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LIGHT REDUCTION AND MOISTURE STRESS EFFECTS
ON GROWTH AND WATER RELATIONS
OF WESTERN LARCH SEEDLINGS

By

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B.A., University of Maryland, 1970

Presented in partial fulfillment of the requirements for the degree of
Master of Science
UNIVERSITY OF MONTANA
1983

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Forestry

Light reduction and moisture stress effects on growth and water relations of western larch seedlings (32 pp.)

Director: Dr. Steven W. Running

Ten week old western larch (*Larix occidentalis* Nutt.) seedlings were grown in a greenhouse under 70, 37, and 27% full sunlight from late July to early October. In August seedlings under each light treatment were stress cycled until predawn seedling water potential ($B\psi_p$) reached one of 3 levels: no stress (> -0.4 MPa), moderate stress (-0.7 to -1.0 MPa) and severe stress (-1.5 to -1.8 MPa). Seedlings were sampled for height, diameter, shoot and root dry weights and analyzed by ANOVA. Shoot/root ratios were calculated and time of terminal bud set noted. Diurnal leaf conductance (K_l) and seedling water potential (ψ_p) were measured and water relations compared to those of other species.

Moisture stressing significantly reduced height and diameter of seedlings grown under 70% light. Light reduction reduced biomass accumulation in shoot and root. A positive linear relation was found between root dry weight and light intensity. The largest seedlings (on a weight basis) received the highest light, were unstressed and had the lowest shoot/root ratios. Terminal bud set was not affected by light reduction or moisture stressing but occurred under a 14 hour photoperiod and reduced nighttime temperatures. Stressed and shaded seedlings had significantly reduced diurnal K_l and stress cycled seedlings showed an adjustment to stressing. The K_l of unstressed seedlings was correlated with humidity deficit (ABHD), of stressed seedlings, with $B\psi_p$ and ABHD. Maximum K_l declined with decreasing $B\psi_p$ but not to a level indicating complete stomatal closure.

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INTRODUCTION

Western larch (*Larix occidentalis* Nutt.) is valued as a commercial species (Owens and Molder 1979, Schmidt et al. 1976), although its range is restricted to the interior northwestern United States and southern portions of western Canada. Highly intolerant, this pioneer species grows best under full sunlight of clearcuts (Schmidt et al. 1976). Yet drought, named as one of the most important causes of seedling mortality in western larch, reduces the survival rates of out planted seedlings.

A major goal in rearing conifer seedlings is to produce seedlings morphologically and physiologically suited for withstanding the rigors of planting and the site (Cleary et al. 1978, Tinus and McDonald 1979). Meeting that objective is difficult with western larch, an atypical deciduous conifer species which is usually reared under growing regimes adjusted by trial and error. Nursery personnel regularly moisture stress western larch seedlings to stop height growth and induce dormancy without knowing the effects of plant water stress on the seedlings since this species has received little formal physiological study. Yet the increased use of nursery and greenhouse grown western larch seedlings for reforestation emphasizes the need for basic physiological, morphological and growth data.

The effects of manipulating the greenhouse environment on seedling morphology and physiology should be determined before deciding on the characteristics that can be correlated with survival. Since changes

in the moisture and light environment strongly affect seedling growth and physiology (Kozlowski 1971, Levitt 1972, Larson 1974), the objective of this study is to examine moisture stressing and light intensity reduction effects on height, diameter, dry matter accumulation and distribution, and timing of bud set. The study also will examine the effects of moisture stressing and light reduction on seedling water potential and leaf conductance.

MATERIALS AND METHODS

Western larch seed were obtained from Montana Department of State Lands, Forestry Division. Seed were randomly selected from seed lot 776-SDF, collected Fall 1980 from Big Creek, Mt. at about 1200 m elevation and 48°35' latitude, and cold stored. Seed were stratified for 23 days, sown in Ray Leach tubes (#4) and grown in the Montana State Nursery greenhouse, Missoula, Montana during the Spring and Summer of 1982. Seedlings were grown in a peat-vermiculite medium (Grace Products) and under controlled environmental conditions of an operational greenhouse: 30/20° C temperatures, 50 to 80% RH, with a 24 hour photoperiod by supplemental lighting. Seedlings were watered by an overhead sprinkling system and fertilized with a commercial fertilizer which included micronutrients (Peters, 9-45-15 and 20-20-20). At the end of July when the seedlings were about 10 weeks old, a set of 15 randomly sampled seedlings were harvested and baseline measurements of height; stem diameter, measured just above the root collar;

shoot and root oven dry weight (70° C for 48 hr) were determined. Supplemental photoperiod lighting was discontinued and treatments began.

Light readings taken with a quantum sensor (LI-COR 190S) and averaged during peak photosynthesizing hours indicated that on the average photosynthetic photon flux density at peak irradiance was about $1400 \mu E m^{-2} s^{-1}$ having been reduced 30% through the greenhouse glazing. Two light reduction treatments were applied by using commercial shade cloths. Each shade shelter covered 600 seedlings (3 container trays) and another 600 were left uncovered for the highest of the three light treatments. The uncovered and the two shade treatments provided a growing environment under 70%, 37% and 27% full irradiance.

After all seedlings were watered to saturation, a subset of 200 seedlings from each light treatment were given one of three moisture stress treatments. One set was watered at a frequency to prevent significant moisture stress or predawn seedling water potential ($B\psi_p$) above -0.4 MPa. Water was withheld from another set until $B\psi_p$ reached -0.7 to -1.2 MPa (moderate stress), and from a third set until $B\psi_p$ reached -1.5 to -1.8 MPa (severe stress). Stress development was monitored by measuring $B\psi_p$ with a pressure chamber on sampled seedlings clipped above the root collar (Ritchie and Hinckley 1975). The stress treatments involved two consecutive moisture stress cycles, each taking from 1 to about 2 weeks to complete. During the moisture stress cycling fertilizer was withheld so as not to confound effects of the stress

treatments. Morphological changes and date of bud set were noted. At the end of the period (August 16) 15 seedlings randomly sampled from each light and moisture stress treatment (135 seedlings) were harvested and height, diameter, shoot and root dry weight were measured.

Following the moisture stress cycling, seedlings were fertilized weekly with 5-11-26 (Peters). In August the greenhouse temperatures were lowered to 25/13° C to prepare seedlings for dormancy and cold hardening. Seedlings were moved outside by the end of September to continue cold hardiness development under short days and cool nights and final data were taken the first week in October. Shoot dry weight was not measured because of extensive needle drop. Data results were treated by analysis of variance. Significant differences in treatment effects were determined by Duncan's multiple range test.

Diurnal moisture stress development in shaded and unshaded seedlings from the unstressed treatments was measured August 16 at approximately 2 hour intervals with the pressure chamber. Measurements of water potential (Ψ_p) were taken of the entire seedling shoot clipped above the root collar.

Leaf conductance (K_l) was measured August 4 during the first stress cycle and August 16 during the second stress cycle on intact seedlings with a null balance diffusion porometer (Beardsell et al. 1972). Approximately 3 to 4 cm of the seedling terminal generally having about 30 to 50 needles, or about 20-30 cm² of total needle surface area, were enclosed in the cuvette. Photosynthetic photon flux density (PPFD)

was measured with a quantum sensor (LI-COR 190S), temperature with a platinum thermistor and relative humidity with a Vaisala sensor at the same time conductance measurements were taken. The following morning before sunrise each seedling was clipped and ($B\psi_p$) was measured. Because the method of measuring $B\psi_p$ was destructive, sample sizes were 3 for each data point unless otherwise stated. All measurements were taken on sunny days.

Leaf area used in the conductance determinations were calculated with a LI-COR portable surface area meter. The planar surface area was corrected to total surface area under a slightly modified method described by Drew and Running (1975). A scanning electron microscope was used on prepared needles (dehydrated in a graded series of ethanol solutions, critical-point dried, and coated with gold) and polaroid photographs obtained. Direct measurements were made on 10 random needle samples to calculate the ratio of leaf curvature to the width of the planar surface. The correction factor for needle curvature used to calculate total surface area was determined to be 2.23.

RESULTS AND DISCUSSION

Growth and Morphology

Mean heights of seedlings harvested October 5, 1982 are presented in Table 1. The effects of light reduction on height growth were not statistically significant at the .05 level of confidence. The mean

Table 1. Analysis of differences in morphology and dry matter accumulation and distribution.

		LIGHT TREATMENT		
		70%	37%	27%
HEIGHT centimeters				
August 16	1.	13.56	12.80	12.65
	2.	12.41	12.77	12.53
	3.	12.54	12.51	12.57
October 5	1.	15.77	15.05	14.89
	2.	12.67	13.71	13.78
	3.	13.19	14.07	13.93
DIAMETER centimeters				
August 16	1.	.197	.180	.173
	2.	.173	.178	.168
	3.	.187	.161	.149
October 5	1.	.251	.206	.196
	2.	.238	.205	.194
	3.	.228	.204	.198
SHOOT DRY WEIGHT grams				
August 16	1.	.405	.345	.352
	2.	.357	.354	.321
	3.	.387	.322	.291
ROOT DRY WEIGHT grams				
August 16	1.	.237	.182	.171
	2.	.203	.162	.132
	3.	.209	.161	.139
October 5	1.	.559	.355	.285
	2.	.537	.343	.267
	3.	.509	.343	.241
SHOOT/ROOT RATIO				
August 16	1.	1.74	2.02	2.14
	2.	1.76	2.31	2.53
	3.	1.86	2.04	2.16

Numbers 1, 2, 3 denote no, moderate and severe moisture stress treatments respectively. Nonsignificant differences for group means at the .05 level by Duncan multiple range test. Nonsignificant differences connected by solid line.

height (14.89 cm) of seedlings grown under 27% light was about 1 centimeter less than the mean height (15.77 cm) of seedlings grown under 70% light, but the variability within treatment population heights made detecting significant differences impossible. Rehfeldt (1982) also found height variability within populations and attributed it to the exogenous nature of western larch shoot growth.

Despite the variability, statistically significant differences in height were detected as a result of moisture stressing (Figure 1). Moisture stressing effects were significant under 70% light only, however.

Although bud formation was visible before August 16, curiously, there was significant height growth (about 2 cm) of the unstressed seedlings between August 16 and October 5. This may have been due to the continual growth or "free growth" habit of western larch (Rehfeldt 1982, Owens and Molder 1979) and to the late seasonal growth pattern which is characteristic of *Larix* (Tranquillini 1979, Ledig and Botkin 1974, Kozlowski 1971). Growth after August 16 of the moisture stressed seedlings was less than the unstressed seedlings which also suggests that growth after the appearance of the terminal bud did indeed occur, since one of the first responses to moisture stress by a growing plant is inhibition of cell enlargement (Hsiao et al. 1976).

Light reduction treatments significantly decreased mean diameter of seedlings harvested August 16 and October 5 (Table 1). Moisture stress did not affect diameter except for the severely stressed seedlings grown under 70% light which were significantly smaller in diameter (Figure 2).

Figure 1. Change in height of unstressed (●), moderately (○), and severely (○) stressed seedlings under 70% light over the 20 week study. (Each point is the mean of 15 measurements.) Height difference of moisture stressed seedlings under 37% and 27% light was not detected therefore data not shown.

Figure 2. Change in diameter of unstressed western larch seedlings under 70% (●), 37% (▲), and 27% (■) full light over the 20 week study, also, change in diameter of severely stressed (○) seedlings under 70% light. Each point is the mean of 15 measurements. Differences in diameter under other moisture stress treatments not detected therefore, data not shown.

A fungus, *Botrytis cinerea*, infected seedlings in September causing considerable needle drop, so shoot dry weights were not calculated in October. Shoot dry weights were determined on seedlings harvested August 16. Analysis showed a significant difference in dry weight between the means of the severely stressed seedlings under the 70% and the light reduction treatments (Table 1).

There was a significant effect of light reduction treatments on root dry weight (Table 1). The increase in allocation of dry matter to roots by October was greatest in seedlings grown under 70% light (Figure 3) and agreed with Shiroya et al. (1962) who found more photosynthate was transferred to the roots by pine seedlings grown under higher light intensity. A regression analysis of root dry weight with percent light showed a significant positive linear association ($r^2 = .68$). This positive association to light intensity of tolerant as well as intolerant conifer seedlings has also been found by Fairbairn and Neustein (1970) and Logan (1966).

The translocation of photosynthate to the roots between August and October related to seasonal changes in carbon distribution and the ability of the seedlings to continue positive carbon uptake into late Summer and early Autumn (Figure 3). Ledig and Botkin (1974) showed stem and root dry weight in European larch (*Larix decidua* Mill.) and Japanese larch (*Larix leptolepis* (Sieb. & Zucc.) Gord.) increased 5-6 fold between August and October. The high dry weight increase was attributed in part to their relatively high photosynthetic rate in late summer. This data suggest that western larch maintained positive CO₂ uptake late in the growing season as well.

Figure 3. Change in root dry weight of unstressed western larch seedlings under 70% (●), 37% (▲), and 27% (■) light treatments over the 20 week study. Each point is the mean of 15 measurements.

Shoot/root ratios were calculated from seedlings harvested August 16 and results are shown in Table 1. Across two moisture stress treatments, there was a significant reduction in the shoot/root ratio of seedlings grown under 27% light; however, there was no difference due to moisture stressing. Reduction of light intensity apparently affected allocation of photosynthate to the roots more than to the shoots. How light reduction affects shoot/root ratios of conifer seedlings has been rigorously analyzed (Ledig et al. 1970, Ledig and Perry 1965). Ledig et al. (1970) cautioned that while analysis of variance of shoot/root ratio may indicate significant differences among treatments, the difference was related to the total size of the seedling. Larger seedlings had smaller shoot/root ratios regardless of treatment. The results of this study appear to agree with those observations. Seedlings under the 70% light, no stress treatment had the highest mean total weight (.642 g) and correspondingly lowest mean shoot/root ratio (1.74).

Dormancy Induction

No differences in time of terminal bud set across all treatments were detected, and the terminal bud was visible on virtually all seedlings within 72 hours. Although buds in greenhouse grown western larch seedlings often rebreak these were the final resting buds of the season. This suggests that photoperiod was a more critical factor than light intensity or moisture stress for inducing a final resting bud and dormancy under the environmental conditions of this study.

The importance of photoperiod in inducing the formation of resting buds and the onset of dormancy in European larch (*Larix decidua* Mill.) is well known (Wareing 1969). Vaartaja (1959) found photoperiodic ecotypes in eastern larch (*Larix laricina* (Du Roi) K. Koch) corresponded with latitude (critical daylength increased with latitude north), but Rehfeldt (1982) also noted genetic variation occurred in western larch with elevation (earlier bud set with higher elevation seed source). That the seed for this study originated from a single source (latitude and elevation), most likely contributed to the uniformity of bud set regardless of treatment.

Terminal buds first appeared on August 13 when daylength was approximately 14 hours. Vaartaja (1959) found that in 1-year-old eastern larch seedlings from as far south as 46° latitude, critical daylength for terminal dormancy was also 14 hours.

Water Relations

Diurnal leaf conductance (K_l) of unstressed and stressed seedlings measured August 4 are shown in Figure 4. The unstressed seedlings at that date responded poorly to ABHD (Table 2) compared to seedlings measured later. This may be attributable to immaturity of the terminal needles which had not developed stomatal mechanics, although stomatal closure did occur when there was internal moisture stress. Richards (1980) detected a similar dampening of stomatal response in immature needles of alpine larch (*Larix lyallii* Parl.). The reduction in K_l of the stressed seedlings (mean $B\psi_p = -1.65$ MPa) was similar to that of

Figure 4. Diurnal measurements taken August 4, 1982 of photon flux density (PPFD), absolute humidity deficit (ABHD) and leaf conductance (K_l) of unstressed ($B\psi_p > -0.4$ MPa) and stressed seedlings ($B\psi_p = 12.5-20.0$ MPa). Stressed and unstressed seedlings denoted by (○) and (●) respectively. All points are means of 3 seedlings with one standard error indicated (bars).

Table 2. Summary of regressions of leaf conductance with humidity deficit, predawn xylem water potential, and both independent variables entered stepwise.

DATE	SEEDLING WATER STATUS	k vs ABHD r^2	k vs $B\psi_p$ r^2	k vs $B\psi_p$ & ABHD r^2
August 4	Unstressed	.02 NS	.11 NS	.38 NS
	Stressed	.01 NS	.74***	.75***
August 16	Unstressed	.82***	.01 NS	.83***
	Stressed	.27**	.15*	.75***

Significance difference at the .001 level, ***; significant difference at the .01 level, **; significant difference at the .05 level, *; no difference, NS.

stressed seedlings (mean $B\psi_p = -1.7$ MPa) measured August 16 (Figure 5) and agreed with a comparable pattern described by Hinckley et al. (1978) and Davies et al. (1981).

Diurnal K_1 patterns of the shaded and unshaded seedlings from the unstressed treatment measured August 16 are shown in Figure 5. Although maximum K_1 was not significantly different between the shaded and unshaded seedlings, K_1 was significantly lower at high levels of ABHD. The greater decline in K_1 of the shaded seedlings having the same water status may have been due to stomatal response to reduced light intensity and was also noted by Havranek and Benecke (1978) and Kaufmann (1976). The decrease in K_1 which reduced transpirational water loss probably contributed to the difference in diurnal pattern of water potential (ψ_p) of shaded and unshaded seedlings measured August 16 (Figure 5). Shaded seedlings showed a significantly higher minimum (-0.59 MPa) than the unshaded seedlings (-0.85 MPa).

Diurnal measurements of K_1 and ABHD, and corresponding $B\psi_p$ were further analyzed by regressing K_1 with ABHD and $B\psi_p$ individually, and K_1 with ABHD and $B\psi_p$ in a stepwise multiple regression. A summary of the results is shown in Table 2. Except for the unstressed seedlings measured August 4, the relation between K_1 and ABHD and $B\psi_p$ is significant. The lack of significance in the August 4 unstressed seedlings is attributed to the variability in stomatal behavior of the immature terminal needles. The relationship between $B\psi_p$ and K_1 has been shown by Running (1976, 1980). As $B\psi_p$ decreased, or internal moisture stress

Figure 5. Diurnal measurements taken August 16, 1982 of absolute humidity deficit (ABHD), seedling water potential (Ψ_p), and leaf conductance (K_l) of unshaded ($\bullet$), shaded ($\blacksquare$), and stressed ($\circ$) seedlings. All points are means of 3 seedlings with one standard error indicated (bars).

increased, its influence on K_j correspondingly increased until at some critical level it overrode not only stomatal response to ABHD, but the photoactive response as well, which agrees with Hinckley et al. (1978).

The direct relationship of $B\psi_p$ and maximum K_j is demonstrated for western larch and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) from Running (1980) in Figure 6. Although the fitted regression line indicated the response of western larch to declining $B\psi_p$ was similar to that of lodgepole pine, maximum K_j did not decline as rapidly to increasing internal water stress. At even severe stress levels ($B\psi = -2.0$ MPa), levels of maximum K_j ($> .10 \text{ cm} \cdot \text{s}^{-1}$) indicated stomata were still partially open. Seedlings stressed to $B\psi_p = -1.5$ MPa still opened stomata photoactively (Figures 4, 5 and 6) whereas lodgepole pine stomata did not (Figure 6) indicating less ability by western larch seedlings to conserve water under stress. This agrees with Havranek and Benecke (1978) who found that stomata of two-year-old eastern larch did not react as sensitively as lodgepole pine to declining ψ_p .

The curves in Figure 7 resemble soil moisture tension release curves and suggest close coupling of $B\psi_p$ to the water potential of the container soil. This assumes equilibrium conditions existed when $B\psi_p$ was measured (Havranek and Benecke 1978, Hinckley et al. 1978). The second moisture stress cycle took several days longer to produce the same $B\psi_p$ in comparable seedlings. There were no changes in the greenhouse environment over the time span of the stress cycles that could have accounted for

Figure 6. A second degree regression from a least squares curve fit of maximum morning leaf conductance (K_1) on predawn seedling water potential ($B\psi_p$). The solid line is from the equation fitting the data points for western larch. The dashed line is for lodgepole pine from Running (1980).

Figure 7. Seedling predawn xylem pressure potential ($B\psi_p$) during two consecutive stress cycles. Each point is the mean of 3 measurements taken of seedlings under 70% (○) and 27% (□) light treatments. The first stress cycle is denoted by (—), the second cycle by (--).

this. Changes in seedling stem and needle morphology over the stress cycling period could have possibly accounted for the apparent adaptation; however these and physiological adjustments were not quantified. In studies by Johnson and Ferrell (1982) and Newville and Ferrell (1979) seedlings were placed under 2 consecutive stress cycles, and although the second cycle also took longer for seedlings to achieve the same $B\psi_p$, the means of the apparent adaptation including greater stomatal control or osmotic adjustment were not ascertained.

CONCLUSIONS

Seedling height growth responded significantly to moisture stress and continued after bud set. The considerable variability in height suggests height growth is not very predictable with this species and less emphasis should be placed on it as an attribute of seedling quality. The direct relationship of root dry weight to light intensity and the dramatic increase in root dry weight late in the growing season under relatively high light suggests that as long as moisture is available shading larch after bud set is contraindicated. Although shoot dry weight also increased with increased light intensity, relatively more dry matter was allocated to the shoots than the roots with light reduction. In general, the highest light intensity produced the largest seedlings by weight with the lowest shoot/root ratios.

Bud set timing was not influenced by moisture stressing or light intensity reduction but by the 14 hour photoperiod. This suggests

that while moisture stressing may induce a temporarily resting bud in larch, truly dormant buds could best be induced by photoperiod control.

Despite western larch seedlings' apparent fragility and relative needle succulence, water relations were generally characteristic of other conifers. Data indicated that stomatal closure occurred at a threshold level of ψ_p ; however, seedlings had a persistent photoactive response even under stressful conditions which resulted in less stomatal control in reducing transpirational water loss. Nevertheless, seedlings were able to recover from predawn moisture stress as great as -1.5 MPa and displayed an adjustment to stressing which could provide the seedling with a protective mechanism against subsequent episodes of moisture stress.

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