ECOPHYSIOLOGICAL ASSESSMENT OF WESTERN HEMLOCK AND WESTERN RED CEDAR GREENHOUSE STOCKTYPES

BY

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Date April 23/90
Western hemlock (Tsuga heterophylla (Raf.) Sarg.) and western red cedar (Thuja plicata Donn) seedlings from four dormancy induction treatment(s) (DIT) (i.e. long-day dry, long-day wet, short-day dry, and short-day wet) were planted on a high available soil moisture field site in British Columbia and monitored for physiological response and morphological development over the first growing season. Stomatal conductance (gwv) and net photosynthesis (Pn) were recorded over an environmental matrix of photosynthetically active radiation (PAR) (0 - 2.2 mmol m$^{-2}$ s$^{-1}$) and vapour pressure deficit (VPD) (0 - 2.5 or 4.0 kPa) on both first year grown and fully developed second year foliage. To compare stocktypes, physiological data were collected and analyzed in the following ways: (1) replicated data at stable environmental conditions once a month, (2) physiological response to one increasing environmental variable using boundary line analysis, and (3) physiological response surface to two simultaneously changing environmental variables.

For western hemlock first year needles, short-day DIT had a higher gwv response to both increasing VPD and PAR. Both short-day and moisture stressed DIT improved Pn response to PAR, and the combination had the highest response. Short-day DIT seedlings initially were smaller, shorter, had a better seedling water balance ratio and lower
shoot to root ratio. Short-day second year needles showed a slightly higher gwv response to both increasing VPD and PAR as compared to long-day seedlings; however, they showed no treatment differences for Pn versus PAR. All stocktypes had similar final morphological parameter values.

For western red cedar first year foliage, moisture stressed DIT seedlings had greater Pn response to increasing PAR and VPD. Also, moisture stressed seedlings gwv response to increasing VPD and PAR was higher when compared to its' non moisture stressed daylength counterpart. The long-day wet seedlings initially had a larger root and shoot system as compared to the other stocktypes. Second year foliage exhibited no treatment differences for gwv and Pn response to PAR and VPD. All stocktypes had similar final morphological parameter values.

Attempts to test stocktypes at stable environmental conditions proved, at times, difficult. Potentially large measurement variation due to atmospheric environmental changes, and not stocktype effect, could result. Boundary line analysis, when used correctly and with sufficient data, offers a good stocktype assessment method which enables the isolation of a physiological response to one environmental variable. Three dimensional surface response technique was required to provide a clear conceptual representation of two primary environmental variables' influence on seedling physiological response.
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<tr>
<td>@</td>
<td>rate of change</td>
<td></td>
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<tr>
<td>( \psi x )</td>
<td>xylem water potential</td>
<td>MPa</td>
</tr>
<tr>
<td>Ci</td>
<td>internal carbon dioxide concentration</td>
<td>ppm</td>
</tr>
<tr>
<td>( CO_2 )</td>
<td>carbon dioxide</td>
<td>ppm</td>
</tr>
<tr>
<td>DIT</td>
<td>dormancy induction treatment</td>
<td></td>
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<tr>
<td>E</td>
<td>transpiration</td>
<td>mol m(^{-2}) s(^{-1})</td>
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<tr>
<td>g(_{wv} )</td>
<td>stomatal conductance</td>
<td>cm s(^{-1})</td>
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<td>Long-day dry</td>
<td></td>
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<tr>
<td>LDW</td>
<td>Long-day wet</td>
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<td>PAR</td>
<td>photosynthetically active radiation</td>
<td>mmol m(^{-2}) s(^{-1})</td>
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<tr>
<td>Pn</td>
<td>net photosynthesis</td>
<td>umol m(^{-2}) s(^{-1})</td>
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<tr>
<td>RGR</td>
<td>relative growth rate</td>
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<td>SDD</td>
<td>Short-day dry</td>
<td></td>
</tr>
<tr>
<td>SDW</td>
<td>Short-day wet</td>
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</tr>
<tr>
<td>VPD</td>
<td>vapour pressure deficit</td>
<td>kPa</td>
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INTRODUCTION

Successful reforestation demands an understanding of both the morphological and physiological responses of available species and stocktypes to field site environmental conditions. Cultural treatments, such as moisture stress and modified daylength, can be introduced at a reasonable cost in the greenhouse to produce stocktypes that may be better prepared for field planting. Reforestation site studies have shown stocktype differences in morphological development over a number of growing seasons (Arnott 1975, Wood 1983). Physiological response may be the basis for these differences. Few studies have been published which show the physiological response of pre-conditioned trees after field planting (Hobbs 1984, Seilor and Johnson 1985, Vance and Running 1985).

The goal of this ecophysiological research study was to characterize the response of western hemlock and western red cedar greenhouse cultural stocktypes to changing atmospheric environmental conditions before and after bud flush development. The two main gas exchange parameters to be assessed on a field site were; net photosynthesis (PN), because it is basic to primary production, and stomatal conductance (gwv) because it regulates water loss. One method used to study the effect of cultural treatments is to measure these indicators in response to different environmental conditions. Since there are various factors...
involved, it would be prudent to examine the seedling response to primary environmental variables.

The literature review examines the following areas: (1) and (2) response of gwv and Pn to major environmental variables, (3) influence of greenhouse cultural treatments, (4) use of boundary line analysis, (5) physiological response models, and (6) species background.
LITERATURE REVIEW

Stomatal Conductance

Stomata are the primary pathway for carbon dioxide (CO₂) transfer from the atmosphere into the mesophyll of needles. Stomatal conductance is a measure of microscopic pore opening which open and close in response to the environment and allow gas exchange. They are controlled by complex means and the exact mechanisms which operate the opening and closing are not fully understood (Kramer 1983). It is known that stomata respond to: light intensity, evaporative demand, temperature, internal CO₂ (Ci), and plant water status. These factors will each be discussed briefly.

Light Intensity

Stomatal conductance response to photosynthetically active radiation (PAR) generally exhibits a dramatic increase at low light levels (up to 0.1 mmol m⁻² s⁻¹), and then a slight increase with further PAR increases (which has also been described as a rectangular hyperbola shaped response) (Leverenz 1981, Beadle et al. 1985b, Higgins et al. 1987). Seasonally, this response may vary for conifers. During the summer, gwv for Pseudotsuga menziesii (Mirb.) Franco was similar to the above, but during the autumn and winter gwv showed insensitivity to changing PAR (Meinzer 1982b).
Currently there are two theories, direct and indirect response, describing the mechanism of gwv response to PAR (Sharkey and Ogawa 1987). In direct response, guard cells initiate stomatal movement via light absorbing pigments. In indirect response, as light levels increase and Pn begins, guard cells respond to decreased Ci levels. A review of this hypothesis will be discussed later on in the Ci section.

Observations of light responses in epidermal strips with stomata (Ogawa et al. 1978) and in isolated guard cell protoplasts (Zeiger 1983) have brought forth evidence that stomatal response to light is separate from the Ci level. In addition, photosynthesis system II inhibitors have been introduced which stabilized Ci, and have provided evidence that stomata are sensitive to light only (Sharkey and Raschke 1981). Sharkey and Ogawa (1987) concluded that experimental evidence thus far indicates that gwv response to light is independent of changes in Ci and that direct response to light can be very strong.

The magnitude of gwv response to PAR is dependent on the environment in which needles were developed. Sun needles (needles developed in full sunlight) could have up to 100% higher gwv response to increasing light intensity as compared to shade needles (needles developed in a shaded environment), e.g., Larix decidua Mill. (Leverenz and Jarvis 1979), and Picea sitchensis (Bong) Carr. (Benecke et al. 1981). It has also been observed that shade needles opened
at lower PAR, as compared to sun needles (Sharkey and Ogawa 1987).

Evaporative Demand

It has been well documented that gvw of many tree species decreases as vapour pressure deficit (VPD) increases (Benecke et al. 1981, Grossnickle and Blake 1986, Sandford and Jarvis 1986). This factor has been cited as the major determinant of gvw during most of the growing season (Beadle et al. 1985a). Vapour pressure deficit is the amount of atmospheric moisture deficit between needle and air. Vapour pressure deficit is based on air temperature and relative humidity around the needle, needle temperature, and relative humidity in the stomata antechamber.

There are two major, often interacting, control loops proposed for describing gvw response to VPD (Schulze 1986a). Firstly, the feedback response. Exposure of seedlings to increasing VPD initially causes transpiration to increase which in turn leads to decreases in xylem water potential ($\psi_x$). As $\psi_x$ continues to decrease, $\psi_x$ threshold is eventually surpassed and stomatal closure results. Feedback response is mostly initiated by root zone water resistance. Insufficient root water absorption to shoot transpiration balance produces a transpiration lag which is chiefly responsible for the midday stomatal depression (Tenhunen et al. 1987).
Secondly, in the feedforward concept, gwv responds to atmospheric drought by direct drying of guard and epidermal cells, even though $\psi_x$ is well above the turgor loss point. Stomatal responses to VPD changes have been shown to behave independent of changes in $\psi_x$ (Schulze and Kuppers 1979, Leverenz 1981, Osonubi and Davies 1980a). This was first demonstrated by using isolated epidermal strips (Lange et al. 1971), observed in detached leaves (Raschke 1970), and whole plants differing in ecological demands (Schulze et al. 1972). Characteristically, a feedforward response shows a gentle gwv decline to increasing evaporative demand.

**Temperature**

In a review on conifer water relations, Hinckley et al. (1978) found that the effect of air temperature on gwv of conifers is weak between 0 – 40°C with gwv increasing slightly as temperature increases. Beadle et al. (1985a, and b) found gwv was influenced when air temperature was below 10°C. Hall (1982) states that "the variation of gwv response to temperature may be due to measurements under unspecified and varying levels of humidity". However, if VPD is taken into account temperature does not need to be considered because temperature is included in its’ calculation (Kaufmann 1976, Running 1976). Nevertheless, if an overnight frost event precedes measurements, gwv values are significantly reduced and hence temperature must be considered (Delucia 1987, Delucia and Smith 1987).
Conifer research shows that as soil temperatures decrease, gwv decreases (Lopushinsky and Kaufmann 1984, Grossnickle and Blake 1985, Delucia 1986). Stomatal conductance decrease with soil temperature is thought to be due to a greater resistance to water flow through roots within the soil-plant-atmosphere continuum and greater water viscosity (Kaufmann 1976, Grossnickle 1988).

Carbon Dioxide Concentration

Stomata response to Ci is varied and subject to dispute. It has been suggested that changes in gwv to PAR is purely an indirect response, resulting from changes in Ci concentration produced by light-induced changes in Pn (Miedner and Mansfield 1968, Hasio 1973). However, research has shown that varying external CO₂ (hence modifying Ci) had little affect on gwv, e.g., Picea sitchensis (Beadle et al. 1979), Pinus sylvestris L. (Jarvis 1980), and Pseudotsuga menziesii (Meinzer 1982b). Further tests varying Ci conducted at different water stress levels (-0.5 to -2.5 MPa) showed that φx had an effect on gwv, but this was not mediated by Ci (Beadle et al. 1979). In addition, tests varying Ci at various light levels (0 to 1.3 mmol m⁻² s⁻¹) showed no apparent influence on gwv response to PAR (Jarvis 1980). The connection between Ci and gwv has not been rigorously established, and in view of information presented in the light intensity section, gwv response to PAR appears
to be a direct response. Therefore, with certain conifers, there is no evidence for a Ci mediated influence on gwv.

**Plant Water Status**

It has been well documented that gwv tends to decrease when plants are subjected to drought (Kaufmann 1979, Pezeshki and Chambers 1986, Schulte and Marshall 1983). The exact relationship between gwv and $\phi_x$ has been characterized in two distinct ways for many tree species. The first consists of two phases with a threshold potential above which there is little change in gwv, but below which gwv decreases rapidly, e.g., *Picea sitchensis* (Beadle et al. 1979), *Pinus banksiana* Lamb. (Grossnickle and Blake 1986). The second has the appearance of a progressive negative feedback system in which gwv decreases gently with decreasing $\phi_x$, e.g., *Picea mariana* (Mill.) B.S.P., and *P. glauca* (Grossnickle and Blake 1986), and *Pinus contorta* Dougl. (Dykstra 1974).

In order to reconcile the two conflicting models of responses, Hall (1982) suggests that the threshold model reflects short-term stomata response (minutes/hours), and the progressive model reflects a long-term response (days). It has been documented that gwv exhibited threshold type models when the foliage of several species was rapidly disturbed by detaching them (Hall and Hoffman 1976). Progressive models were reported when measurements of predawn water potential taken over the growing season were
plotted against mean daily gvw (Running et al. 1975), and maximum morning gvw (Running 1980). However Grossnickle and Blake (1986) reported both a threshold and a progressive model for species tested over the growing season, and hence feel that these response types may also be inherent.

The mechanics of the plant water status influence on gvw begins with soil water status. In most research it is assumed that the soil water status control is exerted through leaf water status. Evidence is now accumulating on agricultural plants (Gollan et al. 1985, Turner et al. 1985, Schulze 1986b) showing that gvw correlates with soil water supply but not with leaf water status. The mechanism by which the root water status controls gvw is not known but Schulze (1986b) has hypothesized that stomata may respond directly to a signal from the roots under conditions of drought. The signal is thought to be related to root metabolic activity, which may be related to cytokinin production, which tend to open stomata and counteract the effects of ABA in leaves.

The amount of transpiring area as compared to absorbing area can influence stomatal behavior. Comparing gvw diurnal response differences between western hemlock and Douglas-fir, Running (1976) suggests that shoot to root ratio, and/or differing root absorption capabilities, were the causes. A study by Pereira and Kozlowski (1977) points to the counteracting effects of extensive leaf area on gvw.
Photosynthesis

Since carbon assimilation is basic to primary production, a model developed for Pn was constructed to compare stocktypes. It is known that Pn responds to the following factors: light intensity, evaporative demand and plant water status, gwv, temperature, and Ci.

Light Intensity

A major environmental variable regulating Pn is PAR (Beadle et al. 1985b). Photosynthetic rate usually exhibits a hyperbolic response to PAR which is similar to gwv response to PAR. Characteristically, this is seen as a rapid curvilinear increase up to a light saturation level (0.4 - 0.8 mmol m\(^{-2}\) s\(^{-1}\)), and then levels off or increases slightly to full sunlight (2.2 mmol m\(^{-2}\) s\(^{-1}\)) e.g., *Picea sitchensis* (Watts et al. 1978), *Larix decidua* (Benecke et al. 1981), and *Pinus sylvestris* (Beadle et al. 1985a). However, for a forest canopy, Pn versus PAR is a near linear relationship due to mutual shading and the inability of foliage in the lower canopy levels to reach light saturation (Beadle et al. 1985b).

The initial phase of Pn is the trapping of light energy. Photosynthesis is a two step process; a dark reaction and a light reaction. The light reaction involves electron removal from water, release of oxygen, and a reduction process to form pyridine nucleotide (NADH or NADPH), and adenosine triphosphate (ATP). These stable high
energy compounds are used in the dark reaction to reduce CO$_2$ via the Calvin cycle (Salisbury and Ross 1985). Up to a level of light saturation, Pn is limited directly by photochemical energy supply; thereafter, the dark reaction capability to fix CO$_2$ becomes the limiting factor.

Foliage developed in shaded habitats have a lower capacity for Pn than foliage developed in habitats of high solar radiation. (Leverenz and Jarvis 1979, Benecke et al. 1981). These differences in capacity are associated with differences in leaf and stomata anatomy (Schulze and Hall 1982).

**Evaporative Demand and Plant Moisture Status**

Tree species generally show a constant linear decline in Pn, or feedforward response, to increasing VPD e.g., *Pseudotsuga menziesii* (Grieu et al. 1988, Meinzer 1982a), *Pinus contorta* and *Picea sitchensis* (Sandford and Jarvis 1986) *Podocarpus oleifolius* Buchh. and *P. rospigliosii* Pilg. (Meinzer et al. 1984). The same linear response is found for Pn to decreasing soil moisture (Grossnickle et al. 1990a).

In earlier reports it has been assumed that Pn decrease to increasing VPD was largely gwv related (Hasio 1973, Mederski et al. 1975) However, evidence is now gathering which indicates that this response is non stomatal. Many recent studies have shown that Ci does not decline with gwv decrease due to VPD (Briggs et al. 1986, Wong et al. 1985). Sharkey (1984), investigating Pn decline to increasing VPD
showed that by measuring Ci directly, the decrease in Pn occurred at the mesophyll and was not due to the stomata. The author suggested that increased transpiration with higher VPD induced water deficits at the sites of evaporation, and this inhibits Pn. This hypothesis explains in part why soil and atmospheric drought have a similar affect on Pn.

Under moderate environmental conditions, when stomatal and non stomatal limitations to Pn are compared, the stomatal limitation is often quite small. Teskey et al. (1986) estimated that stomatal limitations accounted for 20-30% of the Pn decline in Pinus taeda L. subject to various environmental conditions.

Shoot to root ratios can influence the water relation balance of seedlings, and hence influence the foliage development through the effects of $\Psi$ on leaf expansion. Interwoven through this is the proper balance of needle area available for Pn, and the opportunity to photosynthesize free from water stress. Schulze (1986b), states that at the whole plant level, plants can regulate carbon partitioning to roots in response to water relations, but the underlying mechanisms are obscure.

Stomatal Conductance

Until as late as the early 1970's, it was thought that gwv largely regulated Pn by decreasing Ci levels. This was partially a result of the close correlation found between
gwv and Pn (v. d. Dreissche 1971) and no direct methods of measuring Ci. More recently, a number of studies have shown that a variable amount of Pn can be observed for a given gwv reading (Leverenz 1981, Beadle et al. 1985a), and that changing VPD has a direct affect on the photosynthetic apparatus at the mesophyll (Sharkey 1984).

Photosynthesis and gwv respond to PAR and VPD independently of each other except under extreme conditions (i.e. at low PAR, and at high VPD) (Kuppers and Schulze 1985, Beadle et al. 1985a). The rate of Pn tends to be proportional to gwv only at low gwv, because it is the strongest limitation.

It appears that too much emphasis is placed on water use efficiency and what it may indicate. On a reforestation site, if one particular plant is efficient with water use, other competing plants will use that available water to benefit their own growth. A plant that can tolerate stress and maintain physiological activity as water deficits increase, will grow more than seedlings that avoid stress by closing their stomata. Furthermore, during a period of drought, only stress tolerant seedlings will be able to develop an extensive root system and thereby increase water uptake (Livingston and Black 1988). In a study done with 3 coniferous species, Grieu et al. (1988) found drought resistant *Pseudotsuga macrocarpa* exhibited the least conservative water use efficiency in response to soil and
atmospheric drought as compared to *P. menziesii*, and *Cedrus atlantica*.

Stomatal behavior has been recently described operating in relation to an "optimal" theory (Farquhar et al. 1980) which suggests stomata function to minimize water loss for a given amount of carbon gain. In other words, stomata behave in order to maintain a constant *Pn* and transpiration (*E*) to changes (∂) in gwv ratio (∂*Pn*/∂gwv / ∂*E*/∂gwv) over a variety of environmental conditions within the operational range of plants. This was demonstrated by using daily values in controlled environments to humidity changes by Farquhar et al. (1980) and to humidity and temperature changes by Hall and Schulze (1980). However, Williams (1983), working in the field, and Fites and Teskey (1988), working in the laboratory and field, showed that stomatal behavior generally did not conform to the above optimal behavior hypothesis. Fites and Teskey, studying *Pinus teada*, found that the gain ratio increased with VPD and suggested that stomata function in response to VPD, but that *Pn* may be influenced by non stomatal limitations and hence alter the gain ratio. In another study, Meinzer et al. (1984) working with tropical species in controlled laboratories, found that *Podocarpus oleifolius* exhibited a constant gain ratio, but *Podocarpus rospiglosii* did not remain constant.
Temperature

Leaf temperature response curve for $P_n$ characteristically exhibits an inverted 'U' with a broad plateau in the middle region, e.g. between 15–25°C. $Pseudotsuga$ menziesii (Meinzer 1982c), 10–25°C for $Picea$ engelmannii Parry ex Engelm. (Delucia and Smith 1987) and 10–25°C for $Pinus$ sylvestris (Kuppers and Schulze 1985). It has been observed that optimum temperature and size of plateau for $P_n$ is dependent on climatic preconditioning of the plant material, and can shift in response to seasonal changes (Beadle et al. 1985a, Delucia and Smith 1987).

Low $P_n$ rates were highly correlated with low minimum soil temperature for $Picea$ engelmannii (Delucia and Smith 1987). Delucia (1986) working in a controlled environment, found that root temperature had no effect on $P_n$ between 10 to 20°C. However, gwv and $P_n$ declined dramatically below 8°C. Jurik et al. (1988), studying springtime recovery of $Pinus$ strobus L., observed the same response, and also found that $P_n$ was more highly correlated with soil temperature at a depth of 30 cm than with air temperature, or soil temperature at more shallow depths. It has been suggested that although gwv decreases with $P_n$ at low temperatures the decline in $P_n$ is due to non stomatal limitations because $C_i$ was unchanged (Delucia 1986). At the biochemical level, it has been found that low needle temperatures reduce $P_n$ because of reduced activity of the ribulose biphosphate carboxylase–oxygenase (Rubisco) enzyme and the capacity for
electron transport, and high temperatures reduce electron transport capacity and increase the rates of photorespiration causing Pn to decline (Farquhar and Sharkey 1982).

**Carbon Dioxide Concentration**

Carbon dioxide is one of three basic inputs for photosynthesis, the others being water and light. The CO₂ pathway from the atmosphere to utilization in the chloroplast is restricted due to physical and chemical limitations. According to laws governing diffusion, if there are limitations, larger gradients allow for faster rates of transfer.

Photosynthesis can almost always be increased by raising the level of CO₂ in the atmosphere if there are no other serious limitations to normal growth (Tinus 1974). Adding CO₂ not only increases the rate of flow by diffusion but also suppresses photorespiration in C₃ plants at CO₂ concentrations above 1000 p.p.m. (Tinus 1974, Salisbury and Ross 1985). This higher rate of Pn is accomplished with no change in water consumption, thus improving water use efficiency.

**Greenhouse Cultural Treatments**

Evidence is accumulating which indicates the use of certain seedling stocktypes are better suited to specific reforestation sites (Arnott 1975, Hobbs 1984, Arnott and
Burdett 1988). Current greenhouse container nurseries provide greater control of seedling physiology as compared to the outdoor bareroot nursery. Potential for control of stocktype performance can be realized only by a thorough understanding of seedling response to environmental cues, and the procedures for providing them (Tinus 1981).

In order to improve field planting success and early growth, cultural treatments are applied to seedlings to induce dormancy and/or harden seedlings. Two economically viable methods, daylength and moisture stress, are being used increasingly by nurseries to meet morphological guidelines. However, there is little information on how nursery cultural practices affect seedling physiology and subsequent development (Duryea 1985).

**Daylength**

Growth and development for many tree species is regulated by photoperiod. Extended photoperiods have been shown to promote increased height and diameter growth and dry weight while reduced photoperiod have been shown to decrease these parameters (Arnott and Mitchell 1981). Short-day causes rapid cessation of shoot growth and stimulated bud development, whereas free growth continues under long-day (O'Reilly et al. 1989b). Research into examining seedling quality of western hemlock stocktypes, treated with various daylength and moisture stress DIT, found short-day seedlings superior (Grossnickle et al. 1990a). Short-day
seedlings had the greatest cold tolerance, highest root growth capacity at 5°C, highest osmotic potential, and highest Pn at high soil moisture stress conditions. In field plantations in the interior of B.C. and Alberta, short-day treatment of *Picea glauca* (Moench) Voss and *Pinus contorta* showed higher survival and more rapid growth initiation in the spring (Silim et al. 1989).

**Moisture Stress**

One of the first investigations into the effects of moisture stress, as a preconditioning cultural treatment, on Pn and gwv response was on *Pinus taeda* seedlings (Seiler and Johnson 1985). The study revealed that moisture stressed seedlings were able to maintain Pn to much lower needle water potentials than control treated seedlings. This response was thought to be partially attributed to the significant 0.45 MPa decrease in needle osmotic potential.

On a study using control and prestressed sunflower plants, Matthews and Boyer (1984) found that Pn response to increasing PAR was the same at high leaf water potential, but at low (stressed) leaf water potential, Pn of moisture stressed plants was as much as 100% higher than control plants. In addition, they recorded higher gwv for moisture stressed plants as compared to control plants. It was concluded that the major contributor to Pn acclimation of moisture stressed plants was non stomatal acclimation. Matthews and Boyer (1984) also brought forth evidence that
water stress pre-conditioning provided cytoplasmic protection of chloroplast.

**Boundary Line Analysis**

Attempts to correlate gwv values to particular environmental variables collected in the field have met with limited success because gwv is simultaneously affected by a number of environmental variables (Jarvis 1976), and includes data which show diurnal hysteresis. Hysteresis generally develops after midpoint of the day, showing reduced physiological values for the same environmental conditions (Helms 1970, Livingston and Black 1987). Webb (1972), also attributes the resulting scatter diagram to errors of measurement, variability of the biological material, and the overall variation caused by other interacting factors.

If much data (i.e. Pn) has been collected from a wide range of conditions a scatter diagram will result. The line of best performance will be evident when limits of response are reached, but will not occur if there is no cause-and-effect relationship. A boundary line represents the highest values of a cause factor under conditions of an experiment. Arguments for existence of a boundary line are biological rather than mathematical, because of all the contributing variables, and factors.

Recognition of this line and calculation of its equation may vary. To best describe the data some
researchers used hand-drawn lines connecting the highest values (Goldstein et al. 1985, Livingston and Black 1987). This method places a line so it encloses all points which may include errors, thereby allowing for overestimation. Others developed regression equations using best data (Webb 1972, Chambers et al. 1985, Grossnickle and Arnott 1990). This method derives a line by a logical process which allows some deviation above and below it, minimizing the contribution of error. However, there are no means of calculating a true estimate of real error. The inability to do this is not a serious problem if boundary line is regarded simply as an analytical device requiring intelligent interpretation (Webb 1972).

**Physiological Response Models**

Quantitative description of a physiological function to one or multiple environmental conditions summarizes complex processes for understanding and comparison. Mathematical models of photosynthesis and plant water loss control are a major objective in testing hypothesis or comparing species, genotypes, and stocktypes. Models of biological systems are works of mathematics and art, and only partially simulate reality (Passioura 1973).

Modelling of physiology can be divided into two main categories; deterministic (mechanistic); and predictive (phenomenological). Deterministic models include a variety of studies that are designed to quantify the underlying
biochemical and biophysical processes involved in physiological functions, whereas phenomenological models are involved with empirical studies of physiological behavior in relation to observed environmental conditions (Kaufmann 1982b). Both contribute to understanding the process investigated.

According to Hall (1982) a mechanistic model of gwv response to the environment would require adequate descriptions of the following submodels: (1) mechanics of guard cell wall deformation and physical relations with adjacent cells; (2) biochemistry and biophysics of osmotic potential control within guard cells and relations with other epidermal cells; and (3) characteristics of water solute, and hormonal transport within leaves and throughout plants. Hall continues by saying that a mechanistic model of stomatal response to environment would be cumbersome and highly unreliable.

Predictive models integrate a series of independent steady state environmental conditions. Stomatal conductance response model might include the following independent variables; PAR, VPD, temperature, plant water status, and Ci. The simplest approach is by using multiple correlation statistics which highlight relationships and measure their strength. Hinckley et al. (1975), testing both a multiple and single variable equation found that the multiple equation provided poor estimates for leaf surface resistance. It was stated that caution should be used when
empirical multivariate models are used to determine the contribution of a single variable from natural environments.

Research with predictive models can be strengthened considerably by developing phenomenological models using controlled environments, or by being based on boundary line analysis using least squares regression analysis to obtain input parameters (Hall 1982). The main driving environmental variables for the physiological process of interest must first be identified. To elucidate the main driving variables many studies on various tree species have been studied in controlled environments (Meinzer 1982a, and b, Higgins et al. 1987). Physiological response is recorded in relation to a range of this environmental variable and a regression equation is derived using environmental variable transformations.

Three-dimensional representations to 2 main driving environmental variables were first presented by joining a number of main intersections within the bounds of the environmental matrix. Earliest research presentations of these 3-D graphs are by Hinckley et al. (1975) showing *Quercus alba* L. stomatal resistance to VPD and predawn water potential, Pereira and Kozlowski (1977) showing stomatal resistance and shoot water potential to PAR and temperature, and Osonubi and Davies (1980b) showing *Pn* and *gWv* to PAR and foliage temperature. Studies showing some of the first least square regression calculated 3-D models were Thompson and Hinckley (1977), exhibiting leaf surface resistance and
xylem pressure potential to predawn xylem pressure potential and VPD for *Quercus alba*; Meinzer (1982c) water use efficiency to PAR and VPD for *Pseudotsuga menziesii*; and Grossnickle and Reid (1985) showing gwv to light intensity and VPD, and showing gwv to xylem water potential and VPD. These regression based models have the distinct advantage of providing an equation for predictions within bounds of the environmental range studied.

**Species Background**

**Western Hemlock** (*Tsuga heterophylla* (Raf.) Sarg.)

An important coastal timber species, western hemlock grows along the Pacific coast from Alaska and British Columbia (B.C.) to northwestern California. It grows east to the western slope of the Continental Divide. Best stands are found in the humid coastal regions of B.C., Washington, Oregon, and Alaska where frequent fog and rain provide moisture during the growing season. Western hemlock occurs on a wide variety of soil types from sandstone to igneous rock material. Western hemlock is usually a secondary species growing in association with *Picea sitchensis* and *Pseudotsuga menziesii*, but sometimes dominates and occasionally grows in pure stands (Fowells 1965).

Silvicultural attributes which make western hemlock a desirable tree species are as follows; it is rated very shade tolerant, releases well after long periods of suppression, and has good regeneration potential after using
a wide range of harvest methods. In B.C., approximately 5 million container-grown western hemlock seedlings were planted in 1988-1989 (O'Reilly et al. 1989a).

Western Red Cedar (Thuja plicata Donn ex D. Don)

Western red cedar grows from the coastal regions of southern Alaska, south through the coastal ranges of B.C. through western Washington and Oregon to northern California. It grows inland to the Rocky Mountains, confined to regions having abundant precipitation and high humidity. It seldom occurs in pure stands, and then only over small areas. It is often associated with Tsuga heterophylla, Picea sitchensis, Pseudotsuga menziesii, and true firs. In interior areas, it grows with Pinus monticola Doug. ex D. Don, Larix occidentalis Nutt., Pinus contorta, Picea engelmannii and Abies lasiocarpa (Hook.) Nutt. (Fowells 1965).

The volume of mature western red cedar in B.C. is estimated at 824 million cubic meters. This represents 3.5% and 8.5% of the total mature timber volume of Canada and B.C., respectively (Quenet and Magdanz 1988). Silvicultural attributes which make western red cedar a desirable tree species are; low susceptibility to root rot and insect pests, shade tolerance, and tolerance to planting in mild frost pockets. In 1987, approximately 6.4 million seedlings were planted in the Vancouver Forest Region (Curran and Dunsworth 1988).
RESEARCH HYPOTHESIS AND OBJECTIVES

After reviewing the literature, it was decided to limit the number of environmental factors varied to two. It has been shown that as soil water status decreases, physiological parameters response lines show a similar but progressive decrease to changing VPD and PAR (Turner et al. 1985). Many researchers have found that when soil moisture is not limiting, PAR and VPD are the primary environmental factors that effect gwv and Pn on a field site (Kaufmann 1982b, Meinzer 1982c, Grossnickle and Reid 1985, Landsberg 1986).

Other important factors such as soil moisture, temperature, and Ci would be considered secondary factors and monitored closely or controlled so that Pn and gwv data would not be adversely influenced. High soil moisture level would be maintained by watering regularly, particularly the evening before measurements. Temperature would be recorded with each physiological measurement, and incorporated into the VPD variable. No data would be used if air temperature was less than 0°C the evening prior to measurements. Internal CO₂ would be calculated for all physiological measurements and values above or 100 ppm below ambient would be discarded.

It was hypothesized that western hemlock and western red cedar seedling stocktypes will have different
physiological response patterns over a range of PAR and VPD on a site where soil moisture is controlled on both:

a) first year foliage (greenhouse grown foliage), and
b) fully expanded second year foliage (field site grown foliage).

The following is a brief listing of research objectives. They are expanded in more detail in the next section.

1) Examine the change in selected morphological attributes over one growing season.
2) Compile statistical comparison between stocktypes at stable environmental conditions once a month for the growing season.
3) Examine the 2-D relationship between Pn response to increasing PAR and VPD.
4) Examine the 2-D relationship between gwv response to increasing VPD and PAR.
5) Characterize the 3-D response of Pn to simultaneously changing PAR and VPD levels.
6) Characterize the 3-D response of gwv to simultaneously changing PAR and VPD levels.
MATERIALS AND METHODS

Plant Material

Western hemlock (Tsuga heterophylla (Raf.) Sarg.) seed (British Columbia Forest Service (BCFS) Registered Seedlot no. 3906; Lat. 48° 55' N, Long. 123° 55' W; elevation 340m) was stratified at 1°C for 4 weeks before sowing. Western red cedar (Thuja plicata Donn) seed (BCFS Registered Seedlot no. 7853; Lat. 48° 50' N, Long. 124° 00' W; elevation 525m) was soaked in tap water for thirty-six hours prior to sowing. Both species were sown on March 2nd, 1987 in BC/CFS 313A styroblocks (Beaver Plastics Ltd., Edmonton, Alta.) in a 3:1 mixture of peat and vermiculite with dolomite lime added to adjust the pH to 5.0 and coarse sand as seed cover.

Seedlings were grown at the Pacific Forestry Centre, Victoria, B.C. (Lat. 48° 28' N). The greenhouse environment was maintained at a day/night temperature of 21/18°C, 50% relative humidity, and natural light supplemented at night with high pressure sodium vapor lamps (i.e. 6 μmol m⁻² s⁻¹) to provide a 16 hour photoperiod. Seedlings were watered and fertilized (i.e. 20-20-20 NPK with micronutrients) twice weekly (500 mg l⁻¹), and biweekly with the heptahydrate form of ferrous sulphate (155 mg l⁻¹).

Seedlings were grown under the above greenhouse regime until July 20, 1987 when mean seedling shoot height had reached 15.8 and 16.3 cm for western hemlock and western red cedar, respectively. At this point, one of four dormancy
induction treatments (DIT) were applied to one fourth of the seedling population for each species. The dormancy treatments were as follows:

1. Long-day wet (LDW): (control) seedlings continued to receive the above greenhouse regime until the end of August.

2. Long-day dry (LDD): seedlings had the extended photoperiod as in the above stated greenhouse regime, but on July 20, 1987 a moisture stress treatment was initiated.

3. Short-day wet (SDW): seedlings continued to receive the above stated watering and fertilization regime until the end of August (as in 1), but had photoperiod reduced to eight hours on August 1, 1987.

4. Short-day dry (SDD): seedlings, on July 20, 1987 had the moisture stress treatment initiated and the photoperiod reduced to eight hours on August 1, 1987.

All dormancy induction treatments were concluded on August 29, 1987, after which regular watering, fall fertilization, temperature, and natural daylength regimes were implemented. Fertilizer (10-51-16 NPK with micronutrients) was applied (500 mg l\(^{-1}\)) weekly until November, and biweekly thereafter. Temperatures (day/night) were set at 20/10°C until September 15th, 17/8°C until October 10th, 15/5°C until October 15th, 13/4°C until November 11th, 10/3°C until November 18th, and 8/0°C until
seedlings were put into cold storage (2°C) on January 11th, 1988.

In the moisture stress treatment, styroblocks were allowed to dry down to approximately 2.63 kg below their saturated weight before rewatering with fertilizer solution to saturation, and repeating the drying cycle. Average predawn and noon xylem pressure readings for each species at the end of drying cycles were -0.3 and -0.7 MPa for western hemlock and -0.4 and -1.0 MPa for western red cedar, respectively. Seedlings were subjected to six drying cycles. Many western hemlock shoots were wilted by the afternoon of the last day of each drying cycle. Thus western hemlock shoot wilt was used as the indicator to end a drying cycle.

Treatment statistical design was a modified Latin Square with DIT randomly assigned to four bench positions. The two species were randomly assigned to opposite sides of each treatment block position. Styroblocks within a DIT were rotated every six weeks. No effect of bench location was detected.

From January 15 to February 20, 1988 seedlings were tested with an integrated stock quality assessment procedure. These tests were organized into two areas called material attributes (direct measurements), and performance attributes (whole seedling response), as defined by Ritchie (1984). Material attribute tests included nutrition, morphology (height, diameter, shoot and root dry weights, foliage and root surface areas, related ratios, and needle
primordia development), pressure-volume analysis, soluble sugar analysis, and seedling water movement. Performance attribute tests included root growth capacity (soil pot, 5 and 22°C hydroponic test), frost hardiness, low temperature response, and drought stress response. Stock quality assessment test results for western hemlock are described in Grossnickle et al. (1990a), and for western red cedar in Grossnickle et al. (1988).

Field Site Conditions

The field site was located at University of British Columbia Forest Nursery, on the university campus, Vancouver, British Columbia, Canada (Lat. 49° 15' N, Long. 123° 15' W). An area 20m x 20m was selected which had been previously cultivated, but was left fallow in 1987. Elevation of the area is 25m above sea level, with a gentle south facing slope. The site was roto-tilled in February 1988 prior to field planting. Plow layer soil texture was a sandy-loam with 5.5 % organic matter, and it was moderately well drained (appendix 1A).

Soil nutrient analysis taken in March 1988 showed macronutrient deficiencies in nitrogen and sulfur, and pH of 5.8 (appendix 1a). A 20-20-20 granulated fertilizer with micronutrients was hand broadcasted and irrigated into the site in March 1988. Soil nutrient analysis in July 1988 showed satisfactory nitrogen levels, but low sulfur and potassium levels (appendix 1B).
Seedlings were planted March 17-18, 1988 in a randomized block design with repeated replicates (appendix 2). Two blocks were randomly assigned to each species. Seedlings from each DIT (4) were represented in 5 randomly selected rows for a total of 20 rows per block with 20 seedlings planted in a 0.5m x 0.5m spacing per row. A total of 200 seedlings from each species/DIT were field planted.

A four sprinkler head irrigation system was set up to control soil moisture deficit. The site was watered regularly, particularly on the days before recording of seedling physiological measurements. In addition plant competition was controlled by regularly removing all vegetation from the site mechanically. A soil moisture retention curve was developed for the site to allow soil moisture potential calculations (appendix 3).

**Morphological Assessment**

Seedlings from each species/DIT (n=25) were measured prior to field planting. Morphological parameters assessed include (1) shoot height, (2) root collar diameter, (3) foliage surface area, (4) root surface area, (5) shoot dry weight, (6) root dry weight, (7 & (8) shoot to root ratio by dry weight and by surface area and, (9) seedling water balance ratio (i.e. shoot dry weight/(root dry weight x root collar diameter)). Dry weights were assessed after 48 hours at 65°C. Needle and root area measurements were determined using a Li-3000 (Li-Cor Inc., Lincoln, Nebraska) area meter.
To assess growth after one growing season one randomly selected seedling from each row was planted in buried cylindrical (30 cm diameter, 30 cm length) porous felt root bags (San Jacinto Capital Corp., Houston, Texas). This facilitated removal of 10 seedlings from each DIT 8 months after planting to determine root and shoot development. Further discussion of the root analysis technique can be found in Grossnickle and Reid (1983). Except for root and foliage surface area, the same parameters as the preplant harvest were measured. The following parameters were also measured (1) needle damage index, (2) root dry weight in container plug, and (3) root dry weight outside container plug. Needle damage was quantified by visual assessment of percent needles green where: 1=100%, 2=90-99%, 3=75-89%, 4=50-74%, 5=25-49%, 6=1-24%, and 7=0% green needles.

The two species were analyzed separately. Data at the beginning of the growing season was analyzed using a one way ANOVA and Waller-Duncan mean separation test. Due to blocking, end of the growing season data was analyzed as a two-way ANOVA. Experimental error was not significant, and was combined with the sampling error to form a new mean square error term. The site was plowed and appeared uniform but there was gentle slope hence the blocking. The F-value calculated showed that blocking was not significant (p=0.05).
Measurement of Site Environmental Conditions

When physiological measurements were collected, soil samples were collected at 1200h each day. Soil moisture content was determined gravimetrically, and water potentials were determined from soil retention curves. If the soil water potential was found limiting (below -0.5 MPa), the physiological data for that day were discarded. Photosynthetically active radiation (PAR), and vapour pressure deficit (VPD) were taken simultaneously with net photosynthesis (Pn) and foliage conductance (gwv) readings using a LI-6200 CO₂ porometer (Li-Cor, Inc.). The PAR values were taken with a LI-1905-1 (Li-Cor, Inc.) quantum sensor located on the porometer and was oriented perpendicular to incoming solar radiation at all times. Measurements of VPD were derived by the porometer from chamber air temperature, chamber relative humidity, needle temperature and assumed 100% relative humidity in the stomata antechamber.

Monthly Measurement of Replicated Physiological Data at Standard Environmental Conditions

Once each month during the growing season, April to September, a one day assessment of physiological data was collected for each species. Data collection consisted of predawn xylem water potential, then pressure chamber and porometer measurements taken from 0830h to 1000h and 1300h to 1430h. This was done in order to collect 10 replicates from each DIT during assumed periods of least (i.e. 0830-
1000h) and greatest (i.e. 1300-1430h) physiological stress. Days which were selected had consistent light conditions during collection periods (i.e. clear or constant cloud cover). In addition, soil temperature (-10 cm) at 12h from two locations were recorded using a soil temperature probe.

Shoot water potential ($\psi_w$) was measured on individual branch tips of seedlings using a pressure chamber (Soil Moisture Corp. Model 3005) according to Ritchie and Hinckley (1975). Shoot water potential was measured on 10 seedlings selected randomly from the entire population. Net photosynthesis and gwv were measured with a Li-6200 (Li-Cor Inc.) portable porometer with a 1/4 l (Li-6200-13) sample chamber. Conductance values refer to water vapour, and were calculated from transpiration rate and VPD (Schulze and Hall 1982). For each sampling day, porometer data were collected from 10 preselected seedlings from each DIT. Needles were trimmed from the base of the twig to allow for closure of the gas exchange cuvette. In April and May, porometer samples were from first year foliage, while June through September, samples were from second year foliage. At the end of each data collection period, porometer samples were clipped. Total foliage surface area was determined using an Li-3100 area meter (Li-Cor Inc.), multiplied by 2 for western hemlock, and 2.4 for western red cedar and then porometer measurements were recalculated to represent total surface area. Both sides were included in the calculations because both sides photosynthesize. The value of 2.4 was
determined, after repeated measurements, to best approximate total surface area (including width) of western red cedar.

Morning and afternoon physiological data (i.e. Pn, gwv and ψx) were analyzed with analysis of variance and significant differences between DIT determined by Waller-Duncan mean separation test (Steele and Torrie 1980). Morning and afternoon environmental data were summarized for PAR and VPD. The changes over the season can be observed, but not compared statistically.

**Physiological Response to One Environmental Variable**

Twenty to 30 randomly selected seedlings from each DIT were prepared and marked from the field planted population. The selected seedlings were randomly measured for Pn and gwv over a range of PAR (0 to full sunlight) and VPD (low to the highest possible on the site). Data collection was environmentally driven, by trying to collect data across the PAR x VPD matrix. Special attention was given to selecting hard to obtain PAR x VPD (i.e. high PAR x low VPD and low PAR x high VPD).

To help produce a range of environmental conditions, four 1.2m x 2.4m x 0.6m (w x 1 x h) shade racks were constructed. Two with 33% shade cloth and two with 66% shade cloth were used. Racks were placed over a group of seedlings in advance and measurements were not taken until one half hour after placement.
Second year foliage response is defined as physiological measurements on fully developed second year foliage found on the same field site. Treatment names remain the same to indicate greenhouse treatment history. Data was collected and analyzed for first year foliage (April and May) and for fully developed second year foliage (July and August). Most data were collected over a 3-4 week time period with 125-150 data points obtained for each DIT. To avoid a hysteresis effect, data measurement was restricted from dawn to 1430h.

Since data were collected over a wide range of atmospheric environmental conditions, a boundary line analysis procedure was used to determine seedlings maximum Pn and gwv response to PAR and VPD conditions. This was then used to compare between different DIT. The boundary line analysis concept states that a scatter diagram's upper limit of Pn or gwv measurements (i.e. dependent variable) in response to an environmental variable (i.e. independent), known to limit the dependent variable, indicates the best physiological response to that particular environmental variable when other conditions are not limiting (Jarvis 1976). This concept is valid as long as the two variables being examined have sufficient data to describe their relationship.

Physiological (i.e. Pn or gwv) data in response to an environmental variable was systematically taken from the upper region or layer of a scatter diagram, resulting in a
maximum physiological response data set for regression analysis (Webb 1972). This procedure also reduced any physiological response overestimation to a single environmental variable described by Chambers et al. (1985). In the systematic collection procedure, the independent variable was partitioned into segments with the greatest 3 to 4 physiological measurements from that segment included in the maximum response data set (Grossnickle and Arnott 1990). The maximum response data set included 18 to 23 percent of the entire data set. After some independent variable transformations, regression response models were then tested and compared by selecting one that had each parameter(s) significantly contributing to the model (p=0.05), and having the highest R-squared (Kleinbaum et al. 1988). A total of 64 boundary line response relationships were produced (2 species x 4 DIT x 2 foliage types x 4 relationships).

Physiological Response to Two Independent Environmental Variables

Response surfaces in a 3-dimensional (3-D) coordinate system were generated using an empirical rather than mechanistic approach. The relationship between (1) Pn to PAR and VPD, and (2) gwv to PAR and VPD were analyzed using multivariate linear least squares regression. The same data base used to generate the 2-dimensional (2-D) boundary line response model were used for producing 3-D response surface
models. All data were used except for gwv data collected at relative humidities greater than 80%. This restriction is recommended by the manufacturer of the porometer (Li-Cor Inc.) since calculations can be unreliable (i.e. low gwv).

To best describe the physiological response to two environmental variables, a phenomenological model was developed. It was necessary to transform the independent variables (PAR, VPD) into inverse, natural logarithm, and quadratic values. Various models largely based on the 2-D responses generated were tested. Models were evaluated based on partial F-test on each component of the model. Models with all components significantly contributing (p = 0.05), and with the highest R-square, were considered the best. To compare DIT for a specific foliage type/species combination, the same model was used to generate each DIT. If one component of one of the DIT models was not significant (p=0.05), it was kept for comparison value. A total of 32 response surface models (2 species x 2 foliage types x 4 DIT x 2 relationships) were produced.
RESULTS
WESTERN HEMLOCK

Environmental Conditions

Soil water potentials were only lower than -0.10 MPa three times and never lower than -0.37 MPa during the measurement season (Table 1). Predawn xylem water potentials were measured monthly and were never lower than -.64 MPa (Table 2). In April and May measurement period, soil temperatures (-10 cm) were between 8 - 15°C, and were between 13 - 25°C for the rest of the measurement season. Morphology data showed no blocking effect, or blocking x treatment interaction at p=0.05 (unreported data). Thus experimental and sampling errors were combined for a new data analysis error term.

Preplant Morphology

Seedlings in the LDW DIT had the largest overall shoot system with a greater height, diameter, and shoot dry weight (Table 3). Root dry weight and diameter were greater in non stressed DIT. Short-day DIT had a lower shoot to root ratio and a better seedling water balance ratio than long-day DIT. Long-day wet seedlings had significantly more needle surface area than LDD which had significantly more than short-day seedlings. Non stressed seedlings had a greater root surface area as compared to water stressed seedlings.
TABLE 1. Soil water potential on moisture-controlled field site.

<table>
<thead>
<tr>
<th>Date Sampled (1988)</th>
<th>Soil Water Potential (- MPa)</th>
<th>Date Sampled (1988)</th>
<th>Soil Water Potential (- MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>April 21</td>
<td>0.05</td>
<td>July 6</td>
<td>0.07</td>
</tr>
<tr>
<td>30</td>
<td>0.06</td>
<td>18</td>
<td>0.09</td>
</tr>
<tr>
<td>May 5</td>
<td>0.08</td>
<td>19</td>
<td>0.36</td>
</tr>
<tr>
<td>6</td>
<td>0.04</td>
<td>21</td>
<td>0.04</td>
</tr>
<tr>
<td>19</td>
<td>0.05</td>
<td>25</td>
<td>0.08</td>
</tr>
<tr>
<td>20</td>
<td>0.08</td>
<td>26</td>
<td>0.09</td>
</tr>
<tr>
<td>23</td>
<td>0.06</td>
<td>28</td>
<td>0.04</td>
</tr>
<tr>
<td>24</td>
<td>0.06</td>
<td>29</td>
<td>0.08</td>
</tr>
<tr>
<td>25</td>
<td>0.06</td>
<td>Aug 3</td>
<td>0.08</td>
</tr>
<tr>
<td>June 3</td>
<td>0.07</td>
<td>22</td>
<td>0.11</td>
</tr>
<tr>
<td>29</td>
<td>0.09</td>
<td>23</td>
<td>0.18</td>
</tr>
<tr>
<td>Sept 22</td>
<td>0.05</td>
<td>29</td>
<td>0.06</td>
</tr>
</tbody>
</table>
TABLE 2. Predawn water potential of western hemlock from different dormancy induction treatments and soil temperature from stable environment data collection days.

<table>
<thead>
<tr>
<th>Dormancy Induction Treatment</th>
<th>April 30</th>
<th>June 3</th>
<th>July 6</th>
<th>July 19</th>
<th>Aug 23</th>
<th>Sept 22</th>
</tr>
</thead>
<tbody>
<tr>
<td>LDD &lt;sup&gt;1&lt;/sup&gt;</td>
<td>.12±.01a</td>
<td>.39±.05a</td>
<td>.10±.02a</td>
<td>.57±.09a</td>
<td>.40±.09a</td>
<td>.26±.03a</td>
</tr>
<tr>
<td>LDW</td>
<td>.14±.02a</td>
<td>.41±.08a</td>
<td>.10±.02a</td>
<td>.62±.06a</td>
<td>.47±.08ab</td>
<td>.25±.01a</td>
</tr>
<tr>
<td>SDD</td>
<td>.13±.01a</td>
<td>.37±.01a</td>
<td>.07±.02a</td>
<td>.55±.04a</td>
<td>.64±.05b</td>
<td>.28±.03a</td>
</tr>
<tr>
<td>SDW</td>
<td>.15±.01a</td>
<td>.41±.02a</td>
<td>.10±.01a</td>
<td>.64±.04a</td>
<td>.62±.02b</td>
<td>.26±.04a</td>
</tr>
</tbody>
</table>

Noon Soil Temp. at -10 cm (°C)

<table>
<thead>
<tr>
<th>Date</th>
<th>8</th>
<th>15</th>
<th>19</th>
<th>25</th>
<th>19</th>
<th>13</th>
</tr>
</thead>
</table>

1) LDD = Long-day dry
LDW = Long-day wet
SDD = Short-day dry
SDW = Short-day wet

2) A difference in the letter within each date indicates a significant difference between dormancy induction treatments at p = 0.05 as determined by ANOVA and Waller-Duncan mean separation test.
Morphology After One Growing Season

All seedlings grew approximately 30 cm after 8 months in the field (Table 3). Seedling shoot dry weights and diameters showed no significant (p=0.05) difference. SDW DIT had the lowest stem units per cm and 1.0 needle damage index over the season. LDD DIT had the highest stem units per cm and needle damage index of 1.78 with LDW and SDD showing intermediate values. New root development into the soil showed no significant differences between DIT. Long-day DIT had greater inside the container plug root dry weight than short-day DIT and this difference carried over into total root dry weight sums. The three types of shoot/root ratios tested showed no significant differences between DIT.

Relative growth rates for height, diameter, shoot and root dry weight are found in Table 4.

Monthly Measurement of Replicated Physiological Data at Stable Environmental Conditions.

Afternoon physiological measurements were collected under clear sunny skies (Fig. 1A). Although photosynthetically active radiation (PAR) levels were similar (particularly in the afternoon) the vapour pressure deficit (VPD) levels were variable with afternoon measurements ranging from 1.0 to 3.6 kPa (Fig. 1B).

Net photosynthesis (Pn) for first year foliage was lower than second year foliage under similar environmental conditions (May af. versus September af., Fig. 1C). Pn
Table 3. Morphological development of western hemlock seedlings from different dormancy induction treatments before field planting and after one growing season on a field site.

<table>
<thead>
<tr>
<th>Dormancy Induction Treatment</th>
<th>Shoot Weight (g)</th>
<th>Root Diameter (cm)</th>
<th>Dry Needle Surface Area (cm²)</th>
<th>Needle Damage Index (1)</th>
<th>Stem Area by Weight (cm²)</th>
<th>Container Plug Dry Wt. (g)</th>
<th>In Soil Dry Wt. (g)</th>
<th>Total Shoot Dry Wt. (g)</th>
<th>Root Total Dry Wt. (g)</th>
<th>Root Total Surface Area (cm²)</th>
<th>Total Shoot Stem Water Balance (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LDD (1)</td>
<td>27.18±2.61b (4)</td>
<td>.27±.01b</td>
<td>1.27±.07bc</td>
<td>180.5±9.4b</td>
<td>1.00 (5)</td>
<td>.35±.02c</td>
<td>.35±.02c</td>
<td>68.1±4.4c</td>
<td>3.85±.18b</td>
<td>13.68±.86b</td>
<td>4.80±.73a 4.00±.37ab 6.41±.79b 2.48±.15a 4.76±.40a 2.63±.20a</td>
</tr>
<tr>
<td>LDW</td>
<td>11.52±.96a</td>
<td>.32±.01a</td>
<td>1.96±.10a</td>
<td>272.9±14.5a</td>
<td>1.00</td>
<td>.49±.04ab</td>
<td>.49±.04ab</td>
<td>90.7±6.5ab</td>
<td>4.22±.16b</td>
<td>13.65±.65b</td>
<td>6.44±.37ab 4.00±.37ab 6.41±.79b 2.48±.15a 4.76±.40a 2.63±.20a</td>
</tr>
<tr>
<td>SDD</td>
<td>22.18±.57c</td>
<td>.28±.01b</td>
<td>1.00±.03c</td>
<td>127.6±5.3c</td>
<td>1.00</td>
<td>.40±.03bc</td>
<td>.40±.03bc</td>
<td>82.1±5.5bc</td>
<td>2.75±.18a</td>
<td>10.19±.76a</td>
<td>6.44±.37ab 4.00±.37ab 6.41±.79b 2.48±.15a 4.76±.40a 2.63±.20a</td>
</tr>
<tr>
<td>SDW</td>
<td>23.04±.52c</td>
<td>.31±.01a</td>
<td>1.28±.08b</td>
<td>157.6±9.1b</td>
<td>1.00</td>
<td>.53±.04a</td>
<td>.53±.04a</td>
<td>102.2±7.4a</td>
<td>2.60±.12a</td>
<td>8.69±.55a</td>
<td>6.44±.37ab 4.00±.37ab 6.41±.79b 2.48±.15a 4.76±.40a 2.63±.20a</td>
</tr>
</tbody>
</table>

MARCH 15, 1988 — (Before Outplant)

- NOVEMBER 15, 1988 — (8 Months After Outplant)

(1) Needle damage index was categorized as: 1=100%, 2=90-99%, 3=75-89%, 4=50-74%, 5=25-49%, and 6=1-24% green needles.
(2) Seedling water balance ratio is: shoot dry weight/(diameter x soil root dry weight).
(3) LDD = Long-day dry
LDW = Long-day wet
SDD = Short-day dry
SDW = Short-day wet
(4) Mean and standard error. A difference in the letter for a morphological variable within each harvest date indicates a significant difference between dormancy induction treatment at p = 0.05 as determined by ANOVA and Waller-Duncan mean separation test.
(5) No statistical analysis due to lack of variation in one or more treatment(s).
TABLE 4. Relative growth rate of western hemlock seedlings from different dormancy induction treatments for the first growing season on a moisture-controlled field site.

<table>
<thead>
<tr>
<th>Dormancy Induction Treatment</th>
<th>Relative Growth Rates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Height (cm/cm/mon.)</td>
</tr>
<tr>
<td>LDD</td>
<td>.093</td>
</tr>
<tr>
<td>LDW</td>
<td>.086</td>
</tr>
<tr>
<td>SDD</td>
<td>.102</td>
</tr>
<tr>
<td>SDW</td>
<td>.105</td>
</tr>
</tbody>
</table>

1) LDD = Long-day dry  
   LDW = Long-day wet  
   SDD = Short-day dry  
   SDW = Short-day wet.
Figure 1. Morning (Mn) and afternoon (Af) measurements taken each month across the growing season for: A) photosynthetically active radiation (PAR), B) vapour pressure deficit (VPD), C) net photosynthesis (Pn), D) stomatal conductance (gwv), and E) xylem water potential (ψx) for western hemlock seedlings from dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW). Significant differences determined by ANOVA and Waller-Duncan mean separation test (p=0.05) are shown by different letters. Days with no lettering indicate no statistically significant treatment differences.
increased with time of year. No significant differences were found between DIT for first year or second year foliage.

Stomatal conductance (gwv) measurements for first year needles (April and May) were higher in short-day DIT seedlings than in long-day seedlings, but not significantly (Fig. 1D). Maximum gwv value for first year needles obtained by SDW seedlings reached an average of 0.13 cm s\(^{-1}\) in April. Second year gwv measurements (June - September) showed no consistent treatment trends. Seedlings for all DIT exhibited higher gwv readings than first year foliage having a maximum value of 0.23 cm s\(^{-1}\) in September.

Minimum xylem water potential (\(\psi_x\)) was -1.0 MPa observed in the afternoon readings of July, August and September (Fig. 1E). Pressure-volume analysis taken monthly showed that the turgor loss point was never higher than -1.5 MPa for LDW DIT (unpublished data).

**Physiological Response of First Year Needles**

Stomatal response of all seedlings indicated a sensitivity to changes in VPD particularly between 0.3- 1.0 kPa (Fig. 2). Beyond 1.0 kPa, stomatal response was constant with no further stomatal closure seen up to a moderate VPD value of 2.5 kPa.

Equations contained no constant since it did not significantly contribute to the model, whereas VPD and 1/VPD did at p=0.05. R-square values have been adjusted for the lack of constant and each indicate a reasonably good fit
Figure 2. Stomatal conductance boundary line analysis response to vapour pressure deficit (VPD) from greenhouse needles for western hemlock seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).

Figure 3. Stomatal conductance boundary line analysis response to photosynthetically active radiation (PAR) from greenhouse needles for western hemlock seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).
STOMATAL CONDUCTANCE (cm s\(^{-1}\))

- LDD: \(Y = 0.0262x + 0.0994x^{-1}; r^2 = 0.87\)
- LDW: \(Y = 0.0290x + 0.0891x^{-1}; r^2 = 0.84\)
- SDD: \(Y = 0.0297x + 0.119x^{-1}; r^2 = 0.85\)
- SDW: \(Y = 0.0353x + 0.109x^{-1}; r^2 = 0.74\)

STOMATAL CONDUCTANCE (cm s\(^{-1}\))

- LDD: \(Y = 0.114 + 0.011x; r^2 = 0.14\)
- LDW: \(Y = 0.121 + 0.010x; r^2 = 0.14\)
- SDD: \(Y = 0.152 + 0.007x; r^2 = 0.04\)
- SDW: \(Y = 0.139 + 0.013x; r^2 = 0.17\)
for all DIT.

Regardless of moisture stress treatment photoperiod was observed to have an effect on gwv to VPD response. Both short-day treatments had similar and higher response to VPD than long-day treatments over the whole range of VPD recorded. Short-day gwv response was 0.02 cm s$^{-1}$ higher than long-day at the maximum VPD condition observed.

Stomatal response show insensitivity to increasing PAR from just above 0.1 up to 2.2 mmol m$^{-2}$ s$^{-1}$ (full sunlight) (Fig. 3). There is a slight increase in gwv over this range reflected in the positive PAR coefficients, and greater than zero R-square values.

A linear model best described the data, and both components significantly contributed to the equation. Since a constant was included in the model, no adjustment to R-square was necessary. Although the R-square values were low this does not reflect on how well the line fits, but rather the lack of a strong correlation.

Seedling DIT influenced gwv response to PAR. Both short-day DIT had 0.02-0.03 cm s$^{-1}$ higher than their long-day counterpart over the recorded PAR range. No moisture stress effect was observed.

The model showing seedling gwv to simultaneous changes in PAR and VPD is shown in figure 4A-D for each DIT. At any given level of irradiance, gwv is sensitive to VPD changes particularly between 0.3-1.0 kPa. A leveling off of gwv after 1.0 kPa was observed. A mostly linear response to PAR
Figure 4. Stomatal conductance (g_{wv}) response to photosynthetically active radiation (PAR) and vapour pressure deficit (VPD) from first year needles of western hemlock for: A) long-day dry (LDD), B) long-day wet (LDW), C) short-day dry (SDD), and D) short-day wet (SDW). The regression models are as follows:

LDD: \( g_{wv} = -0.0181 + 0.0330(\text{PAR}) - 0.000402(1/\text{PAR}) + 0.0772(1/\text{VPD}) \):
\( r^2 = .53 \)

LDW: \( g_{wv} = 0.0445 + 0.0112(\text{PAR}) - 0.000566(1/\text{PAR}) + 0.0514(1/\text{VPD}) \):
\( r^2 = .48 \)

SDD: \( g_{wv} = -0.0242 + 0.0384(\text{PAR}) - 0.000422(1/\text{PAR}) + 0.0937(1/\text{VPD}) \):
\( r^2 = .51 \)

SDW: \( g_{wv} = 0.0568 + 0.0192(\text{PAR}) - 0.000667(1/\text{PAR}) + 0.0446(1/\text{VPD}) \):
\( r^2 = .27 \)
best described the gwv response at all VPD levels. From the 3-D response, data for the gwv to VPD 2-D response was most likely collected when PAR was high. Moreover, most of the data for gwv to PAR 2-D response was most likely collected at low VPD (approximately 0.5 kPa).

Modelling incorporated a constant, PAR, inverse PAR and inverse VPD as the best tested equation. All components significantly contributed to the model except inverse PAR. Inverse PAR was kept to correctly describe an observed biological response (position gwv to zero at zero PAR), but at no influence to the rest of the response surface. R-square values obtained with this model are moderate in value. This reflects an averaging of high R-square values achieved for gwv to VPD and low R-square values obtained for gwv to PAR.

Short-day DIT had higher gwv response than long-day at high PAR. At high PAR and low VPD, SDD seedlings maintained a higher gwv than other DIT seedlings. Although water stressed treatments did not have an effect on the gwv to VPD 2-D response, at low PAR moisture stressed seedlings stomata were almost closed at high VPD (Fig. 4A,C). Overall SDW DIT seedlings maintained stomata open over the widest range of atmospheric environmental conditions.

Between 0.05 and 0.6 mmol m\(^{-2}\) s\(^{-1}\) PAR, Pn exhibited a steep positive relationship (Fig. 5). For values greater than 0.6 mmol m\(^{-2}\) s\(^{-1}\), PAR had a slight influence on Pn. Maximum Pn values ranged from 2.8 to 3.4 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) for
Figure 5. Net photosynthesis boundary line analysis response to photosynthetically active radiation (PAR) from first year needles for western hemlock seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).

Figure 6. Net photosynthesis boundary line analysis response to vapour pressure deficit (VPD) from first year needles for western hemlock seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).
NET PHOTOSYNTHESIS (μ mol m\(^{-2}\) s\(^{-1}\))

- LDD: \(Y = 3.18 - 402x + 0.0118x^2 + 0.949\ln x : r^2 = 0.96\)
- LDW: \(Y = 3.67 - 897x + 0.0105x^2 + 1.183\ln x : r^2 = 0.95\)
- SDD: \(Y = 4.72 - 1.269x + 0.0265x^2 + 1.616\ln x : r^2 = 0.94\)
- SDW: \(Y = 3.53 - 0.597x + 0.0125x^2 + 1.132\ln x : r^2 = 0.93\)

NET PHOTOSYNTHESIS (μ mol m\(^{-2}\) s\(^{-1}\))

- LDD: \(Y = 3.00 - 0.196x : r^2 = 0.09\)
- LDW: \(Y = 3.07 - 0.275x : r^2 = 0.48\)
- SDD: \(Y = 3.07 - 0.127x : r^2 = 0.02\)
- SDW: \(Y = 3.21 - 0.365x : r^2 = 0.28\)
LDW and SDD seedlings, respectively. The light compensation point for western hemlock seedlings is 0.02 - 0.03 mmol m\(^{-2}\) s\(^{-1}\) (unreported data).

Equations which best described the data consisted of constant, PAR, inverse PAR, and natural logarithm of PAR. Each component significantly contributed to the response model. R-square values were very high for all treatments indicating that PAR accounts for a large measure of variation found in Pn.

Seedling DIT influenced Pn response to PAR. Below 0.6 mmol m\(^{-2}\) s\(^{-1}\), SDD DIT seedlings had greater Pn response compared to other DIT. At PAR levels greater than 0.6 mmol m\(^{-2}\) s\(^{-1}\), seedlings in SDD had the greatest response followed by SDW, LDD and LDW, respectively. Moisture stressed seedlings had higher values than their non moisture stress counterparts. In addition, short-day seedlings had higher values compared to their long-day counterparts. This indicates that moisture stressed / daylength treatment(s) influenced the Pn response for western hemlock seedlings.

Net photosynthesis decreased with increasing VPD for all treatments (Fig. 6). A linear equation was found to best describe the data with both components significantly contributing to the model. R-square values for each DIT equation were relatively low. Since a boundary line analysis of data was used to describe the response, the low R-square values showed a weak relationship, not a lack of fit between Pn and VPD over the range of VPD values measured.
At low VPD levels (0.5–1.0 kPa) all DIT seedlings showed similar Pn response. As VPD increased, SDD DIT seedlings maintained Pn similar to values found at low VPD.

Net photosynthesis response to simultaneous changes in PAR and VPD for each DIT is shown in figures 7A–D. At any given level of VPD, Pn is very responsive to PAR changes especially between 0 and 0.6 mmol m\(^{-2}\) s\(^{-1}\). Above this light level, or approximate saturation point, Pn remained consistent or increased moderately depending on DIT. Note, it was necessary to position the best model equation through 0 mmol m\(^{-2}\) s\(^{-1}\), thus the light compensation point is not shown. At any selected value of PAR, Pn decreased linearly with increasing VPD.

The best equation included the following components; constant, PAR, inverse PAR, natural logarithm of PAR, and VPD. These components also best described the 2-D boundary line analysis (Fig. 5 and 6). All components significantly contributed to the model. An interaction term was introduced but proved to be non-significant. R-square values are relatively high (0.7–0.85) showing that PAR and VPD strongly account for the Pn variation.

Comparing seedling treatments, Pn response to PAR at low VPD showed a similar ranking and response as the 2-dimensional boundary line analysis (Fig. 5). SDD DIT seedlings had the highest response followed by SDW, LDD, and LDW, respectively. Net photosynthesis dropped 30 to 35% as VPD increased to 2.5 kPa (Fig. 7A–D). Similar ranking, but
Figure 7. Net photosynthesis (Pn) response to photosynthetically active radiation (PAR) and vapour pressure deficit (VPD) from first year needles of western hemlock for: A) long-day dry (LDD), B) long-day wet (LDW), C) short-day dry (SDD), and D) short-day wet (SDW). The regression models are as follows:

LDD: $Pn = 2.993 - 0.263(PAR) + 0.0131(1/PAR) + 0.871(\ln(PAR)) - 0.422(\text{VPD})$; $r^2 = .83$

LDW: $Pn = 3.294 - 0.525(PAR) + 0.0078(1/PAR) + 0.951(\ln(PAR)) - 0.344(\text{VPD})$; $r^2 = .80$

SDD: $Pn = 3.416 - 0.425(PAR) + 0.0202(1/PAR) + 1.066(\ln(PAR)) - 0.446(\text{VPD})$; $r^2 = .70$

SDW: $Pn = 3.115 - 0.333(PAR) + 0.0095(1/PAR) + 0.893(\ln(PAR)) - 0.388(\text{VPD})$; $r^2 = .85$
with not as pronounced Pn differences, occurred at the highest VPD levels. Overall, SDD seedlings were best able to maintain a higher level of Pn over the measured range of environmental conditions compared to other DIT.

**Physiological Response of Second Year Needles**

Stomatal conductance exhibited a curvilinear decrease with increasing VPD with particular sensitivity between 1.0-2.0 kPa (Fig. 8). From VPD levels of 2.0-3.8, gwv continued to decrease, but not as rapidly. At a VPD level of 2.0 kPa, gwv response for SDW DIT seedlings increased 33% and for LDW DIT seedlings gwv response increased 60% over first year needle.

The best equation included VPD and 1/VPD and no constant was used since it did not significantly contribute to the model. The R-square values have been adjusted for lack of constant component and range from 0.60-0.66.

No differences between DIT were observed for gwv at low VPD levels. As VPD increased, SDW DIT seedlings maintained a slightly higher gwv than LDD, SDD and LDW, respectively. Compared to first year needles, treatment ranking was similar except that LDD seedlings performance had improved, and overall DIT differences had decreased.

A gwv increase of 30-50% was observed for all DIT seedlings as PAR increased (Fig. 9). At low PAR (0.1 mmol m⁻² s⁻¹) a moderate gwv increase of 25-30% was observed for all DIT seedlings compared to first year needles. At PAR
Figure 8. Stomatal conductance boundary line analysis response to vapour pressure deficit (VPD) from second year needles for western hemlock seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).

Figure 9. Stomatal conductance boundary line analysis response to photosynthetically active radiation (PAR) from second year needles for western hemlock seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).
greater than 2.0 mmol m\(^{-2}\) s\(^{-1}\), short-day seedlings response increased 40% while long-day seedlings increased by 75-85% compared to first year needles.

A linear model best described the data with both components significantly contributing to the equation. R-square values were relatively low, due to the horizontal relationship between gwv and PAR.

Seedling DIT influenced gwv response to PAR. Short-day DIT performed better than long-day DIT over the entire range of PAR; however, the difference between short-day and long-day DIT seedling response was slight at high PAR.

The figures showing second year gwv response to simultaneous changes in PAR and VPD for all DIT are seen in figures 10A-D. For any PAR, gwv is responsive to VPD changes particularly at values less than 1.5 kPa and greater than 3.5 kPa. From 0 to 1.5 kPa, gwv rapidly decreased with increasing VPD. Between 1.5 and 3.5 kPa, gwv decreased slightly with increasing VPD. For values greater than 3.5 kPa, gwv declined to a point of stomatal closure at approximately 4.0 kPa. From 0.1 mmol m\(^{-2}\) s\(^{-1}\) to full sunlight, a linear response best describes the gwv response to PAR at all levels of VPD. Note the shape of gwv to VPD from the 3-D graph is not the same as the 2-D gwv versus VPD graph. This is because only the best values were used in the boundary line response and hence the method was not able to pick up the overall decrease in gwv at the highest VPD values measured.
Figure 10. Stomatal conductance (g\textsubscript{wv}) response to photosynthetically active radiation (PAR) and vapour pressure deficit (VPD) from second year needles of western hemlock for: A) long-day dry (LDD), B) long-day wet (LDW), C) short-day dry (SDD), and D) short-day wet (SDW). The regression models are as follows:

**LDD:** \[ g_{wv} = 0.0315(PAR) - 0.000171(1/PAR)^2 + 0.161(\text{VPD}) - 0.107(\ln(\text{VPD})) - 0.337(\text{VPD})^2: r^2 = .38 \]

**LDW:** \[ g_{wv} = 0.0415(PAR) + 0.001725(1/PAR)^2 + 0.159(\text{VPD}) - 0.102(\ln(\text{VPD})) - 0.037(\text{VPD})^2: r^2 = .58 \]

**SDD:** \[ g_{wv} = 0.0391(PAR) + 0.001156(1/PAR)^2 + 0.158(\text{VPD}) - 0.106(\ln(\text{VPD})) - 0.035(\text{VPD})^2: r^2 = .40 \]

**SDW:** \[ g_{wv} = 0.0231(PAR) + 0.000334(1/PAR)^2 + 0.189(\text{VPD}) - 0.098(\ln(\text{VPD})) - 0.041(\text{VPD})^2: r^2 = .39 \]
Best equations included the following components; PAR, inverse PAR, VPD, natural logarithm of VPD, and VPD squared. All components significantly contributed to the model except inverse PAR. Inverse PAR was kept to correctly describe an observed biological response (position gwv to zero at zero PAR), but at no influence to the rest of the response surface. A constant did not contribute to the model, hence the R-square values have been appropriately adjusted. R-square values were in the 0.38–0.58 range.

Seedling DIT moderately affected second year needle gwv response to varying PAR and VPD. At low light levels (0.1–0.5 mmol m\(^{-2}\) s\(^{-1}\)) and moderate to high VPD levels (1.5–4.0 kPa) SDW DIT seedlings exhibited the greatest gwv response. During high VPD levels (3.5–4.0 kPa), short-day and LDD DIT seedlings had higher gwv response than the LDW DIT seedlings. At moderately high PAR levels (1.0–1.5 mmol m\(^{-2}\) s\(^{-1}\)), and low to moderate VPD levels (less than 3.5 kPa), all DIT seedlings had similar response.

Second year needles, similar to first year needles, show Pn rise rapidly to a level of light saturation (0.75 mmol m\(^{-2}\) s\(^{-1}\)) (Fig.11). As PAR increases, Pn values remained unchanged. The observed light compensation point did not change significantly from 0.02–0.03 mmol m\(^{-2}\) s\(^{-1}\) as recorded for first year needles (unreported data).

The equation which best described the data consisted of a constant, PAR, inverse PAR, and natural logarithm of PAR.
Figure 11. Net photosynthesis boundary line analysis response to photosynthetically active radiation (PAR) from second year needles for western hemlock seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).

Figure 12. Net photosynthesis boundary line analysis response to vapour pressure deficit (VPD) from second year needles for western hemlock seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).
R-square values for all DIT seedlings were calculated to be greater than 0.90.

No differences in Pn response to varying PAR were found from the second year needles. Maximum Pn for second year needle response (Fig. 11) increased as compared to first year needles (Fig. 5), from 60% for SDD to 95% for LDW DIT seedlings.

A linear decrease in Pn to increasing VPD occurred (Fig. 12). Net photosynthetic response decreased from 50 to 66% in all DIT from 0.5 to 3.8 kPa VPD levels, while xylem pressure potentials were never less than -1.0 MPa (Fig. 1E).

A simple linear equation best related Pn to VPD. R-square values were between 0.73 to 0.88.

Short-day wet seedlings had a greater Pn at high VPD compared to other DIT. When compared to first year needles in figure 6, it can be seen that second year needles show a higher Pn response at comparable values.

Surface response of Pn to varying PAR and VPD for all four DIT are shown in figures 13A–D. Pn response to PAR for any given VPD showed that Pn was extremely responsive to PAR up to 0.7 mmol m$^{-2}$ s$^{-1}$. In addition, Pn is highly responsive to VPD at all light intensities. Again, due to model limitations of the model at very low PAR, a light compensation point cannot be determined.

The equation that best described these variables was identical to the first year needle models, and included the
Figure 13. Net photosynthesis (Pn) response to photosynthetically active radiation (PAR) and vapour pressure deficit (VPD) from second year needles of western hemlock for: A) long-day dry (LDD), B) long-day wet (LDW), C) short-day dry (SDD), and D) short-day wet (SDW). The regression models are as follows:

LDD: \[ Pn = 6.020 -0.828(PAR) +0.0143(1/PAR) +1.688(\ln(PAR)) -0.922(\text{VPD}) : r^2 = .72 \]

LDW: \[ Pn = 6.877 -1.050(PAR) +0.0176(1/PAR) +1.829(\ln(PAR)) -1.123(\text{VPD}) : r^2 = .83 \]

SDD: \[ Pn = 6.230 -1.052(PAR) +0.0171(1/PAR) +1.761(\ln(PAR)) -0.860(\text{VPD}) : r^2 = .75 \]

SDW: \[ Pn = 6.711 -0.969(PAR) +0.0113(1/PAR) +1.785(\ln(PAR)) -0.976(\text{VPD}) : r^2 = .85 \]
following components: constant, PAR, inverse PAR, natural logarithm of PAR, and VPD. All components significantly contributed to the model. R-square values are relatively high (0.76–0.86), and attest to the significance of PAR and VPD in accounting for Pn variation.

At low VPD levels (<1.0 kPa), and at moderate to high PAR (0.7–2.2 mmol m\(^{-2}\) s\(^{-1}\)), both non moisture stressed treatments had higher Pn than moisture stressed seedlings. However, at high VPD (greater than 3.5 kPa) and all PAR levels, short-day seedlings maintained higher Pn rates than long-day seedlings. Short-day wet seedlings had the highest overall Pn performance of all DIT.
Environmental Conditions

Predawn xylem water potentials measured monthly never were lower than -0.33 MPa (Table 5). The lowest soil water potential reading recorded for western red cedar sampling days was -0.11 MPa on August 22, 1988 (Table 1). Soil temperatures (-10 cm) were between 8 and 22°C (Table 5). Morphology data showed no blocking effect or blocking x treatment interaction at p=0.05 (unreported data). Thus, experimental and sampling errors were combined for a new error term for data analysis.

Preplant Morphology

Seedlings in the LDW DIT had the greatest height, diameter, shoot dry weight and foliage surface area (Table 6). Moisture stress DIT seedlings were smaller than non moisture stressed seedlings, but the differences were not significant. Moisture stressed DIT seedlings had better shoot to root and seedling water balance ratios.

Morphology After One Growing Season

Each DIT grew approximately 50 cm in height after 8 months on the controlled field site (Table 6). Shoot dry weights and diameters were not significantly different (p=0.05) between DIT. No foliage damage occurred after 8 months of growth. There were no significant differences
TABLE 5. Predawn water potential of western red cedar from different dormancy induction treatments and soil temperature from stable environment data collection days.

<table>
<thead>
<tr>
<th>Dormancy Induction Treatment</th>
<th>April 21 $\pm$ 1 S.E.</th>
<th>May 30 $\pm$ 1 S.E.</th>
<th>June 29 $\pm$ 1 S.E.</th>
<th>July 18 $\pm$ 1 S.E.</th>
<th>Aug 22 $\pm$ 1 S.E.</th>
<th>Sept 29 $\pm$ 1 S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>LDD$^1$</td>
<td>.13 $\pm$ .01a$^2$</td>
<td>.28 $\pm$ .02a</td>
<td>.31 $\pm$ .03a</td>
<td>.17 $\pm$ .01b</td>
<td>.18 $\pm$ .02b</td>
<td>.15 $\pm$ .01a</td>
</tr>
<tr>
<td>LDW</td>
<td>.15 $\pm$ .01a</td>
<td>.22 $\pm$ .01a</td>
<td>.33 $\pm$ .05a</td>
<td>.18 $\pm$ .02b</td>
<td>.14 $\pm$ .01a</td>
<td>.14 $\pm$ .01a</td>
</tr>
<tr>
<td>SDD</td>
<td>.15 $\pm$ .01a</td>
<td>.29 $\pm$ .06a</td>
<td>.28 $\pm$ .02a</td>
<td>.15 $\pm$ .01a</td>
<td>.12 $\pm$ .01a</td>
<td>.14 $\pm$ .01a</td>
</tr>
<tr>
<td>SDW</td>
<td>.14 $\pm$ .01a</td>
<td>.28 $\pm$ .03a</td>
<td>.33 $\pm$ .02a</td>
<td>.12 $\pm$ .02a</td>
<td>.13 $\pm$ .01a</td>
<td>.11 $\pm$ .01a</td>
</tr>
</tbody>
</table>

| Noon Soil Temp. at -10 cm (°C) | 8  | 18  | 22  | 20  | 18  | 13  |

1) LDD = Long-day dry  
LDW = Long-day wet  
SDD = Short-day dry  
SDW = Short-day wet

2) A difference in the letter within each date indicates a significant difference between dormancy induction treatments at $p = 0.05$ as determined by ANOVA and Waller-Duncan mean separation test.
Table 6. Morphological development of western red cedar seedlings from different dormancy induction treatments before field planting and after one growing season on a field site.

<table>
<thead>
<tr>
<th>Dormancy Induction Treatment</th>
<th>SHOOT</th>
<th>ROOT</th>
<th>SHOOT/ROOT RATIOS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Height (cm)</td>
<td>Root Collar Diameter (cm)</td>
<td>Dry Weight (g)</td>
</tr>
<tr>
<td>LDW (2)</td>
<td>77.50 ± 3.30a</td>
<td>1.32 ± 0.3a</td>
<td>39.94 ± 1.91a</td>
</tr>
<tr>
<td>LDW (2)</td>
<td>82.00 ± 1.84a</td>
<td>1.40 ± 0.05a</td>
<td>47.40 ± 2.89a</td>
</tr>
<tr>
<td>SDW (2)</td>
<td>76.56 ± 2.66b</td>
<td>1.34 ± 0.05a</td>
<td>41.53 ± 2.65a</td>
</tr>
<tr>
<td>SDW (2)</td>
<td>78.72 ± 1.15a</td>
<td>1.44 ± 0.05a</td>
<td>47.39 ± 2.46a</td>
</tr>
</tbody>
</table>

(1) Needle damage index was categorized as: 1=100%, 2=90-99%, 3=75-89%, 4=50-74%, 5=25-49%, and 6=1-24% green needles.
(2) Seedling water balance ratio is: shoot dry weight/(diameter x soil root dry weight).
(3) LDW = Long-day dry
LDW = Long-day wet
SDD = Short-day dry
SDW = Short-day wet
(4) Mean and standard error. A difference in the letter for a morphological variable within each harvest date indicates a significant difference between dormancy induction treatment at p = 0.05 as determined by ANOVA and Waller-Duncan mean separation test.
(5) No statistical analysis due to lack of variation in one or more treatments.
TABLE 7. Relative growth rate of western red cedar seedlings from different dormancy induction treatments for the first growing season on a moisture-controlled field site.

<table>
<thead>
<tr>
<th>Dormancy Induction Treatment</th>
<th>Relative Growth Rates</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Height (cm/cm/mon.)</td>
<td>Diameter (cm/cm/mon.)</td>
<td>Shoot Dry Wt. (g/g/mon.)</td>
<td>Total Root Dry Wt. (g/g/mon.)</td>
</tr>
<tr>
<td>LDD (^1)</td>
<td>.121</td>
<td>.194</td>
<td>.396</td>
<td>.381</td>
</tr>
<tr>
<td>LDW</td>
<td>.122</td>
<td>.201</td>
<td>.396</td>
<td>.392</td>
</tr>
<tr>
<td>SDD</td>
<td>.135</td>
<td>.200</td>
<td>.408</td>
<td>.391</td>
</tr>
<tr>
<td>SDW</td>
<td>.138</td>
<td>.209</td>
<td>.417</td>
<td>.433</td>
</tr>
</tbody>
</table>

\(^1\) LDD = Long-day dry  
LDW = Long-day wet  
SDD = Short-day dry  
SDW = Short-day wet.
between DIT for root dry weights or any of the measured shoot/root ratios. Relative growth rates for height, diameter, shoot and root dry weight are found in Table 7.

Monthly Measurement of Replicated Physiological Data at Stable Environmental Conditions

Except for morning measurements in May and June, PAR data showed all measurements were taken under clear sunny skies (Fig. 14A). Vapour pressure deficit range for data collection was moderate from 1.0 to 2.5 kPa (Fig. 14B).

Maximum Pn was 2.5 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for first year foliage in May, and 5.4 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for second year foliage in August under similar environmental conditions (Fig. 14C).

On 2 of the 4 measurement occasions in April and May (first year foliage) moisture stress DIT had significantly higher gwv readings (Fig. 14D). LDD seedlings ranked first on 3 of the 4 occasions, while SDD seedlings ranked first on the other. Second year foliage gwv (June - September) exhibited no DIT or seasonal trends.

From April to September all measured xylem water potentials (\( \psi_x \)) were between \(-0.4\) and \(-0.8\) MPa (Fig. 14E). Pressure-volume analysis taken monthly on LDW DIT had a minimum turgor loss point of \(-1.3\) MPa (unpublished data). Average \( \psi_x \) for each DIT were similar for most of the growing season.
Figure 14. Morning (Mn) and afternoon (Af) measurements taken each month across the growing season for: A) photosynthetically active radiation (PAR), B) vapour pressure deficit (VPD), C) net photosynthesis (Pn), D) stomatal conductance (gwv), and E) xylem water potential ($\Phi_x$) for western red cedar seedlings from dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW). Significant differences determined by ANOVA and Waller-Duncan mean separation test (p=0.05) are shown by different letters. Days with no lettering indicate no statistically significant treatment differences.
Physiological Response of First Year Foliage

As VPD levels increased from 0.5-1.0 kPa, gwv rates decreased quickly (Fig. 15). For VPD values greater than 1.0 kPa, gwv showed a slight decrease as VPD increased. No evidence of stomatal closure was found.

The best equation describing the gwv to VPD data included VPD and inverse VPD. No constant was used in the equation, since it did not significantly contribute at p=0.05. R-square numbers have been adjusted for removal of the constant component.

Overall, LDW seedlings had the lowest gwv response to changing VPD. Above 1.0 kPa, SDD seedlings maintained a 0.01 cm s\(^{-1}\) greater gwv rate than SDW and LDD DIT seedlings. For most of the VPD range, moisture stressed DIT seedlings maintained a higher gwv than their non moisture stressed DIT seedling counterparts.

Stomatal conductance response showed an insensitivity to increasing PAR from 0.10 to 2.2 mmol m\(^{-2}\) s\(^{-1}\) (full sunlight) (Fig. 16). There is a slight increase in gwv over this range reflected in the positive PAR coefficients.

A linear model was found to best represent the data. Both components, constant and PAR, significantly contributed to the equation. Even though the R-square values are low this does not reflect the line fit, but more so the lack of a strong relationship.

Seedling DIT influenced gwv response to PAR. LDW seedlings had the lowest response over the entire PAR range.
Figure 15. Stomatal conductance boundary line analysis response to vapour pressure deficit (VPD) from first year needles for western red cedar seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).

Figure 16. Stomatal conductance boundary line analysis response to photosynthetically active radiation (PAR) from first year needles for western red cedar seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).
STOMATAL CONDUCTANCE (cm s\(^{-1}\))

LDD: \(Y = 0.0691 + 0.0880x\), \(r^2 = 0.80\)
LDW: \(Y = 0.0763 + 0.0686x\), \(r^2 = 0.87\)
SDD: \(Y = 0.1114 + 0.0447x\), \(r^2 = 0.57\)
SDW: \(Y = 0.0925 + 0.0579x\), \(r^2 = 0.73\)

STOMATAL CONDUCTANCE (cm s\(^{-1}\))

LDD: \(Y = 0.146 + 0.010x\), \(r^2 = 0.13\)
LDW: \(Y = 0.123 + 0.017x\), \(r^2 = 0.24\)
SDD: \(Y = 0.128 + 0.023x\), \(r^2 = 0.34\)
SDW: \(Y = 0.140 + 0.008x\), \(r^2 = 0.08\)

PAR (mmol m\(^{-2}\) s\(^{-1}\))
Moisture stressed DIT had a moderate affect on gwv. Long-day dry seedlings were 0.01 to 0.02 cm s\(^{-1}\) higher as compared to LDW seedlings for any PAR values. Short-day dry seedlings showed a higher response for the PAR range measured.

The graphs illustrating gwv response to PAR and VPD for the four DIT are found in figures 17A-D. All treatments showed a strong response to VPD below 1.0 kPa at all PAR. Beyond that point, gwv leveled off maintaining a nearly constant value up to 2.5 kPa. The highest gwv values for any segment of VPD were at high PAR. Response of gwv to PAR was a weak linear response across PAR values greater than 0.1 mmol m\(^{-2}\) s\(^{-1}\). Data used for the gwv to VPD 2-dimensional (2-D) boundary line analysis were most likely collected at high PAR levels.

The modelling equation which was used to best fit the data for all treatments included a constant, PAR, and the inverse of VPD. Moderate R-square values (0.33 - 0.65) were computed. These values were a result of combining a strong gwv to VPD relationship (Fig. 15), to a weak gwv to PAR relationship (Fig. 16).

For environmental conditions having VPD values less than 1.0 kPa, the 3-D response shows that LDD DIT seedlings had a slightly higher gwv response at all PAR levels. When VPD values were between 1.0 and 2.5 kPa, moisture stressed DIT seedlings maintained higher gwv than their non moisture stressed seedling counterparts, especially at low PAR. The LDW DIT seedlings showed the lowest overall gwv values over
Figure 17. Stomatal conductance (gwv) response to photosynthetically active radiation (PAR) and vapour pressure deficit (VPD) from first year needles of western red cedar for: A) long-day dry (LDD), B) long-day wet (LDW), C) short-day dry (SDD), and D) short-day wet (SDW). The regression models are as follows:

LDD: \( gwv = 0.0449 + 0.0100(PAR) + 0.0661(1/VPD) \); \( r^2 = .50 \)
LDW: \( gwv = 0.0112 + 0.0204(PAR) + 0.0627(1/VPD) \); \( r^2 = .46 \)
SDD: \( gwv = 0.0691 + 0.0055(PAR) + 0.0374(1/VPD) \); \( r^2 = .33 \)
SDW: \( gwv = 0.0187 + 0.0175(PAR) + 0.0701(1/VPD) \); \( r^2 = .65 \)
the environmental conditions measured, whereas both water stressed treatments showed the highest values. It would appear that daylength had little or no influence on gwv.

Western red cedar seedling Pn rapidly increased with PAR to 1.0 mmol m\(^{-2}\) s\(^{-1}\) and continued to increase but at a diminishing rate up to full sunlight (Fig. 18). It would appear that there is no easily-defined light saturation point. Light compensation value was between 0.02 and 0.03 mmol m\(^{-2}\) s\(^{-1}\) (unreported data).

The equation used to best describe the data consisted of the following components; constant, PAR, inverse PAR, and natural log of PAR. Each component significantly contributed to the response model. For all treatments, R-square values were very high ranging from 0.94-0.96.

Both moisture stressed DIT seedlings had higher Pn response than their non moisture stressed seedling counterparts. Moisture stressed seedling response began to separate at approximately 0.2 mmol m\(^{-2}\) s\(^{-1}\) and maintained a 0.1-0.3 μmol m\(^{-2}\) s\(^{-1}\) Pn rate difference up to full sunlight. Daylength DIT had no influence on Pn versus PAR response, except at the highest PAR levels, LDW seedlings had a higher Pn than SDW seedlings.

The response to increasing VPD (0.5-2.0 kPa) shows Pn decreasing linearly with Pn rate declining by 20-30% depending on DIT (Fig. 19).

A linear equation best described the data with both components significantly contributing to the model. R-square
Figure 18. Net photosynthesis boundary line analysis response to photosynthetically active radiation (PAR) from first year needles for western red cedar seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).

Figure 19. Net photosynthesis boundary line analysis response to vapour pressure deficit (VPD) from first year needles for western red cedar seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).
NET PHOTOSYNTHESIS (µ mol m\(^{-2}\) s\(^{-1}\))

**PAR (mmol m\(^{-2}\) s\(^{-1}\))**

- **LDD:** \(Y = 4.23 - 0.730x \quad r^2 = 0.48\)
- **LDW:** \(Y = 4.31 - 0.830x \quad r^2 = 0.42\)
- **SDD:** \(Y = 4.19 - 1.048x \quad r^2 = 0.53\)
- **SDW:** \(Y = 3.76 - 0.656x \quad r^2 = 0.50\)

**VPD (kPa)**

- **LDD:** \(Y = 4.23 - 0.730x \quad r^2 = 0.48\)
- **LDW:** \(Y = 4.21 - 0.830x \quad r^2 = 0.42\)
- **SDD:** \(Y = 4.75 - 1.048x \quad r^2 = 0.53\)
- **SDW:** \(Y = 3.76 - 0.656x \quad r^2 = 0.50\)
values for each DIT equation were moderate (0.42-0.53). The R-square values are not seen as a lack of fit, but a lack of a strong relationship between Pn and VPD over the range of VPD levels tested.

Moisture stressed DIT seedlings exhibited higher Pn as compared to the non moisture stressed DIT seedlings. SDD seedlings showed the best Pn response for VPD values less than 1.5 kPa, while LDD seedlings produced the highest values up to 2.3 kPa. Short-day wet seedlings showed the lowest Pn values over the VPD range measured.

Surface response models of Pn to PAR and VPD levels showed that Pn was sensitive to both variables (Fig. 20A-D). Net photosynthesis was responsive to PAR changes from 0 to 2.2 mmol m$^{-2}$ s$^{-1}$ with the greatest sensitivity up to 0.6 mmol m$^{-2}$ s$^{-1}$ and thereafter showing a positive but weaker response. Seedling Pn response to VPD showed a significant linear response for all PAR values. Note that due to the nature of the equation selected, light compensation point can not be determined from the graph.

The equation which best described the data included the following components; constant, inverse PAR, natural log of PAR, PAR squared, and VPD. Note, this equation does not have a linear PAR term (non-significant at p=0.05), but includes a PAR square term. Each component of the equation contributes significantly to the model (p = 0.05). R-square values are relatively high (0.75 - 0.87) showing a strong relationship of Pn to both PAR and VPD.
Figure 20. Net photosynthesis (Pn) response to photosynthetically active radiation (PAR) and vapour pressure deficit (VPD) from first year needles of western red cedar for: A) long-day dry (LDD), B) long-day wet (LDW), C) short-day dry (SDD), and D) short-day wet (SDW). The regression models are as follows:

LDD: \( Pn = 3.479 + 0.0125(\frac{1}{\text{PAR}}) + 1.089(\ln(\text{PAR}) - 0.168(\text{PAR})^2 - 0.699(\text{VPD}) \quad r^2 = .75 \)

LDW: \( Pn = 2.894 + 0.0032(\frac{1}{\text{PAR}}) + 0.781(\ln(\text{PAR}) - 0.044(\text{PAR})^2 - 0.559(\text{VPD}) \quad r^2 = .77 \)

SDD: \( Pn = 3.284 + 0.0097(\frac{1}{\text{PAR}}) + 1.014(\ln(\text{PAR}) - 0.117(\text{PAR})^2 - 0.689(\text{VPD}) \quad r^2 = .76 \)

SDW: \( Pn = 2.960 + 0.0048(\frac{1}{\text{PAR}}) + 0.822(\ln(\text{PAR}) - 0.064(\text{PAR})^2 - 0.587(\text{VPD}) \quad r^2 = .87 \)
Net photosynthesis response to PAR at low VPD exhibited very similar DIT ranking and response as the 2-D boundary line analysis (Fig. 18). Seedlings in LDD, followed by SDD seedlings, showed the highest response followed by SDW and LDW. At the highest measured VPD levels, Pn response was similar for all DIT seedlings. Overall, LDD seedlings were best able to maintain a high level of Pn over the range of environmental conditions measured as compared to other DIT seedlings.

Physiological Response of Second Year Foliage

Stomatal conductance shows a curvilinear response to changing VPD, with a rapid decline in gwv up to VPD values of 2.0 kPa (Fig. 21). Thereafter gwv exhibited a slow constant decline to 4.0 kPa. Second year foliage maintained a higher gwv at similar VPD as compared to first year foliage. Both foliage types were sensitive to VPD, but at different levels.

Like first year foliage response, the best equation included VPD and inverse VPD. No constant was used since it did not significantly contribute to the equation. As a result, R-square values were adjusted. R-square values were moderate having values ranging from 0.60 to 0.81.

No differences between DIT seedlings were observed for gwv at low to moderate VPD levels (1.0 - 3.0 kPa). At higher VPD levels (3.0-4.0 kPa) gwv was slightly higher for short-day as compared to long-day seedlings.
Figure 21. Stomatal conductance boundary line analysis response to vapour pressure deficit (VPD) from second year needles for western red cedar seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).

Figure 22. Stomatal conductance boundary line analysis response to photosynthetically active radiation (PAR) from second year needles for western red cedar seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).
STOMATAL CONDUCTANCE (cm s$^{-1}$)

- **LDD:** $Y = 0.00889x + 0.320x^{-1}; r^2 = 0.81$
- **LDW:** $Y = 0.00854x + 0.323x^{-1}; r^2 = 0.81$
- **SDD:** $Y = 0.01596x + 0.279x^{-1}; r^2 = 0.60$
- **SDW:** $Y = 0.01534x + 0.302x^{-1}; r^2 = 0.69$

STOMATAL CONDUCTANCE (cm s$^{-1}$)

- **LDD:** $Y = 0.114 + 0.061x; r^2 = 0.72$
- **LDW:** $Y = 0.112 + 0.060x; r^2 = 0.56$
- **SDD:** $Y = 0.120 + 0.050x; r^2 = 0.63$
- **SDW:** $Y = 0.121 + 0.059x; r^2 = 0.74$
Stomatal conductance versus PAR showed a moderately strong relationship (Fig. 22). On average, gwv increased 85%, from 0.13 cm s\(^{-1}\) at 0.1 mmol m\(^{-2}\) s\(^{-1}\) to 0.24 cm s\(^{-1}\) at 2.1 mmol m\(^{-2}\) s\(^{-1}\). Compared to first year foliage (Fig. 16), no differences were observed at low PAR (0.1 mmol m\(^{-2}\) s\(^{-1}\)); however, at high PAR levels (2.1 mmol m\(^{-2}\) s\(^{-1}\)) second year foliage had on average 40% greater gwv values.

Statistically, the best equation to describe the data was a linear model. R-square values of the linear model were between 0.56 and 0.74.

Unlike first year foliage, second year foliage of different DIT seedlings did not influence gwv response to PAR.

Figures 23A–D show the second year foliage response surface model of gwv to simultaneous changes in PAR and VPD for all dormancy induction treatments. For any PAR level, gwv is responsive to VPD up to 1.5 kPa. Thereafter depending on light levels, gwv was relatively constant with only a gradual decrease. No evidence of stomatal closure was found up to the maximum measured VPD level (4.0 kPa). With increasing PAR, gwv exhibited a linear response up to approximately 1.5 mmol m\(^{-2}\) s\(^{-1}\), and thereafter maintained a constant or decreasing trend depending on DIT.

The best equation included the following components; PAR, natural log of PAR, PAR squared, and inverse VPD. All components significantly contributed to the model. A constant component was not significant, and thus R-square
Figure 23. Stomatal conductance (g_wv) response to photosynthetically active radiation (PAR) and vapour pressure deficit (VPD) from second year needles of western red cedar for: A) long-day dry (LDD), B) long-day wet (LDW), C) short-day dry (SDD), and D) short-day wet (SDW). The regression models are as follows:

LDD: $g_{wv} = 0.145(PAR) - 0.0169\ln(PAR) - 0.0429(PAR)^2 + 0.0668(1/VPD); \ r^2 = .29$

LDW: $g_{wv} = 0.127(PAR) - 0.0118\ln(PAR) - 0.0330(PAR)^2 + 0.0688(1/VPD); \ r^2 = .32$

SDD: $g_{wv} = 0.121(PAR) - 0.0229\ln(PAR) - 0.0285(PAR)^2 + 0.0616(1/VPD); \ r^2 = .21$

SDW: $g_{wv} = 0.160(PAR) - 0.0222\ln(PAR) - 0.0467(PAR)^2 + 0.0474(1/VPD); \ r^2 = .22$
values were adjusted. R-square values were low (0.21 - 0.32) probably reflecting the large flat area for environmental conditions where gwv readings were relatively constant (VPD values greater than 1.5 kPa and PAR values greater than 0.1 mmol m^{-2} s^{-1}).

The moisture stressed seedlings were able to maintain a constant level of gwv at values greater than 1.5 mmol m^{-2} s^{-1} whereas non moisture stressed seedlings showed a decrease in gwv, particularly at high VPD. Otherwise differences between DIT were minor.

Net photosynthesis for all seedlings rose rapidly up to 0.3 mmol m^{-2} s^{-1} and then increased linearly with increasing light intensity (Fig. 24). First year foliage 2-D responses (Fig. 18) are very similar to second year foliage up to 0.5 mmol m^{-2} s^{-1}. Thereafter, first year foliage begins to show diminishing Pn with increasing PAR; whereas, second year foliage maintains a linear Pn increase with increasing PAR up to a rate of 5.9 \mu mol m^{-2} s^{-1} at 2.1 mmol m^{-2} s^{-1}. Measurements at full sunlight produced the greatest relative difference (60%) between first year (Fig. 18) and second year foliage (Fig. 24). Light compensation point of 0.02 - 0.03 mmol m^{-2} s^{-1} did not change from that obtained with first year foliage (unreported data).

The model that best described the data included a constant, PAR, and natural log of PAR. All equation components contributed significantly to the model. R-square values were very high ranging from 0.94 to 0.96.
Figure 24. Net photosynthesis boundary line analysis response to photosynthetically active radiation (PAR) from second year needles for western red cedar seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).

Figure 25. Net photosynthesis boundary line analysis response to vapour pressure deficit (VPD) from second year needles for western red cedar seedlings in dormancy induction treatments: 1) long-day dry (LDD), 2) long-day wet (LDW), 3) short-day dry (SDD), and 4) short-day wet (SDW).
NET PHOTOSYNTHESIS ($\mu$ mol m$^{-2}$ s$^{-1}$)

**PAR (mmol m$^{-2}$ s$^{-1}$)**

- **LDD**: $Y = 1.84 + 1.68x + 0.547 \ln x$ \(r^2 = 0.95\)
- **LDW**: $Y = 1.32 + 2.10x + 0.400 \ln x$ \(r^2 = 0.94\)
- **SDD**: $Y = 1.65 + 1.86x + 0.508 \ln x$ \(r^2 = 0.96\)
- **SDW**: $Y = 1.76 + 1.70x + 0.541 \ln x$ \(r^2 = 0.94\)

**VPD (kPa)**

- **LDD**: $Y = 6.05 - 1.81x$ \(r^2 = 0.96\)
- **LDW**: $Y = 6.56 - 1.95x$ \(r^2 = 0.94\)
- **SDD**: $Y = 7.89 - 1.77x$ \(r^2 = 0.80\)
- **SDW**: $Y = 7.20 - 1.42x$ \(r^2 = 0.57\)
No differences in Pn response to PAR between DIT were detected.

The relationship of Pn versus VPD is seen in figure 25. The results show strong linear decrease in Pn (from 5.9 to 1.9 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) with increasing VPD (from 1.0 to 3.8 kPa) producing an average decrease of 66% for all DIT. Note, the strong response occurred while plant moisture stress was never lower than -1.0 MPa during measurement. For both first year and second foliage, the rate of decrease was approximately the same.

Net photosynthesis was best related to VPD using a simple linear regression. Both components contributed significantly to the equation. R-square values were moderately high ranging from 0.57 to 0.94.

Second year foliage showed no differences between DIT seedlings Pn response to VPD.

Response surface models of second year foliage Pn to combined PAR and VPD changes for all treatments are found in Figures 26A-D. At all levels of PAR, Pn decreased linearly with increasing VPD. Note that at high VPD values the model showed no photosynthesis occurring at low light levels (0 - 0.2 mmol m\(^{-2}\) s\(^{-1}\)). Photosynthesis increased dramatically with initial PAR levels and showed less of a response as PAR increased to full sunlight. Depending on the treatment, it was also observed that Pn was slightly inhibited at PAR values approaching full sunlight. Net photosynthesis response to PAR is not exactly the same as represented in
Figure 26. Net photosynthesis (Pn) response to photosynthetically active radiation (PAR) and vapour pressure deficit (VPD) from second year needles of western red cedar for: A) long-day dry (LDD), B) long-day wet (LDW), C) short-day dry (SDD), and D) short-day wet (SDW). The regression models are as follows:

LDD: \[ Pn = 2.097 + 2.566(PAR) + 0.532(\ln(PAR)) - 0.741(PAR)^2 - 0.600(VPD): \ r^2 = .69 \]

LDW: \[ Pn = 1.818 + 3.345(PAR) + 0.417(\ln(PAR)) - 0.980(PAR)^2 - 0.721(VPD): \ r^2 = .66 \]

SDD: \[ Pn = 2.557 + 1.740(PAR) + 0.664(\ln(PAR)) - 0.425(PAR)^2 - 0.668(VPD): \ r^2 = .68 \]

SDW: \[ Pn = 1.364 + 3.750(PAR) + 0.376(\ln(PAR)) - 1.188(PAR)^2 - 0.550(VPD): \ r^2 = .66 \]
the 2-D graph (Fig. 24). Although they are similar, the difference is due to the analysis procedure for the 2-D graph.

The equation which best modelled Pn to PAR and VPD includes: constant, PAR, natural log of PAR, PAR squared, and VPD. Each component was significant (p=0.05). R-square values range from 0.66 to 0.69.

Similar to the gwv 3-D response graphs, moisture stressed seedlings were able to maintain a constant or increasing Pn at PAR levels above 1.5 mmol m$^{-2}$ s$^{-1}$, while non moisture stressed seedlings showed a decline in Pn. Otherwise, all treatments showed similar response for all other areas of the environmental matrix measured.
DISCUSSION

There are numerous factors which must be considered when assessing the effect cultural treatments have on seedling growth and survival on a reforestation site. Tree seedlings are linked to their atmospheric environment by gas exchange through stomata. Hence, stomatal control of water loss and \( \text{CO}_2 \) uptake are of considerable importance in determining the capacity of seedlings to develop on a particular site (Osonubi and Davies 1980a). In this research study the testing of the hypothesis, "do different stocktypes have different gas exchange responses to atmospheric conditions?", was approached three ways: (1) replicated measurements at stable environmental conditions, (2) physiological response to one increasing environmental variable using boundary line analysis, and (3) physiological response surface to two simultaneously changing environmental variables. First, morphology results for both species will be discussed.

Morphological Response of Western Hemlock

Initial shoot dry weight of the LDW DIT was significantly higher than the LDD, SDD, SDW treatments. Shoot dry weights after one year growth were not significantly different. Reduced treatment differences was shown in a higher shoot dry weight relative growth rate (RGR) for LDD, SDD, and SDW seedlings as compared to the
LDW seedlings. Greater growth by LDD, SDW, and SDD than LDW could possibly be a reflection of first year foliage higher net photosynthesis (Pn) response rate to photosynthetically active radiation (PAR) (Fig. 2) and vapour pressure deficit (VPD) (Fig. 3).

Final average shoot heights were highest for the long-day seedlings (Table 3), however short-day seedlings showed greater height RGR (Table 4). The more balanced, physiologically modified, seedlings were quickly approaching the same size as the LDW seedlings which had begun with the largest needle area and dry weight. Similar to these results, O'Reilly (Pers. Comm.) studying the same stocktypes planted on a reforestation site on Vancouver Island found the long-day treatments to have the greatest height and diameter at the end of the first growing season.

Long-day seedlings had the greatest final total root dry weight, reflecting the adjustment required to reach a shoot to root balance. In particular, the adjustment was more pronounced with LDD seedlings, since they started with the lowest root dry weight and highest seedling water balance ratio.

Seedling treatments grown on a high available soil moisture site, when compared to the same seedling treatments planted on a reforestation site grown for 8 months (data in Grossnickle et al. 1990b), exhibited large morphological differences. Seedling growth on the high available soil moisture site showed, on average, 3 times the height and
root dry weight and 6 times the diameter and shoot dry weight as compared to those on the reforestation site. Large differences in growth were probably due, in large part, to lack of drought and weed competition on the control site.

As for stocktype effect on a coastal reforestation site, the short-day seedlings showed the best response, after one year growth, by having the lowest needle damage and best seedling water balance, and the best growth as shown by the number of stem units per centimeter on the leader (Grossnickle et al. 1990b). Calculated RGR over the same period on the reforestation site showed that LDD, SDD, and SDW seedlings had the highest height, diameter, and shoot dry weight RGR values (unreported data).

Morphological Response of Western Red Cedar

The LDW DIT (control) seedlings were noticeably larger prior to field planting (Table 6). After the eight month growing season, there were no significant differences in seedling morphology among stocktypes. A possible reason the initial morphological differences were reduced, is the slightly higher Pn response to PAR and VPD from first year foliage of moisture stressed seedlings.

Seedlings from the control site exhibited, on average 5.5, times the height, diameter and root dry weight growth, and 15 times the shoot dry weight growth as compared to similar treatments on the reforestation site (Unreported data). It is noteworthy that western red cedar seedlings
exhibited remarkable growth, showing a 25-fold increase in shoot dry weight compared to an average 14-fold increase for western hemlock. This species difference could possibly result from the non saturating Pn response to PAR (of the second year needles) of western red cedar as compared to a saturating irradiance response for western hemlock.

For western red cedar, daylength had a negligible effect on gas exchange, and marginal effect morphologically, perhaps because western red cedar do not develop a true bud (Hosie 1979). Moisture stress showed a positive, yet marginal, effect physiologically, and it has been suggested that its beneficial effect may be improved by increasing the moisture stress levels used to precondition the seedlings (Grossnickle and Arnott Pers. Comm.). It therefore can be seen from this study that moisture stress is a more effective preconditioning treatment, as compared to daylength, for balanced shoot/ root ratios and that more research into stronger stresses may prove fruitful.

Physiological Measurements at Stable Environmental Conditions

This procedure attempted to collect monthly measurements of replicated physiological data at stable environmental conditions (western hemlock Fig. 1, western red cedar Fig. 14). It was thought that this procedure would provide a method to monitor changes in stocktype physiology over the first growing season. As response data, developed
later, indicated (western hemlock Fig 2-13, western red cedar Fig. 15-26), the physiological interpretation could change dramatically, depending on the environmental conditions under which the data was collected. Hence, environmental changes during measurement could confound stocktype physiological differences.

In the field, it was difficult to measure 40 seedlings (10 replicates per treatment) in 60 to 80 minute period and have climatic conditions constant throughout this time period. Every effort was made to collect data under clear skies and this objective was achieved for afternoon readings. Clear skies kept PAR and VPD variations, for the most part, to a minimum. Under cloudy skies, collecting data was more difficult because of continually changing conditions, and this meant that data collection was disrupted due to wide PAR variations which extended the sampling period, and increased VPD variations.

Replicated measurements method of data analysis has been used in controlled environments (Blake 1983), on characterizing species differences (Running 1976, Fry and Phillips 1977), or comparing values at different dates (Running 1980). Grossnickle et al. (1990b) used this method for data collected on a reforestation site with these same stocktypes, but found non-consistent trends. In further analysis Grossnickle and Arnott (1990) used boundary line analysis, and judged this method better to separate stocktype differences because each data point was
independent with its own climatic information, and thus was a better measure of physiological response. For the aforementioned reasons it is inherently difficult to discern true differences between stocktypes in the field using replicated measurements.

It would appear that data collection, of this nature, should be obtained in a controlled environment for more reliable results. Seedlings could be planted in water permeable pots in the field and moved into a controlled environment the day before measurements were to be taken. Data could be collected at an effective predetermined stable and constant environment and then seedlings taken back to the field. This could most likely be done over the growing season with minimal disturbance to the seedlings.

Physiological Response: One Environmental Variable

Basic Physiology

Stomatal conductance (gwv) values of 0.1-0.3 cm s\(^{-1}\), determined from this study are comparable to other studies for western hemlock (Running 1976, Livingston and Black 1987). No such data have been published for western red cedar by which to compare values. Stomatal response to increasing VPD and/or PAR for these species have not been previously reported in the literature, except for a relative gwv term for western hemlock (Livingston and Black 1987). The decreasing curvilinear response to increasing VPD is
similar to that observed for most conifers species (Sandford and Jarvis 1986, Jarvis 1980). Xylem water potentials were always higher than -1.0 MPa and minimum turgor loss point was approximately -1.3 MPa, hence declining gwv with increasing VPD is thought to be a feedforward stomatal response.

In a feedforward system, stomata respond to atmospheric drought by direct drying of guard and epidermal cells, even though seedling water potential is well above turgor loss point (Schulze et al. 1987). Stomatal response to humidity can be independent of changes in bulk leaf water potential (Schulze and Kuppers 1979). Mechanics of a direct stomatal response to humidity is a property of the epidermis, and is related to its steady state turgor (Losch 1977). Lange et al. (1971) suggested that an equilibrium between epidermal water uptake from the mesophyll and a cuticle transpiration (determined by VPD) corresponds to a certain stomatal aperture. Exact mechanisms will remain unclear until more is known about the needle water movement pathway (Schulze 1986b).

Stomatal response to increasing PAR showed gwv increasing as PAR increased (i.e. Fig. 3). Research conducted on several conifer species has shown that stomatal opening in response to light exhibited two phases: first, a rapid increase in gwv over low PAR levels and, second, a very gradual increase of gwv over higher PAR levels e.g., *Picea engelmannii* (Kaufmann 1976), *Pinus sylvestris* (Jarvis
and Abies lasiocarpa (Kaufmann 1982a). The low light level response has been obscured by the boundary line analysis method (i.e. Fig. 3), but is seen in 3-dimensional (3-D) surface response graphs (i.e. Fig. 4A-D).

Research has shown that two photoreceptors, blue and red light pigments, are involved in stomatal opening with blue light important for low light level response and red light important at high light intensity (Zeiger 1983). Chlorophyll is accepted as the red photoactive pigment and flavin as the blue photoactive pigment but the exact mechanism causing stomatal opening is unknown (Ogawa et al. 1978). It is hypothesized that blue light functions as a switch to start stomatal opening, causing protons to be pumped into the guard cells (Zeiger 1983).

Measurements of Pn for western hemlock, other than Grossnickle et al. (1988, 1990a, 1990b) and Grossnickle and Arnott (1990), have been documented in a drought study by Brix (1979) (rates were in difficult to convert units, mg CO₂ hr⁻¹ dm⁻¹) and Fry and Phillips (1977). There are no reported studies on Pn of western red cedar. Carbon dioxide assimilation increased in an asymptotic manner, with increasing light intensity for all four stocktypes similar to other tree species (Beadle et al. 1985b, Vu et al. 1986). The light saturation range of 0.6 - 0.8 mmol m⁻² s⁻¹ has not been reported for western hemlock, but was similar to saturation levels reported for other conifers, e.g. Picea
sitchensis (Bong.) Carr. (Beadle et al. 1985a), *Pinus teada* (Teskey et al. 1986).

Western red cedar first year foliage also had a saturating irradiance for Pn (Fig. 18); however, the second year foliage showed no saturating irradiance level (Fig. 24). *Larix leptolepis* also exhibited a non saturating type of response (Fry and Phillips 1976), as well as *Pinus sylvestris* at moderate to high air temperatures (Beadle et al. 1985a). First year foliage showed a saturating irradiance possibly because seedlings were grown in high density styroblocks which led to "shade" foliage development. On the control site, foliage was developed in an open area which allowed for "sun" foliage development. Sun foliage is generally thicker and has a higher Pn response to PAR as compared to shade foliage (Leverenz and Jarvis 1979, Benecke et al. 1981). Beadle et al. (1985a) suggested that non saturating response is related to large gradients of light within needles resulting from predominantly unidirectional illumination in the field from the sun, and that thick needles would not have all reaction centers saturated at the same incident PAR, as in thin leaves. Hence, it is possible that second year foliage Pn increased with increasing PAR because, once the top of the thicker foliage was saturated, the bottom part continued to contribute to foliage Pn until it reached a light saturation level.
The finding that second year foliage of western hemlock had a lower saturating irradiance for Pn, and a greater Pn efficiency at low irradiance as compared to western red cedar is consistent with the known high degree of shade tolerance of *Tsuga* species (Hosie 1979).

Net photosynthesis reduction with increasing VPD was observed for both species, and for both first year and second year needles. Net photosynthesis reduction is not thought to be induced by lowering internal CO$_2$ (Ci) (via stomatal closure), but by transpiration stress (Sharkey 1984). Direct measurements of Ci (Sharkey et al. 1982) have revealed that Ci remains constant during various physiological stresses (Sharkey 1984, Briggs et al. 1986, Scarascia-Mugnozza et al. 1986). Calculated Ci values showed between 250 - 350 ppm for the entire study (unreported data). Sharkey (1984) found that high transpiration produced water stress over small areas within a leaf and reduced mesophyll Pn. He proposed that large water potential gradients within leaf areoles, between the xylem and site of evaporation, are responsible for Pn decline observed after transpiration stress. The limitation is considered to be attributed to reduced ribulose-1,5-bisphosphate regeneration capacity at the mesophyll (Farquhar and von Caemmerer 1982), and/or losses in chloroplast capacity to fix CO$_2$ (Sharp and Boyer 1986).
Stocktype Effect

It was found that greenhouse cultural treatments affected both the gwv and Pn response of western hemlock and western red cedar first year needles. In western hemlock, the short-day seedlings had a higher gwv response to increasing PAR (Fig. 2) and to increasing VPD (Fig. 3). The explanation may be attributed to one, or all three, of the following possible factors. Grossnickle et al. (1990a) working with the same stocktypes found that at low root temperatures, long-day seedlings had significantly higher resistance to water movement as compared to short-day seedlings through the plant-atmosphere continuum. If resistance difference influenced gwv, it is thought that it would most probably be through a minor feedback response. A second explanation is through morphological modification of stomata or physiological response modification of the epidermis and guard cells (feedforward system). Subtle differences in cuticle thickness could influence this response. Thirdly, perhaps a modification of the feedforward system tolerance to evaporative demand was better developed in the short-day seedlings. It was found that the short-day seedlings had a lower osmotic potential at saturated, and at turgor loss point water potential, as compared to long-day seedlings just before field planting (Grossnickle et al. 1990a).

For western hemlock, moisture stress and daylength greenhouse cultural treatments have an independent, and
combined, influence on Pn response to increasing PAR. Moisture stressed seedlings had equal or higher Pn response particularly at greater PAR than non moisture stressed seedlings. Moisture stress preconditioning has been reported to positively influence other plant species' Pn by possibly decreasing non stomatal mesophyll limitations (Matthews and Boyer 1984, Sen Gupta et al. 1989). For western hemlock, short-day seedlings exhibited a higher Pn response than did long-day seedlings (Fig. 5). Seilor and Johnson (1985) cite differences in osmotic potential, as found in western hemlock daylength treatments, could influence Pn response. Also, short-day treatments have a lower resistance to water movement along with better shoot to root ratios which may contribute to better water availability at the mesophyll (Grossnickle et al. 1990a).

Western red cedar first year needles moisture stressed seedlings had a higher Pn response to changing VPD. Again, decreased non stomatal limitation of moisture stressed seedlings might contribute to this response (Matthews and Boyer 1984). Additionally, the osmotic potential for western red cedar moisture stressed seedlings was marginally lower, as compared to non moisture stressed seedlings prior to field planting (Grossnickle et al. 1988).

For western hemlock, it was interesting after observing the higher gwv to VPD response of short-day as compared to long-day, not to see SDW with as high Pn response as SDD seedlings. This is most likely due to the independent nature.
of Pn and gwv (Kuppers and Schulze 1985), and the higher Pn response of moisture stress as compared to non moisture stressed seedlings. Western hemlock LDD seedlings did not have a higher Pn response than might be expected, possibly because the shoot to root imbalance, or higher seedling water resistance countered the moisture stress treatment advantage.

For both species, cultural treatment effect did not manifest itself in Pn response of second year foliage (Fig. 11, 24). It seems reasonable that new foliage, developed in the same environment with no soil water restrictions, would have similar mesophyll architecture and hence Pn response to increasing PAR.

Stomatal response of second year needles, however, showed a much reduced, but noticeable, treatment difference. It is possible that for western hemlock greenhouse cultural DIT differences continued to influence gwv response through differences in shoot to root ratio. This was not seen with western red cedar second year foliage probably because initial western red cedar DIT morphologies were similar.

Physiological Response: Two Environmental Variables

Three dimensional models are a series of 2-D models which show important interactions of two variables. For example, Pn to increasing PAR 2-D figure does not show the possible effect VPD has on Pn over the entire PAR range. Likewise, second year gwv response to VPD 2-D figure does
not show the gwv decline that occurs at high VPD over the range of PAR. Development of 3-D phenomenological models describing gwv and Pn, using primary environmental factors, helps to further define gas exchange processes. For these reasons, gwv and Pn response surfaces were modelled to PAR and VPD.

It became apparent from the 2-D graphs that large differences between stocktypes would not be discerned, but that small differences in magnitude would have to be detected. Knowing the 2-D response type, a number of different empirical models were tested.

One input environmental variable physiological response models are more numerous than simultaneously changing two input response models. Authors who have modelled the effects of simultaneously changing PAR and VPD on tree species are Grossnickle and Reid (1985) on *Picea engelmannii* for gwv and Meinzer (1982c) on *Pseudotsuga menziesii* for water use efficiency. These response surfaces showed that gwv is strongly influenced by VPD and that PAR only has a modifying effect.

Net photosynthesis versus PAR and VPD response surfaces show that light intensity is the dominant factor, and that VPD has a strong modifying effect. Photosynthesis under most conditions responds exponentially to increased PAR, and then levels off at a saturation level (western red cedar second year needles were an exception). Increasing VPD decreased the magnitude of this response. A representation of this
type has not been published for any forest tree species. However, it is noted that Meinzer (1982c) used this type of representation for *Pseudotsuga menziesii* water use efficiency.

The 3-D response surfaces indicated an independent behavior of gwv and Pn. When gwv was reduced dramatically by increasing VPD, Pn was reduced only progressively. When gwv opened at low PAR (< 0.1 mmol m\(^{-2}\) s\(^{-1}\)) to a near maximum, Pn did not reach full capacity until 0.6 - 0.8 mmol m\(^{-2}\) s\(^{-1}\) or more. Recent findings describe the relationship between Pn and gwv as independent, except under extreme conditions (Beadle et al. 1985a, Kuppers and Schulze 1985).

Unique species differences were observed. Western hemlock second year foliage showed the typical gwv reduction with low to moderate VPD (1.0 - 2.0) with gwv near zero at VPD levels above 3.5 kPa. Since water potentials (\(\psi_x\)) were above turgor loss, it is felt that this species exhibited a drought avoidant response (Levitt 1972). Western red cedar second year foliage also had a reduced gwv at mild to moderate VPD, but had gwv values of approximately 0.1 cm s\(^{-1}\) at a VPD of 4.0 kPa and may be defined as a drought tolerant response (Levitt 1972).

Stocktype 3-D surface response differences were consistent with the 2-D responses. Upon close examination, western hemlock LDD, SDD, and SDW DIT first year needles had the highest Pn response, in particular, SDD seedlings. For western red cedar first year foliage, moisture stressed
seedlings had the highest Pn response. For both species, second year foliage of various stocktypes showed almost identical Pn response.

Whether a higher or lower gwv is better under test conditions remains unclear. It would seem that a higher gwv would be better for optimum Pn; however, these parameters for the most part are unrelated, except under extreme conditions (Beadle et al. 1985a). Perhaps a lower gwv would be better to conserve soil water, but realistically, this is of little consequence on a coastal reforestation site throughout most of the year. If one species does not use the water, another adjacent competing species will use the water. The important factor is to keep the stomata open as long as possible under water stressed conditions, up to moderately dry condition, particularly in the first year of establishment. Open stomata are necessary for new root growth because current year photosynthate is necessary for new root development (v. d. Driessche 1987).

Perhaps the higher gwv under moderate VPD, are indicative of moisture stress tolerance. The western hemlock short-day seedlings had the greatest gwv response to high VPD levels, and also had the highest Pn and gwv response when drought tested up to -1.8 MPa predawn water potential prior to field planting (Grossnickle et al. 1990a).
Advantages and Limitations of Phenomenological Models

Two and three dimensional empirical models were constructed depicting gwv and Pn response to VPD and PAR. Advantages of using phenomenological models to various other types of physiological analysis are described below.

Two-dimensional models enable the effects of single environmental factors to be separated. Factors such as optimum temperatures (Beadle et al. 1985a), VPD and PAR (Jarvis 1976) have been studied by this method. Empirical models are relatively easy to create, and do not require complete understanding of biochemical mechanisms involved in the parameters measured (Hall 1982). The 2-D models enable species, stocktype, and possibly genotypic comparisons, without having to test the seedlings at the exact same time or environment, because all recorded data are treated independently. The developed equation can also serve to calculate response given climatic input. Equations have been used for a number of studies (Kuppers and Schulze 1985, Thompson and Hinckley 1977). Three-dimensional models provide a complete conceptual picture of gwv or Pn behavior for 2 interacting environmental variables. Models of these types could be used as submodels in a larger system such as watershed management or ecosystem studies.

Limitations to response modelling, as presented, need to be recognized. Phenomenological models do not contain a time variable, as much as this is an advantage, the model may break down without it being used as an input parameter.
(Thompson and Hinckley 1977). For example, phenomenological models do not describe hysteresis which can occur during the day, nor consider endogenous rhythms which may affect gwv or Pn.

Integrated steady state models can not correctly describe the effects of quickly changing dynamic conditions, such as sun flecks under a forest canopy, or midday "sun shower". Photosynthetic rate dynamics in response to light occurs in a matter of seconds (Salisbury and Ross 1985). However, for stomata response to changing VPD, Watts and Neilson (1978), studying *Picea sitchensis*, reported that gwv changes began after 4-5 minutes, and a new steady state value was reached in about 30-40 minutes. Johnson and Ferrell (1983), studying *Picea engelmannii* and *Pseudotsuga menziesii* found stomata responded quickly to changes in VPD, with the average response time being 30 seconds at high VPD, and 2 minutes at low VPD. The authors credit discrepancies in response time for the two studies to the time constant of instruments used.

Major determinants of gwv and Pn are light and VPD, but under certain conditions soil temperature, freezing overnight temperatures, and soil moisture can have modifying or dominating effects. These factors were not included in this study, but could be incorporated in future model development by producing additional 3-D models (i.e. Pn to PAR and VPD), but at specific secondary factor levels (i.e. -0.5, -1.0, -1.5 MPa soil drought). If it is determined that
these models, which are essentially 4-D in nature, are similar in shape but lower in magnitude, models could be lowered or raised through the x-y plane by determining responses (i.e. Pn) at only a few PAR x VPD combinations. Multiple 2-D models have been produced this way (Turner et al. 1985), but multiple 3-D models of this nature have not been reported in the literature.

Two-dimensional phenomenological models require many data points to ensure that the limit of a physiological variable has been reached over most of the defined range. In 3-D modelling, sufficient data must be collected for all combinations of the 2 environmental variables. As much as the linear relationship between PAR and VPD was overcome by using shade cloth, it was difficult to record conditions at low PAR and high VPD or high PAR and low VPD. Thus, Pn and gwv responses in these corners might be speculative interpretations of what the model predicts.

A model should be tested for validity, using actual data which had not been included in the original development (Thompson and Hinckley 1977). Testing was not done for the models developed. However, it could be argued that, after a model was developed for a particular species / foliage type / physiological response for one treatment, it was tested at least 3 times using data from the three remaining treatments. Additionally, the identical models (same components) were used for both first year and second year foliage for western hemlock. The exception was gwv to PAR
and VPD response model, because a wider VPD range was measured for second year foliage. Although the tests were not independent assessment for each stocktypes, they do validate model components used.

Establishment of strong relationships between Pn or gwv and multiple environmental factors was made difficult by the interdependence of all variables involved. No single model can account for all possible events, or else it becomes too complex and bulky to manage. Despite these limitations, simple models are necessary to understand seedling physiological response to driving environmental parameters (Kuppers and Schulze 1985). Phenomenological models can be important for comparing species / stocktype sensitivities to potential environmental conditions. Research into integrated steady-state measurements of physiological response (i.e. gwv and Pn) over a wide range of environmental conditions together with environmental condition quantification of potential site types might possibly improve forest regeneration success.

Applications of Phenomenological Models

The proper definition of seedling quality is "fitness for purpose" (Sutton 1988). This definition implies that we must not only quantify the seedling stocktypes' physiological characteristics, but also must know beforehand in some detail the environmental conditions of the site to be planted. The idea of knowing the physiological
characteristics does not require stocktypes from each year from each nursery to be intensively tested, but that a one time intensive assessment of stocktypes be made and catalogued. Selection of stocktype for specific sites would then be based on the one time intensive assessment. An annual "mini" test could be performed to ensure stocktypes are developing to standards set by the intensive test.

Phenomenological models of \( P_n \) and \( gwv \) were established using steady-state responses of gas exchange to a range of PAR and VPD. Hence, it predicted carbon assimilation and water loss from known environmental inputs. Phenomenological models allow conceptual comparisons of species, genotype, or greenhouse cultural treatment for potential reforestation sites. After using phenomenological models, it could be speculated that the order of greatest to least response differences which could be detected are: species, stocktype, and genotype. These divisions will each be discussed briefly.

Tree species have inherent genetic differences which are suited to specific sites. Species found on a site prior to harvesting do not necessarily indicate which species is best for growth and survival on the reforestation site. A closer examination of species physiological response characteristics will alert foresters to the shortfalls or advantages of species on certain planting sites. Phenomenological models can point to species overlaps, so
that multiple species could be planted with a better degree of confidence.

It would appear that species physiological response can be modified, depending on greenhouse cultural regime. All stocktypes tested in this study were of good quality (Grossnickle et al. 1990a). However, it would appear that certain stocktypes were better suited for certain environments. More work is necessary to determine the greenhouse cultural treatment effect on physiological response of other tree species and genotypes.

Leaf gas exchange processes have been used to assess poplar clones (Ceulemans and Impens 1980). For conifers, gas exchange studies have been used to assess genetic families, e.g., *Pinus banksiana* (Blake and Yeatman 1989), and *Pinus teada* (Seiler and Johnson 1988). Using the tools of biotechnology the advent of viable embryogenesis (cloning) is currently available for a conifer species, e.g., *Picea glauca* (Roberts et al. 1990). It is possible that genetic combinations which prove to be superior after testing, can be cyropreserved in a deep freeze to form a library of genotypes (Sutton, Ben, Pers. Comm.). Along with genome storage, a physiological "fingerprint" of genotype response can be stored on a computer disk. Cell tissue of a desired genotype could be pulled out in the future, when the need for a specific physiological response arises.

In order to complete the idea of fitness for purpose, it is necessary to have climatic information for the site,
or a site similar to the one to be planted (i.e. "site type"). Climatic data should be catalogued for hourly averages of daylight PAR and VPD on a monthly basis. A ten by ten PAR x VPD defined matrix ranging from 0 to full sunlight, and 0 to the highest seasonal VPD would need to be created. Hourly environmental combinations would be categorized (average VPD and PAR level determined for each hour of the day each month) and then added together. Hourly environmental conditions could be presented as 3-D response surface figures (i.e. z-axis = accumulated hours, y-axis = PAR, x-axis = VPD) summarizing the main atmospheric variables for a site type. When compared with potential seedling physiological response it forms a risk assessment methodology. These response graphs could quickly indicate reforestation site environmental limitations and/or point to the need for specific species, genotype and/or stocktype.

In review, the necessary ingredients for using a seedling fitness for purpose selection program would be as follows. First, select sites which are designated for intensive forest management such as those near mills, private property, and/or sites of good quality. Second, develop a catalogue of species, genotype and stocktype physiological response, and accompanying morphological makeup. Third, collect specific reforestation site environmental parameters, in particular accumulated hourly PAR and VPD for each site type and noted monthly limitations to growth (i.e. temperature, drought). Fourth, develop an
ability to produce (or clone) species, genotype, and/or stocktype combination economically. The implications are that foresters could select in advance the proper combinations of seedling inputs (species, genotype, and greenhouse cultural stocktype) to best fit prospective reforestation sites.
SUMMARY AND CONCLUSIONS

The findings show that daylength and moisture stress nursery cultural treatments, as applied in this study, influenced physiological and morphological characteristics of western hemlock and western red cedar. In this research study, ecophysiological response of 4 DIT were monitored and related to PAR and VPD on a high available soil moisture site.

The major findings for western hemlock are as follows:

First Year Needles
1) Short-day DIT had a higher gwv response to both increasing VPD and PAR.
2) Both short-day and moisture stress treatments improved Pn response to PAR, and the combination, SDD, had the highest response to increasing PAR.
3) SDD DIT had the greatest Pn in response to VPD.
4) The above 2-D responses were reflected in the gwv and Pn 3-D response surface with short-day DIT having higher gwv and Pn.
5) Short-day DIT seedlings were smaller, shorter, had a better seedling water balance ratio and lower shoot to root ratio prior to field planting.
Second Year Needles

1) Short-day DIT had a slightly higher gwv response to both increasing VPD and PAR.

2) No treatment differences were found for Pn versus PAR.

3) The 3-D response surfaces showed both VPD and PAR were primary determinants of gwv and Pn. Stomata exhibited closure at VPD greater than 3.5 KPa.

4) At the end of the growing season, LDD, SDD, and SDW DIT seedlings had higher shoot dry weight RGR. All stocktypes had similar final morphological parameter values.

The conclusion drawn is that greenhouse cultural treatments can influence physiological response of western hemlock first year needles. On first year needles, short-day DIT appears to primarily influence gwv, while moisture stress DIT influences Pn. Growing in high available soil moisture conditions, short-day DIT continued to influence gwv of second year foliage. There was no continued influence of moisture stress DIT on Pn of second year foliage.

The major findings for western red cedar are as follows:

First Year foliage

1) Moisture stress DIT seedlings had greater Pn response to increasing PAR and VPD.

2) Moisture stress DIT seedlings maintained a higher gwv response to changing PAR and VPD as compared to its non moisture stress daylength counterparts.
3) The above 2-D responses were reflected in gwv and Pn 3-D response surfaces with moisture stressed DIT having higher gwv and Pn.

4) LDW DIT seedlings had the largest shoot and root systems prior to field planting.

Second Year foliage
1) Second year foliage exhibited no treatment difference for gwv and Pn response to PAR and VPD.
2) Pn response to increasing PAR showed no irradiance saturation level.
3) The 3-D response surfaces of gwv and Pn showed that both VPD and PAR are primary determinants of gwv and Pn. Stomata exhibited no signs of closing up to VPD levels of 4.0 kPa.
4) All stocktypes had similar final morphology parameter values.

In conclusion, western red cedar greenhouse cultural treatments can influence physiological response. Moisture stress appears to be the most influential DIT exhibiting moderate effects on Pn and gwv. Stocktype treatments showed no influence on second year foliage Pn and gwv response to PAR or VPD.

Three physiological response assessments were used to characterize stocktypes. Attempts to test stocktype response at stable environmental conditions proved at times difficult to control in the field, and potentially can produce large
measurement variation which may not be attributed to stocktype effect. Boundary line analysis, if used correctly and with sufficient data, offers a good stocktype assessment method which enables the isolation of a physiological response to one environmental variable. Three dimensional surface response technique is required to provide a clearer conceptual representation of 2 primary environmental variables influence on a seedlings physiological response.

The selection for a best performing species / genotype / cultural treatment for a specific field site type must be based on foreknowledge of potential stocktype response and limiting environmental conditions of the reforestation site. Boundary line and 3-D response surface analysis contribute to understanding potential physiological response to environmental conditions. Stocktype selection based on this methodology should improve reforestation success.
Literature Citation


Beadle C.L., Talbot, H., Neilson, R.E., Jarvis, P.G. 1985b. Stomatal conductance and photosynthesis in a mature Scots pine forest. III. Variation in canopy conductance


Hinckley, T.M., Schroeder, M.O., Roberts, J.E., and Bruckerhoff, D.N. 1975. Effect of several environmental variables and xylem pressure potential on leaf surface resistance in white oak. Forest Sci. 21:201-211.


**Sample description:** SOIL SAMPLE

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<th>PHOSPHATE</th>
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<th>SULPHATE</th>
<th>CALCIUM</th>
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**EXCESS**

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**TOTAL LBS/ACRE**

| 7 | 12 | 304 | 208 | 0.7 | 1696 | 114 | 99 | 1.2 | 5.7 | 0.9 | 9 |

**SOIL QUALITY**

- Ph (Acidity): 5.78
- E.C. (Salinity): 0.07
- Organic Matter: 5.5
- Texture: Min

**RECOMMENDATIONS**

**Soil:**

**Crop Environment Condition:**

- Excellent
- Average
- Poor

**Crop Choice:**

- Trees and Shrubs

**Expected Yield:**

- N
- P
- K
- S
- Ca
- Na
- Mg
- Fe
- Cu
- Zn
- Mn
- Mo

**Crop:**

**Crop Environment Condition:**

- Excellent
- Average
- Poor

**Crop Choice:**

- Trees and Shrubs

**Expected Yield:**

- N
- P
- K
- S
- Ca
- Na
- Mg
- Fe
- Cu
- Zn
- Mn
- Mo

**Lime and Micronutrients:**

- Add Potassium at a rate of 0.5 lb K20/1000 sq.ft.
- Do not exceed 2 lb per application.
- Add 50 lb/1000 sq.ft. of lime (not evergreens).
- Mg low. Add Magnesium at 1.0 lb-MgO per 1000 sq.ft.
- Sulphur low. Add Sulphur at 0.5 lb-S per 1000 sq.ft.
- At least one micronutrient is rated as low.

- Apply Boron using Borax at rate of 1/4 lb/1000 sq.ft.

A ton of manure (650 lb) will supply approximately 6 lb-N, 2 lb-P205 & 5 lb-K20 per 1,000 sq.ft. Soluble salts may be high.

**Conversions:**

- 1 acre = 43,560 square feet = 0.40 hectares
- 1 cubic yard = 0.8 cubic meters
- 1 lb/acre = 1.2 kg/ha
NORWEST LABS
NORWEST SOIL RESEARCH INC.
203 20771 LANGLEY BYPASS,
LANGLEY, B.C., V3A 5E8
GROWER
B.C. RESEARCH
3650 WESTBROOK MALL
VANCOUVER, B.C. V6B 2L2
Attention of: JOHN MAJOR
LEGAL LOCATION
Sample description: SOIL

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**EXCESS**

**OPTIMUM**

**MARGINAL**

**DEFICIENT**

### NUTRIENT ANALYSIS (P.P.M.)

For growing trees & shrubs apply NITROGEN at a rate of 1.5 lb per 1000 sq. ft. prior to planting or at 1.0 lb/1000 sq.ft. in early spring to established plants. Additional N can be added up to 1.5 lb/1000 sq.ft. with last application before September. No PHOSPHORUS application required.

**RECOMMENDATIONS**

CROPPING PRACTICE:

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**CONVERSIONS:**

1 Acre = 43,000 square feet = 0.40 Acres
1 cubic yard = 0.8 cubic meters
1 lb/acre = 1.12 kg/ha
**APPENDIX 2**

Experimental Design of Field Layout

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(1) There are five (5) rows of each treatment in each block. There are twenty (20) replicates in each row. For morphological evaluation, one tree was randomly selected from each row.

(2) LDD = Long-day dry  
LDW = Long-day wet  
SDD = Short-day dry  
SDW = Short-day wet
Appendix 3. Soil water retention curve of U.B.C. field site. Three intact core samples were used. Analysis and curve by Soilcon Laboratories, 105 - 2931 Olafson Ave., Richmond, B.C., V6X 2R4.