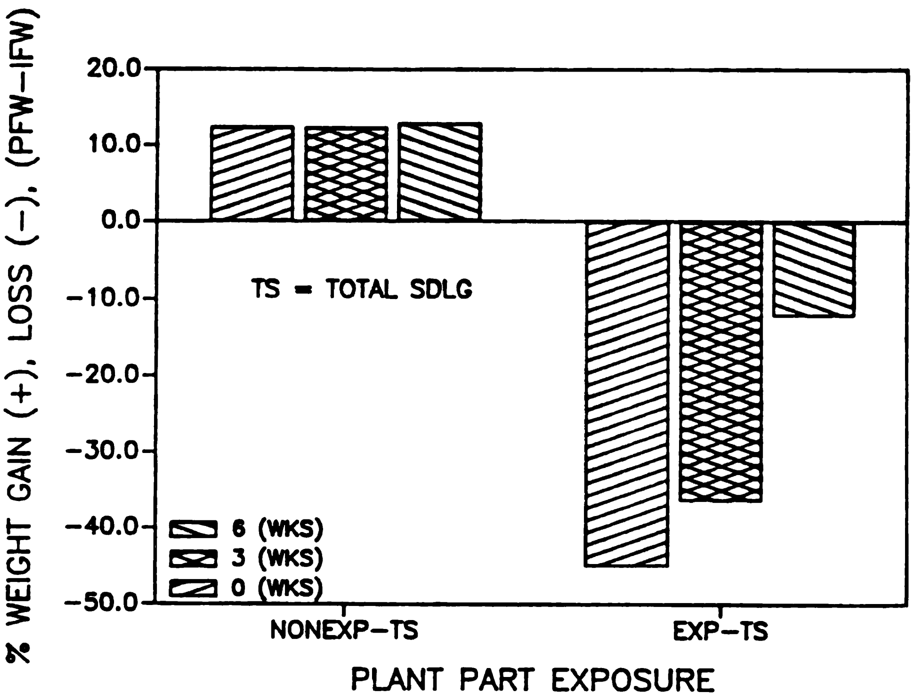
[z]SE± = standard error of the mean.

Table 7. The interaction of plant part exposure and sampling period on seedling moisture contents and white root production following a 20 day growth period.[z]

Factors	(wks)	Potted total seedling	Potted shoot	Potted root	No. white roots >1 mm(length)
		moisture content gm H_2O gm $D.W.^{-1}$			
Nonexposed total seedling	0	2.94	2.73	4.00	51
	3	2.70	2.39	4.00	131
	6	2.35	2.09	3.45	116
Exposed total seedling	0	1.57	1.48	2.28	0
	3	1.80	1.70	2.73	6
	6	2.22	2.18	2.48	21
SE$\pm$		0.11	0.12	0.14	7

[z]SE$\pm$ = standard deviation.

Figure 2. Percent weight gain (+) or loss (-) of initial fresh weight following exposure to 1.5 kPa VPG for 2 hours and a 20 day growth period. Means presented are the plant part exposure and sampling period interaction averaged over daylength and species. Standard error equals ±3.12.


% WEIGHT GAIN (+), LOSS (−), (PFW−IFW)
20.0
10.0
0.0
−10.0
−20.0
−30.0
−40.0
−50.0
TS = TOTAL SDLG
6 (WKS)
3 (WKS)
0 (WKS)
NONEXP−TS
EXP−TS
PLANT PART EXPOSURE

Potted fresh weight (PFW) minus initial fresh weight (IFW) represents the percent weight gain or loss as a result of the 20 day growth period (Table 5). The nonexposed seedling averaged a 12.4% gain over their initial fresh weight whereas the exposed seedlings were still exhibiting a 31.1% loss as a result of desiccation. Weight loss during sampling periods decreased between the first period and the end of the experiment; however, a better picture of the gain/loss relationship between PFW and IFW can be seen in the plant part exposure and sampling period interaction (Fig. 2). The decrease in seedling sensitivity between the 3rd and 6th week period was expressed as a 66% increase in percent fresh wgt; however, it still represented a 12% loss from the seedling fresh weight prior to treatment.

The influence of plant part exposure and sampling period interaction on potted moisture contents and white root production is presented in Table 7. Potted moisture contents in the nonexposed seedlings showed a reduction between the first and the last sampling period. White roots also increased over the period. The increase in white roots averaged over daylength and species could be related to a slowdown in shoot growth in the LD treatment or the cessation of shoot growth in SD treatment. There were no significant differences between LD and SD. The effects of the desiccation on moisture content could still be seen on the potted seedling and shoot moisture content during the first 2 sampling periods. Moisture contents in the seedling and shoots on the last sampling period were similar to the nonexposed seedlings. Root moisture contents were significantly reduced from the nonexposed seedling when compared to the exposed seedlings regardless of sampling period.

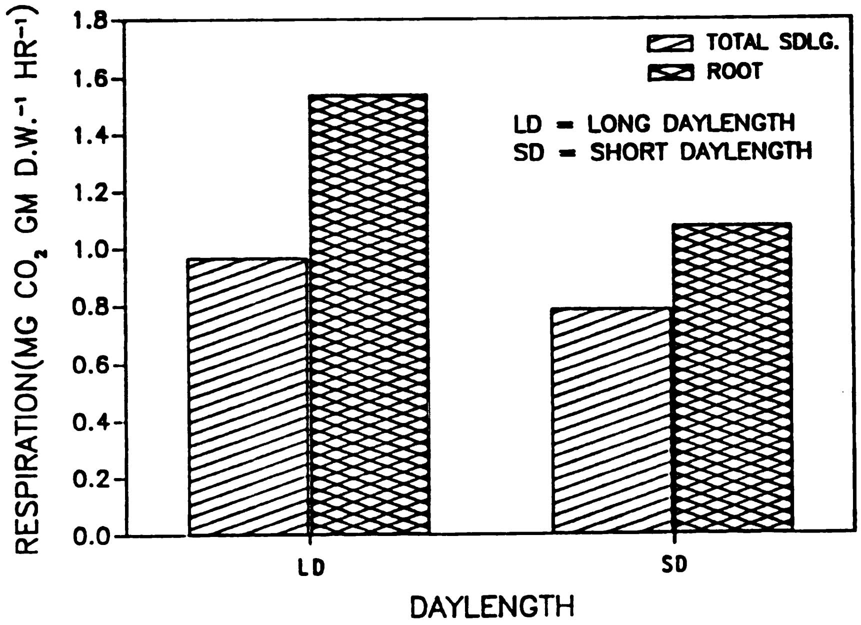
White root production was drastically reduced in the exposed seedlings. The tolerance of the seedling to an approximately 21% loss in fresh weight increased during the six weeks; however, it was not substantial enough to be considered a positive indicator of future performance. Root growth was similar to the growth recorded in Chapter I for the 3 hour exposure treatment. The similarities in number of white roots in the 3 hour treatment could reflect the longer period under short daylength in the Chapter I seedlings. The lack of any significant difference in root growth between the daylength treatment is not in agreement with results reported by other researchers (Lavender and Wareing, 1972). Similarities between seedling response could have been influenced by light intensity when compared to greenhouse condition. The LD seedlings remained actively growing during the six week period, however, the relative rate of growth was reduced from that in the greenhouse. Comparison of seedling dry weights in the moisture study and the root growth study suggest that the six week period may not have been long enough to produce a measurable difference.

Table 8. Respiration and water-vapor loss during 2 hour desiccation treatment at 1.5 kPa VPG.[z]

Factors	Respiration ($mg\ CO_2\ gm\ D.W.^{-1}hr^{-1}$)	Water vapor loss ($mg\ gram\ D.W.^{-1}hr^{-1}$)
<u>Daylength</u>		
Long Day	1.25	0.10
Short Day	0.93	0.10
<u>Species</u>		
White Spruce	1.17a	0.10b
Blue Spruce	1.00b	0.11a
<u>Plant Part Exposure</u>		
Total Seedling	0.87b	0.04b
Root	1.30a	0.16a
<u>Sampling Period (weeks)</u>		
0 weeks	1.23a	0.14a
3 weeks	1.20a	0.09b
6 weeks	0.83b	0.08b
<u>Time Interval (mins)</u>		
20	1.19a	0.12a
40	1.14ab	0.12a
60	1.16ab	0.10b
80	1.09abc	0.09bc
100	1.00bc	0.09bc
120	0.95c	0.08d

[z]Means within vertical column followed by the same letter are not significantly different at P=0.05 using Duncan's Multiple Range Test.

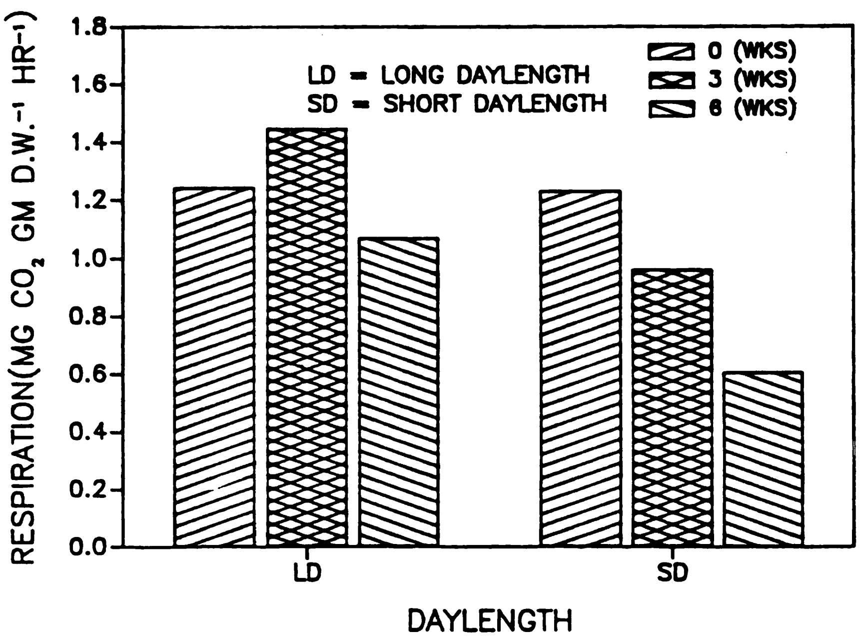
Figure 3. Respiration for daylength and plant part exposure interaction averaged over species and sampling period. Rates are the means of the 20 minute interval measurements within the 2 hour exposure treatment at 1.5 kPa VPG. Standard error equals ± 0.045.


RESPIRATION(MG CO_2 GM D.W.$^{-1}$ HR^{-1})
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
TOTAL SDLG.
ROOT
LD = LONG DAYLENGTH
SD = SHORT DAYLENGTH
LD
SD
DAYLENGTH

Respiration and Water Vapor Loss

The effects of desiccation on respiration and water loss are presented in Table 8. Significant differences were found within species, plant part exposure, sampling period, and time interval. White spruce respiration rate averaged over other main effects was 1.17 mg CO_2 gm D.W.$^{-1}$hr^{-1}. Blue spruce was significantly lower at 1.00 mg CO_2 gm D.W.$^{-1}$hr^{-1}. These results are similar to the rates found in the 2 hour exposure treatment in Chapter II. Respiration in the root exposure treatment was significantly higher (1.04) than in the total seedling (0.87). The results found in this experiment are supported by data reported in Chapters II, III and by previous researchers (Ledig et al., 1976). The reduction in respiration rate observed at the 6th week sample period could be a consequence of tissue maturation and lower rates of metabolism. The lack of significance in the daylength main effect was changed by its interaction with plant part exposure (Fig. 3). Short daylength resulted in a decreased rate in both total seedling and root respiration when averaged over species, sample period, and time interval. The reduction in rate was attributed to the cessation of shoot growth and reduced root activity. Research has correlated changes in respiration with changes in shoot and root growth (Ledig et al., 1976). Significance was also found in the daylength and sampling period interaction (Fig. 4). LD seedlings exhibited a peak in their rate during the 3rd week, followed by a reduction in

Figure 4. Respiration for daylength and sampling period interaction averaged over species and plant part exposure. Rates are the means of the 20 minute interval measurements within the 2 hour exposure treatment at 1.5 kPa VPG. Standard error equals ± 0.055.



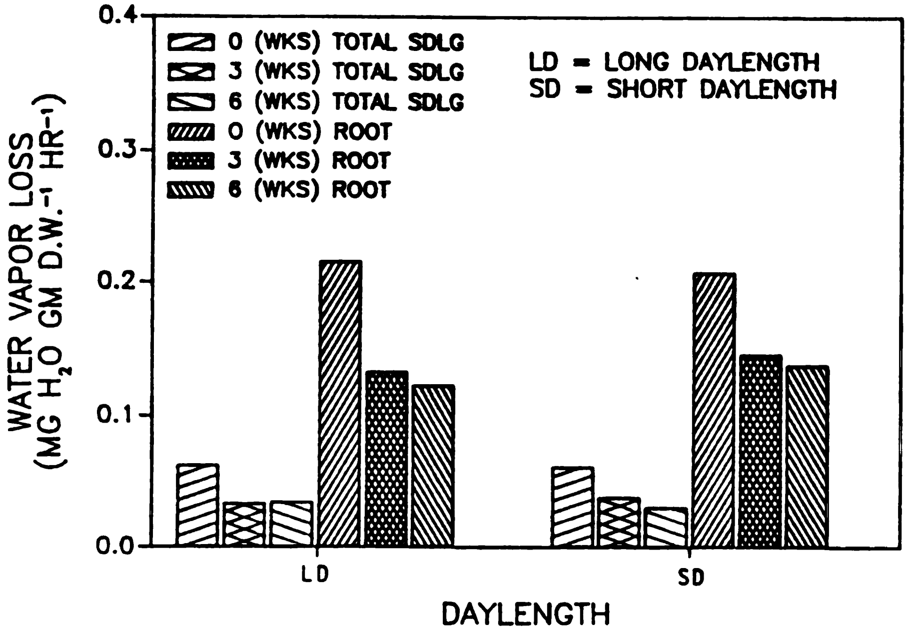
RESPIRATION(MG CO_2 GM D.W.$^{-1}$ HR^{-1})
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
LD = LONG DAYLENGTH
SD = SHORT DAYLENGTH
0 (WKS)
3 (WKS)
6 (WKS)
LD
SD
DAYLENGTH

the 6th week. SD respiration exhibited a steady decrease with each successive sampling period. The respiration rate for the SD 6th week sample was significantly lower than the corresponding LD rate. There was an overall decrease in respiration of 25% in the 2 hour desiccation treatment as reported in the time interval main effect. A reduction of 33% was observed in the 2 hour treatment in Chapter III. The differences between environmental conditions and the duration of the sampling in Chapter III may have influenced the decrease.

Water vapor loss for the main effects is presented in Table 8. Blue spruce rate of water loss was significantly higher than white spruce. A reduction in water vapor loss was found in the sampling period main effect during the 3rd week. Vapor loss monitored during the 2 hour treatment showed a decline after 40 and 100 minutes. The degree of loss in the time intervals was considerably higher than the loss observed in Chapter III for the same main effect. The increased rates in this experiment may be due to differences in developmental state of the tissue. The averaged vapor loss in Chapter III reflect the influence in seasonal temperature change.

A significant interaction was observed between daylength, plant part exposure, and sampling period (Fig. 5). The pattern observed between sampling period was similar for daylength and plant part exposure. There was a sharp decrease in the vapor loss rate after the first

Figure 5. Water vapor loss for daylength, plant part exposure and sampling period interaction averaged over species. Rates are the means of the 20 minute interval measurements within the 2 hour exposure treatment at 1.5 kPa VPG. Standard error equals ± 0.004.


0 (WKS) TOTAL SDLG
3 (WKS) TOTAL SDLG
6 (WKS) TOTAL SDLG
0 (WKS) ROOT
3 (WKS) ROOT
6 (WKS) ROOT
LD = LONG DAYLENGTH
SD = SHORT DAYLENGTH
WATER VAPOR LOSS
(MG H_2O GM D.W.$^{-1}$ HR^{-1})
0.0
0.1
0.2
0.3
0.4
LD
SD
DAYLENGTH

f

e 2

sampling period. This decrease in vapor loss rate could reflect changes in tissue sensitivity with time in the growth frame.

In conclusion, preconditioning container grown white and blue spruce with short daylength will have an influence on the seedling moisture content and the rate of moisture loss. The influence may be due to changes in tissue development as a result of cessation of growth. Six week preconditioning did not appear to be sufficient to resist desiccation and promote root growth following planting. Seedling tolerance to water loss may require additional time or the coupling of low temperature as was found naturally in fall acclimation.

REFERENCES

Arnott, J.T. 1979. Effect of light intensity during extended photoperiod on growth of amabilis fir, mountain hemlock, and white and Engelmann spruce seedlings. Can. J. For. Res. 9:82-89.

Arnott, J.T. and A. Mitchell. 1981. Influence of extended photoperiod on growth of white and Engelmann spruce seedlings in Coastal British Columbia. In: Proceedings of the Canadian Containerized Tree Seedling Symposium. September 14-16, 1981. Toronto, Ontario. Ed. by J.B. Scarratt, C. Glerum and C.A. Plexman. Can. For. Ser. Great Lakes For. Res. Cent. COJFRC Symp. Proc. 0-P-10. pp. 139-152.

Arnott, J.T. and D.E. Macey. 1985. Effect of supplemental light intensity on white spruce, Engelmann spruce and mountain hemlock seedlings grown under an extended photoperiod. Can. J. For. Res. 15:295-300.

Arnott, J.T. and C.S. Simmons. 1985. The effects of failure in extended and intermittent photoperiodic lighting on the growth of white spruce container seedlings. Can. J. For. Res. 15:734-737.

Barney, C.W. 1950. Effects of soil temperature and light intensity on root growth of loblolly pine seedlings. Plant Physiol. 26:146-163.

Bongarten, B.C. and J.W. Hanover. 1985. Accelerating seedling growth through photoperiod extension for genetic testing: A case study with blue spruce (*Picea pungens*). For. Sci. 31:631-643.

Colombo, S.J., D.P. Webb and C. Glerum. 1981. Cold hardiness and bud development under short days in black spruce and white spruce seedlings. In: Proceedings of the Canadian Containerized Tree Seedling Symposium. September 14-16, 1981. Toronto, Ontario. Ed. by J.B. Scarratt, C. Glerum and C.A. Plexman. Can. For. Serv. Great Lakes For. Res Cent. COJFRC Symp. Proc. 0-P-10. pp. 139-152.

Coutts, M.P. 1981. Effects of root or shoot exposure before planting on the water relations, growth and survival of Sitka spruce. Can. J. For. Res. 11:703-709.

Drew, A.P. 1983. Optimizing growth and development of 2-0 Douglas fir seedlings by altering light intensity. Can. J. For. Res. 13:425-428.

Fraser, D.A. 1962. Growth of spruce seedlings under long photoperiods. Canadian Dept. of For. For. Res. Branch Tech. Note No. 114.

Gucci, R. 1988. The effect of fruit removal on leaf photosynthesis, water relations and carbohydrate partitioning in sour cherry and plum. Ph.D. Thesis, Michigan State University. p. 199.

Hanover, J. 1980. Control of tree growth. BioScience 30:756-762.

Hanover, J.W., E. Young, W.A. Lemmien and M. VanSlooten. 1976. Accelerated-optimal-growth: a new concept in tree production. Mich. State Univ. Agric. Exp. Stn. Rep. 317, 16 p.

Heckman, J. 1985. Environmental control of spruce seedling growth and shoot development. Ph.D. Thesis, Michigan State University. 181 p.

Johnson, J.R. and J.R. Havis. 1977. Photoperiod and temperature effects on root cold acclimation. J. Am. Soc. Hortic. Sci. 102:306-308.

Krueger, K.W. and W.K. Ferrell. 1965. Comparative photosynthetic and respiratory response to temperature and light by Pseudotsuga menziesii var menziesii and var. glauca seedlings. Ecology 46:794-801.

Lavender, D.P. 1980. Effects of the environment upon the shoot growth in trees. Ed. C.H.A. Little. Maritimes Forest Research Centre, Fredericton, New Brunswick, Canada. pg. 76-106.

Lavender, D.P. and P.E. Wareing. 1972. Effects of daylength and chilling on the responses of Douglas fir (Pseudotouga menziesii (Mirb.) Franco.) seedlings to root damages and storage. New Phytol. 71:1055-1067.

Lavender, D.P. and S.G. Stafford. 1985. Douglas fir seedlings: some factors affecting chilling requirement, bud activity and new foliage production. Can. J. For. Res. 15:309-312.

Ledig, F.T., A.P. Drew and J.G. Clark. 1976. Maintenance and constructive respiration, photosynthesis and net assimilation rate in seedlings of pitch pine (Pinus rigida Mill). Ann. Bot. 40:289-300.

Levitt, J. 1980. Responses of plants to environmental stress. Vol. 1: Chilling, freezing and high temperature stress. 497 pp. Academic Press, New York, NY.

Moon, J.W. and J.A. Flore. 1986. A basic computer program for calculation of photosynthesis, stomatal conductance and related parameters in an open gas exchange system. Photosynthesis Res. 7:269-279.

Owston, P.W. and T.T. Kozlowski. 1981. Growth and cold hardiness of cold hardiness of container-grown Douglas fir, noble fir, and sitka spruce seedlings in simulated greenhouse regimes. Can. J. For. Res. 11:465-474.

Pellet, N.E. and D.B. White. 1969. Relationship of seasonal tissue changes to cold acclimation of Juniperus chinensis 'Hetzi'. J. Amer. Soc. Hort. Sci. 94:460-462.

Pollard, D.F.W. and K.T. Logan. 1979. The response of bud morphogenesis in black spruce and white spruce provinances to environmental variables. Can. J. For. Res. 9:211-217.

Sams, C.E. and J.A. Flore. 1982. The influence of age position and environmental variables on net photosynthetic rate of sour cherry leaves. J. Amer. Soc. Hort. Sci. 107:339-344.

Smit-Spinks, B., B.T. Swanson and A.H. Markhart, III. 1985. The effect of photoperiod and thermoperiod on cold acclimation and growth of Pinus sylvestris. Can. J. For. Res. 15:453-460.

Sucoff, E., C. Buschema and P. Tamte. 1985. Desiccation and water potential in the roots, leaves and shoots of bare-root red pine and white spruce. Can. J. For. Res. 15:989-992.

Timmis, R.W. 1981. Environmental control of seedling physiology. In: Proceedings of the Canadian Containerized Tree Seedling Symposium. September 14-16, 1981, Toronto, Ontario. Ed. by J.B. Scarratt, C. Glerum and C.A. Plexman. Can. For. Serv. Great Lakes For. Res. Cent. COJFRC Symp. Proc. 0-P-10. pp. 139-152.

Timmis, R. and J. Worrall. 1975. Environmental control of cold acclimation in Douglas fir during germination, active growth and rest. Can. J. For. Res. 5:464-477.

Tyree, M.T., Y.N.S. Cheung, M.E. MacGregor and A.J.B. Talbot. 1973. The characteristics of seasonal and ontogenetic changes in tissue water relations of Acer, Populus, Tsuga and Picea. Can. J. Bot. 56:635-647.

Vance, N.C. and S.W. Running. 1985. Light reduction and moisture stress: effects on growth and water relations of western larch seedlings. Can. J. For. Res. 15:72-77.

Van den Driesche, R. 1969. Influence of moisture supply, temperature and light on frost hardiness changes in Douglas fir seedlings. Can. J. Bot. 47:1765-1772.

Webb, D.P. 1976. Root growth in Acer Saccharum Marsh. seedlings: effects of light intensity and photoperiod on root elongation rates. Bot. Gaz. 137:211-217.

Wheeler, N. 1979. Effect of continuous photoperiod on growth and development of lodgepole pine seedlings and grafts. Can. J. For. Res. 9:276-283.

Young, E. and J.W. Hanover. 1976. Accelerating maturity in Picea seedlings. Acta Hort. 56:105-114.

Young, E. and Hanover, J.W. 1977. Development of shoot apex of blue spruce (Picea pungens). Can. J. For. Res. 7:614-620.

SUMMARY AND CONCLUSIONS

Desiccation has an adverse effect on the quality of container-grown white and blue spruce. The extent of the injury is dependent on the developmental stage of the seedling and the severity of the stress.

Differences between white and blue spruce moisture holding characteristics were observed. Blue spruce initial seedling moisture contents tended to be higher than white spruce. Shoot and root moisture contents following desiccation varied with each experiment; however, blue spruce generally exhibited higher moisture levels. A tendency for higher moisture loss was also observed in blue spruce, and may be linked to the higher initial moisture contents.

Seedling desiccation was influenced by VPG, species, plant part exposed and duration of exposure. Seedling moisture loss increased with an increase in VPG from 0.5 to 1.5 kPa. Losses ranged from 24-41% when averaged over duration of exposure. Practitioners may use this information to control moisture loss through modifying handling procedures during extended planting seasons.

Total seedling and root exposure treatment losses were at least doubled that of the shoot. The root system accounted for approximately 78% of total seedling moisture loss. The root system of container-grown seedlings are extremely vulnerable to desiccation injury due to the relatively high portion of white roots. Fortunately, the container provides protection during processing. Maintaining adequate container moisture and minimizing exposure during the planting process is essential to the success of outplantings. Shoot exposure resulted in approximately 21% of seedling loss; however, under normal conditions light may further elevate these values. An appropriate sequel to this treatment would be to investigate the influence of light on seedling photosynthesis and transpiration during desiccation.

Seedling recovery following desiccation was based on percent gain or loss in fresh weight. Increased fresh weight provided an indication of rehydration following treatment. This parameter can be deceiving because rehydration can occur in both living and dead root tissue. A reasonable indication of recovery from the desiccation was provided by root growth capacity. One hour exposure reduced root growth by 46%. An additional 2 hours of exposure resulted in a further reduction of 59%. Drastic decreases were also found between exposed and nonexposed seedlings in both the fall acclimation and photoperiod studies. A question that needs to be answered concerns the relationship between the root and the shoot during seedling recovery. The present research did not examine physiological or metabolic processes during recovery; however, future research will be designed to investigate the interrelationship between water uptake, photosynthesis and root growth capacity following planting.

Fall acclimation decreased the sensitivity of the seedlings to desiccation. Seedling moisture loss decreased from August through November. Seedling rehydration and root growth capacity in the exposed seedlings increased between August and November, however, the levels were significantly less than the nonexposed seedlings. The decrease in sensitivity through fall is supported by other research and is attributed to increased cold hardiness and/or the level of physiological rest.

The relationship between short daylength and dormancy led to the investigation of daylength on seedling sensitivity to desiccation. Short daylength initiated a change in tissue maturation, decreased seedling moisture content and decreased seedling sensitivity to desiccation, however, the degree of influence after six weeks was not appreciable.

Seedling respiration rate depended on the developmental stage of the seedling. Respiration rates recorded in these experiments were comparable to values reported by other researchers. Respiration differed between the plant part exposure treatments. Root respiration rate was generally higher than that of the shoot or total seedling. This result was expected due to the relatively active nature of the container seedling root system. An exception was found in the fall acclimation study. August total seedling respiration was higher than the root because the shoots were still actively growing. Respiration rate, however, shifted in September with the cessation of shoot growth.

A linear relationship was found between respiration and water vapor loss. Respiration declined as water vapor loss decreased. Root respiration appeared to be most affected. Respiration rates were monitored during the desiccation treatment. Previous researchers have documented a correlation between desiccation and root respiration during recovery. Future research will be designed to examine seedling respiration throughout the desiccation and the recovery period in an effort to increase our understanding of planting shock and seedling establishment.

This information may have practical importance in developing preconditioning treatments for container-grown nursery stock. Sensitivity to moisture loss varied depending on the developmental state of the seedlings. Increased resistance to desiccation, in terms of moisture loss and root growth capacity were observed in Chapter III. The gradual decrease in seedling moisture content coupled with an increase in dry weight during fall acclimation decreased the severity of desiccation on white and blue spruce. Preconditioning treatments which mimic fall changes in moisture contents may reduce the effects of planting and/or site related stress on seedling performance.

The results from these experiments may also be used to modify storage and handling of container grown seedlings. In many cases, the container accompanies the seedling from production to field planting. Proper preconditioning may allow the removal of the container at the end of production, without an adverse effect on the root system. This would increase efficiency during storage, shipping and subsequent planting of container grown seedlings.