Topographic influence of microclimate and tree physiological activity in early spring

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TOPOGRAPHIC INFLUENCE OF MICROCLIMATE
AND TREE PHYSIOLOGICAL ACTIVITY IN EARLY SPRING

By

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B.A., University of Montana 1970

Presented in partial fulfillment of the requirements for the degree of
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The influence of topography on microclimate and tree physiological activity was studied during winter/spring in Western Montana. Air temperature, soil temperature, radiation, humidity and snowmelt rates were measured on opposing north and south aspects. Xylem temperatures and leaf water potentials of three conifer species were monitored. The north site received 43% of the amount of radiation received by the south site, had a .4°C cooler mean daytime temperature, and 20% fewer degree days above 0°C. This resulted in a 10 to 20 day lag in soil warming on the north site. Xylem tissue of branches and small stems thawed quickly on both sites when air temperatures rose above 0°C, but larger stems remained frozen. Leaf water potentials of all three species showed similar seasonal and diurnal patterns. Long periods of freezing temperatures resulted in gradual dessication of the trees, but they quickly rehydrated during brief warm periods by utilizing thawed water reserves. Water potential differences between sites were greatest during the period when snowmelt was complete on the south site but not the north site, suggesting restricted water uptake on the north site due to cold soils.
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CHAPTER I

INTRODUCTION

Tree growth and survival in Western Montana is variable and highly dependent on the microclimate of a given site. A significant limiting factor is lack of available water late in the growing season when temperatures are still favorable for growth. During early spring, when soil water is ample from snowmelt and air temperatures are warm, the potential for physiological activity would appear to be high. Larcher (1980) states that by late February at intermediate latitudes, the post dormancy period has ended and the potential for physiological activity is greatly increased.

Under certain conditions this may be true. Warm weather can trigger increased transpiration from stomatal opening (Fahey, 1979; Turner and Jarvis, 1975), but this transpiration may quickly close the stomates (Turner and Jarvis, 1975) by reducing the leaf water potentials to the threshold level. The ability of the tree to recover overnight (Running, 1980) may be severely restricted due to an already depleted water reserve from winter cuticular
transpiration (Tranquillini, 1982) combined with limited water uptake from cold soils of spring snowmelt (Evans and Reid, 1976).

One objective of this study was to assess the potential for water movement by conifers during winter / spring in Western Montana through examination of environmental conditions, tree water status, and tree xylem temperatures. A second objective was to compare and quantify the differences in microclimate between contrasting sites with north and south exposures during the same period.

Water movement through the soil-plant-atmosphere continuum is necessary for physiologically active conifers. Therefore a major focus of this study was the environmental conditions of the winter / spring period which may restrict water movement through the system. Air temperatures, soil temperatures, radiation and snowpack were monitored. Concurrently, xylem temperatures and tree water potentials were measured. Two different sites, three different conifer species, and two size classes were chosen for comparisons.

This study was designed to shed light on the following questions: What are the seasonal and diurnal patterns of water potentials in conifers during the winter / spring period? What conditions result in the thawing of xylem tissue in conifers? During warm winter / spring days do conifers develop water stress due to restricted water movement within cold soils? Are there species
differences or microsite differences in the water relations of conifers during winter/spring? Are there significant differences in microclimates between adjacent sites in winter/spring?
CHAPTER II

REVIEW OF LITERATURE

Tree Physiology and Microclimate

Macroclimate has a major impact on tree growth and survival. Numerous researchers have used climatic variables to classify and describe forest types and stand structure (Waring et al., 1972; Grier and Running, 1977; Franklin and Dryness, 1973).

In addition most foresters and ecologists recognize that there are significant differences in sites due to microclimatic differences (Hungerford and Babbitt, 1976). A major cause of microclimatic differences is the effect that slope and aspect have on the amount of incoming solar radiation. This generally results in warmer and dryer conditions for those sites with a southerly exposure.

Microclimate differences between sites can have a significant impact on vegetation. In Michigan it was found that south facing slopes had consistently higher radiation, air and soil temperatures than did north facing slopes (Cooper, 1961). The south slope had a warm xeric micro-environment and the
north slope a cool mesic micro-environment. The canopy of the south slope was dominated by *Quercus velutina* and the north slope by *Quercus alba*.

Small differences in microclimate can result in large differences in growth potential for different sites. Even on sites considered to be not limited by available water, basal area growth was much greater on north facing slopes. This amounted to a 35% greater stand volume on the north vs. south facing slope in the wet humid climate of West Virginia. Lee and Sypolt (1974) concluded that although there were no significant differences in available moisture between the north and south slopes, the microclimate differences of air and soil temperatures and radiation resulted in significant differences in the physiological processes of the trees on the two sites.

This was illustrated in studies of microclimate differences and their effects on trees growing at timberline. In Switzerland, four year old seedlings of *Pinus montana* were transplanted on adjacent east and north facing slopes only 25 meters apart. Measured summer transpiration and net photosynthesis revealed that the seedlings on the north slope averaged a 29% lower rate of net photo-synthesis and a 42% lower rate of transpiration than the east slope seedlings. These differences in tree physiology resulted from an average of 9% less light, 1.8 cooler temperatures and 25% lower v.p.d. levels on the north slope (Hassler,
The microclimate differences between sites results in differences in physiological response by the trees and subsequent differences in site productivity and seedling survival. The microclimate differences found between north and east facing slopes at an elevation of 2200 M in the Swiss Alps were considerable. Snow melt was 5 days earlier on the east slope and soil temperatures during the growing season were 3 - 4 degrees C higher than the north slope. This resulted in the initiation of the growing period 5 - 10 days earlier on the east slope. Although the growing period for Pinus cembra and Pinus montana were about the same length for the two sites, the microclimate differences caused a shift in timing of the growing period. Actual production period for the evergreens was 4 weeks longer on the east slope. After 6 years the dry weight production for east slope conifers was 2 - 3 times greater than the north slope. In addition, after 12 years the survival rate and height growth for seedlings was less on the north site (Turner et al., 1982).

Wolf et al. (1977) report microclimatic affects on the water potentials of trees growing in cold soils of Alaska. Although the wet soil conditions on both sites tended to minimize the differences, the ridge site showed a smaller diurnal range of xylem pressure potential than the lowland site. The lowland site had colder soil temperatures and
warmer air temperatures. For the entire growing season the greatest difference in minimum water potential values occurred in May when the air and soil temperatures were coldest.

Kincaid and Lyons (1976) recognizing that winter micro-environment may have an effect on tree dessication, studied four different sites on a southwest slope differentiated by elevation. They noted marked microclimate differences, but minimal differences in tree water status.

Slatyer (1976) created microclimatic differences with screens to reduce radiation and/or night frosts on vegetation. Greater water stress was noted in the coldest microsite in winter. The warm microsite showed greater transpiration and water absorbtion.

Lindsay (1971) found microclimatic differences affected water stress development in timberline trees. Needles exposed to the environment developed water potentials down to -35 bars, while needles protected by snow only decreased to -20 bars.

In addition to elevation, slope and aspect, the vegetation cover itself creates microclimate differences. Researchers have found a high correlation between the basal area or density of a timber stand and transmissivity of solar radiation (Muller, 1971; Soloman et al., 1976). Thus the snowmelt process in spring will not be the same for two different forest stands since short wave radiation is a
significant energy source for snowmelt (Soloman et al., 1976).

Individual trees can be affected by the amount of canopy closure. Sakai (1966) found a strong coupling of tree stem temperatures to radiation flux. At 1200 hours the temperature of the outer xylem (2.5 cm below bark) on the south side of the tree was 15 degrees C yet the air temperature never exceeded 2 degrees C. The temperature at 1.5 cm below bark on the north side of the tree was within 1 - 2 degrees C of the air temperature. Herrington (1969) found that stem temperatures within a dense canopy showed very little variation due to angular position.

Microclimate Measurements

Spomer (1973) maintains that it is necessary to study and understand the "operational environment" when looking at biological processes. By measuring and monitoring certain environmental parameters, this "operational environment" or the influence of microclimate on vegetation can be better understood.

Hungerford and Babbitt (1976) identified a number of environmental parameters that should be accurately measured and monitored on remote forest sites; soil temperature, air temperature, organism temperature, solar radiation, plant water potential, snow accumulation, snow melt rate and relative humidity.
To understand the temperature regime of a given site or organism, hourly and daily minimum to maximum measurements should be recorded (Hungerford and Babbitt, 1976). To obtain temperatures with precision greater than 1 degree C measurements must be averaged over a period of 15 to 30 minutes (Campbell, 1977).

Thermistors may be used to measure soil, air and organism temperatures. These measurements have been successfully monitored and recorded on an automated electronic data logger in remote forest sites in the field (Hungerford, 1979). Thermocouples have also been used to measure tree temperatures as well as air temperature (Sakai, 1966, 1968; Herrington, 1965, 1969; Steele and Henderson, 1967; Derby and Gates, 1966; Wolf et. al., 1977).

Another approach to monitoring or predicting the effect of temperature on biological processes is to calculate the amount of heat accumulation above a given threshold value over a given period of time. The amount of heat accumulation can be expressed in degree days (Baskerville and Emin, 1969).

Degree days have been used to estimate date of crop maturity (Holmes and Robertson, 1959), and to predict bud burst in trees (Thomas and Moncrieff, 1982). It is a commonly used method for estimating heating and cooling requirements for buildings or greenhouses (Williams and MacKay, 1970) and to compare climates of a given region
(Konigsberg, 1980). Thawing degree-days and freezing degree-days have been calculated in studies of freezing and thawing of soil and ice (Thompson, 1963). The degree-day accumulation can be calculated using the mean daily temperature obtained from hourly readings or the maximum and minimum readings for the day (Williams and MacKay, 1970).

Water Potential Measurements

The pressure chamber technique for measuring the water potential of trees has become a widely accepted field method in forestry, botany and agriculture. One source of error in the use of the pressure chamber is the temperature of the twig sealed within the chamber. Evans and Reid (1974) found that the pressure chamber gave erroneous measurements when twig temperatures were less than -.5 degrees C. Measurements made below -.5 degrees C consistently showed lower xylem pressure potential values than the controls. In addition the lower the temperature of the tissue the greater was the error. When the temperature approached -10 degrees C errors as great as -15 bars were recorded. Under such conditions, Evans and Reid (1974) suggested warming the tissue at 15 - 20 degrees C for 10 minutes in a humidity chamber before placing in the pressure chamber. Using this technique with Engelmann Spruce resulted in a -1.5 bar error.

Others have stored detached twigs for longer periods
without significant changes in water potential (Kincaid and Parsby, 1976). Using double bags of polythene Hellkvist and Parsby (1976) stored twigs of Pinus sylvestris at 4 degrees C for 26 hours. The water potential measurements varied by .5 to 1 bar from those measured immediately. Karlic and Richter (1979) explored methods for storing detached twigs of a number of broad leaves as well as conifers. Spruce twigs placed between wet foam rubber mats proved to be adequate storage for up to 24 hours without a significant change in water potential.

Kincaid and Lyons (1981) stored red spruce shoots at a temperature of near 0 degrees C for 4 hours in sealed plastic bags. Measurements of water potential of these shoots were found to be not significantly different than those measured on site.

Noting that subfreezing temperatures may influence pressure chamber measurements (Evans and Reid, 1974), Fahey (1979) allowed the twigs to thaw before taking measurements during the winter.

**Physiological Implications of Cold Soils**

Dessication of conifers during the winter months has often been attributed to low soil temperatures coupled with warm sunny days. During these periods transpiration occurs, yet the low soil temperatures restrict movement of water through the roots and xylem tissue. The result is
dehydration of leaves, twigs and upper stems (Sakai, 1970; Tranquillini, 1982; Lindsay, 1971).

Reviewing the literature in more detail by looking at the individual parts of the soil-plant-atmosphere continuum (SPAC) can provide some insight into the water status of trees during the winter and spring.

Trees growing in regions with long cold winters are exposed to months of cold, sometimes frozen soil. Cold and frozen soils have been documented by numerous researchers (Tranquillini, 1982; Rieger, 1973; Johnson and Billings, 1962; Sakai, 1970).

Whether the soil freezes or not depends on the depth of snow cover (Tranquillini, 1976). In Japan, Sakai (1970) recorded subzero temperatures in the soil to a depth of 30-40 cm with the soil temperature at 10 cm remaining below 0 degrees C for four months. Minimum soil temperature was -5 degrees C. The soil was frozen in areas with little snow cover; soil remained unfrozen where snow depths exceeded 40-60 cm.

With 2.1 meters of snow on the ground in the Sierra Nevadas of California, Smith (1972) recorded a soil temperature of 0.4 degrees C at a depth of 2.54 cm.

Sartz (1967) found that the temperature threshold for frozen soil was -1 degrees C, yet temperature alone was a
poor indicator of frost depth due to the temperature variation within the frozen layer. Later Sartz (1969) found that despite the fact that the soil was frozen, water moved freely through the profile. Infiltration from midwinter snow melt occurred during short periods of thaw and percolation was evident during the frozen period.

Low soil temperatures can restrict water movement into trees. This restriction is not entirely due to the increased viscosity of water at low temperatures.

Anderson and McNaughton (1973) found that reducing soil temperature from 20 degrees C to 3 degrees C did not significantly decrease transpiration or photosynthesis in a majority of montane species studied. The low soil temperature did reduce leaf relative water content, indicating a reduction in water absorption at low soil temperatures. The high elevation species showed greater root permeability at low soil temperatures than did the low elevation species.

Kaufmann (1977) found increased resistance to flow at root temperatures of about 12 degrees C in Monterey pine and at 7.5 degrees C in Engelmann spruce. Very large resistances occur at root temperature of 5 degrees C. With root temperatures at 5 - 8 degrees C the midday xylem pressure potential was -12 bars as compared to -8 bars at 20 degrees C. The rate of transpiration was not affected by soil temperatures since the critical level of leaf water
potential for stomatal closure was not reached.

Kaufmann (1975, 1977) concludes that these increased root resistances at low temperatures are the result of membrane effects to permeability since the magnitude is greater than can be accounted for by the viscosity of water alone.

Studying root permeability of Engelmann spruce under snowmelt conditions, Evans and Reid (1976) found that water uptake was three times greater at 7.5 degrees C than at 0 degrees C. This indicated a high temperature phase and low temperature phase for root permeability. At the high temperature phase, the viscosity of water at a given temperature is the major resistance to flow, whereas at the low temperature phase, a change in membrane permeability creates a greater resistance.

Running and Reid (1980) found high root resistance to water uptake in *Pinus contorta* seedlings when root temperatures dropped below 7 degrees C. Root resistance was 67% of total plant resistance at 7 degrees C and 93% at 0 degrees C. Due to these high resistances, the leaf water potential was lower at lower temperatures, but all seedlings were able to recover to -2 MPa overnight. Like Kaufmann (1975, 1977), Running and Reid conclude that the high root resistance at low temperatures is due to a change in membrane permeability.

From the literature it appears that water absorption
does occur at low soil temperatures, however the rate is severely limited by the combination of increased viscosity of water and increased root resistance.

**Physiological Implications of Frozen Xylem**

Assuming the tree has been able to absorb water from the cold soil and into the root xylem tissue, then continued movement up the tree must occur to avoid dessication of the leaves. To consider the conductance of water within the stem during the winter / spring it is necessary to examine the stem and the conducting area of the stem.

Using heat pulse velocity measurements it has been determined that there is considerable variation in the conducting area (sapwood) of lodgepole pine and Engelmann spruce (Swanson, 1967, 1974). Both species showed very little movement of water in the five most recent annual rings. Sap velocity was greatest in sapwood older than 10 years and decreased in both species beyond a depth of 2 cm.

In Colorado, Swanson (1967) found the wet zone (wood with moisture content greater than 100% dry weight basis) to vary annually. The depth of the wet zone in lodgepole pine ranged from 5.5 to 7.3 cm. The wet zone depth was the least in March and the greatest in April. In Engelmann spruce the wet zone depth ranged from 3.4 cm to 6.1cm. The wet zone depth was least in late February and greatest in May. Thus the wet zone area increased sharply for both species during
the spring. The actual wet zone moisture content fluctuated greatly between February and June with the highest values in March and lowest values in April.

Assuming that sapwood area is of importance in conducting water, the effect of temperature on conductance must be examined. How does air temperature influence stem temperatures? Does all of the stem of just parts of the stem remain frozen at any given time? What factors have the greatest influence on stem temperatures?

During extensive energy budget studies of a Pinus resinosa stand, Herrington (1969) made numerous springtime measurements of the temperatures within a tree stem. Choosing a stem with minimum influence from incoming solar radiation, he found the surface temperatures to be maximum at about 1300 hours. At a depth of 3 cm into the stem, maximum temperature was not reached until 1700 hours. Under these conditions the temperature of the surface and the interior of the stem was not a function of angular position. Measuring the cambium temperature of an aspen in the south edge of a stand in April, Derby and Gates (1966) found that the incoming radiation was a significant factor influencing stem temperatures. Increasing stem temperatures were recorded on the east side first, then south, west and north. The southern side of the tree reached the highest temperature and continued to be the warmest side of the tree from 1200 hours to 1700 hours.
In winter in Sapporo, Japan, the center of tree stems as large as 86 cm in diameter were found to be frozen. During the day when air temperature was barely above freezing the south side of the stem 2.5 cm below the bark surface was almost 15 degrees C. Other positions within the stem remained near freezing. Stem temperatures taken 10 cm below the snow surface showed as much as 6 degrees C fluctuation in temperature yet remained frozen throughout the day. The temperatures within the stem were influenced by such factors as radiation, air temperature, diameter of the tree, position within the stem, height above the ground and color of the bark. Sakai (1968) found that tree stems 5 - 30 cm below the snow level usually remain in a frozen state throughout the winter.

Sakai (1970) observed that in January tree stems on both north-western and north-eastern slopes thawed during the day. The stem on the southern exposure reached 17 degrees C at midday and was unfrozen for 6 hours. The stem on the northern exposure remained unfrozen for 2 hours and reached a maximum temperature of 6 degrees C. Tree stems on the lowest part of the northern slope remained below 0 degrees C throughout the day.

Mid-stem temperatures of red spruce (dbh 7.0 - 8.0 cm) during the winter in New Hampshire were found to be very close to ambient air temperature at mid-day (Kincaid and Lyons, 1981).
The evidence indicates that stems and portions of stems can be frozen for considerable periods of time. How does the freezing of the sapwood affect water conductance within the tree?

Sakai (1968) determined that when a limited part of the basal stem of conifers is kept frozen at temperatures below \(-0.55\) degrees C, the ascent of the water within the stem is completely blocked. He concluded that the temperature of the stem is the determining factor as to whether water movement occurs and not the temperature of the soil. Thus if the temperature of the soil is near 0 degrees C and the depth of the frozen soil minimal, the xylem remains unfrozen. Water ascent can occur under these conditions but will stop if air temperature reduces the temperature of the xylem to its freezing point (\(-0.55\) degrees C).

Apparently, freezing the xylem does not physiologically impair its ability to conduct water. The xylem tissue of frozen spruce was able to conduct water immediately upon thawing (Hygen, 1965). Frozen xylem was able to conduct water at a rate of 1.5 cm/h which is about 3% of the summer rate. He demonstrated that the amount of unfrozen water in the xylem tissue is over 30% (dry weight basis) even down to \(-20\) degrees C and this may allow for some translocation through the winter.

Blocking the ascent of water by freezing the xylem tissue of *Picea glauca* (Sakai, 1970) caused a significant
decrease in water content of leaves, twigs and buds. A stem temperature of -1.5 degrees C for less than one month resulted in defoliation with the water content of the leaves decreasing from 52.9% to 20.7%.

Sucoff (1969) and Hammel (1967) found that freezing of conifer xylem to -4 degrees C terminated water uptake, but thawing of the tissue resulted in a resumption of uptake within three minutes. The thawing of frozen xylem resulted in an initial surge of uptake greater than that before freezing, however it dropped to the control rate within about 2 hours.

Although there is disagreement as to whether freezing completely stops the movement of water within the sapwood, it has been shown that even if a small part of the sapwood conducting area is not blocked significant amounts of water can be conducted. Mackay and Weatherly (1973) demonstrated that single cuts severing 90% of the cross-sectional area of the stem had no effect on the rate of transpiration or on leaf water stress. Reducing the temperature of the stems had little effect until frozen at -1 degrees C to -2 degrees C.

It would appear that unless the whole stem is frozen, water conduction through the winter / spring period is possible even at relatively low temperatures. During those periods of above freezing temperatures and those periods of high radiation, portions of the stems should be able to
conduct water.

In the Sierra Nevada Mountains of California, radioactive isotope tracers were used to record water movement in trees (Owston, et al., 1972; Smith, 1972). Winter rates of from .3 cm/h to 3.4 cm/h were recorded in red fir. No water movement was recorded for lodgepole pine. In April, the water movement was recorded for 23 days. The rate averaged .45 cm/h for the period. In June with 91 cm of snow still on the ground the water movement ranged from 17 - 18 cm/h. Water use estimates for a single tree were 0.1 liters/h in the winter and 30.6 liters/h in the spring (Smith, 1972).

Although red fir was able to move water in winter and early spring, lodgepole pine was not. Lodgepole pine showed no water movement in April, yet rapid movement in May when snow was still deep. Apparently cold soil temperatures from the melting snow pack did not severely limit transpiration rates when other conditions were favorable (Owston, et al., 1972).

**Transpiration in Winter and Spring**

A discussion of winter / spring dessication of conifers must include a consideration of transpiration during this period. It has been generally accepted that the transpiration rates of evergreen species during the winter are greatly reduced (Kozlowski, 1943; Parker, 1961; Parker,
1963; Neilson and Jarvis, 1976). These lower transpiration rates are the result of stomatal closure which occurs during the normal transition of winter dormancy and frost hardening. With the stomates closed, winter water loss is for the most part attributed to cuticular transpiration (Tranquillini, 1982).

Stomatal conductance of Picea sitchensis in Scotland showed a varied response to temperature depending on the season (Neilson and Jarvis, 1976). Maximum stomatal conductance in the winter was lower than summer and occurred at temperatures between 0 degrees C and 5 degrees C. Temperatures above or below this range resulted in a sharp decrease in leaf conductance. Exposure of the plants to -5 degrees C did not affect the conductance rates the following day for winter / spring plants but did depress the subsequent conductance rates of summer plants.

However Fahey (1979) found that freezing overnight temperatures caused a significant decrease in the rate of leaf conductance the following day in lodgepole pine. When night temperatures were less than -7 degrees C, the conductance rates the following day were always zero.

Fahey (1979) found very low leaf conductance rates during the winter and before the onset of snow melt. After a series of three warm days with non-freezing nights in April, stomatal opening occurred and leaf conductances increased.
Transpiration of hardened seedlings of *Pinus sylvestris* and *Picea abies* was about half the rate observed for dehardened seedlings. *Picea abies* reached maximum transpiration after 4 days of dehardening, while *Pinus sylvestris* required 14 days of dehardening to reach maximum transpiration. The transpiration rate of hardened seedlings is of the same magnitude as the night transpiration rate of unhardened seedlings (Christersson, 1972).

Running (1980) found that dormant *Pinus contorta* seedlings showed a significant decrease (65%) in leaf conductance when root temperatures were at 2 degrees C as compared to 20 degrees C.

A winter / spring comparison of native white spruce in Alaska and introduced species of yellow pine and lodgepole pine showed different patterns of leaf conductances. The white spruce leaf conductances showed a maximum value (cuticular loss and stomatal loss) while the pines showed a steady and minimum leaf conductance only (cuticular loss). The cuticular transpiration rates of the pines increased steadily throughout the period. The cuticular transpiration decreased in the spruce while the maximum transpiration rates increased during the period. These differences between spruce and pines are attributed to differences in strategies; spruce are drought tolerant while pines are drought avoidant (Cowling and Kedrowski, 1980).

At air and soil temperature of 20 degrees C hardened
Picea sitchensis seedlings showed a transpiration rate of 60% compared to unhardened seedlings. The hardened seedlings showed a steady increase in stomatal conductance when irradiated at a soil temperature of 11 degrees C. At a soil temperature of -3 degrees C, the seedlings showed a sharp increase in conductance for one hour and then a steady decrease in conductance. After 5.5 h the stomatal conductance had decreased to nearly 0. Hardened seedlings showed significant stomatal conductance at soil temperatures above -1 degrees C. Transpiration of hardened seedlings at low soil temperatures continued until foliage water potential fell to -27 bars which resulted in stomatal closure. After exposure to one day of warmer temperatures the transpiration rate increased significantly suggesting that conifers can respond quickly to warm periods in the winter (Turner and Jarvis, 1975).

Water Stress in Winter and Spring

Do these water losses by either cuticular transpiration, stomatal transpiration, or both, actually result insignificant water stress in conifers during the winter or spring?

Cowling and Kedrowski (1980) found that the white spruce of Alaska did experience winter / spring water stress while lodgepole and yellow pine on the same site did not. The spruce showed decreasing xylem water potentials during
the period with a minimum of -40 bars in late May. The pines remained stable during the period at 0 bars. The spruce also had a decreasing relative water content of needles from March through May whereas the pines did not. While showing evidence of water stress, the spruce were able to recover significantly during brief periods of above freezing temperatures and precipitation.

Studying water stress during the growing season of black spruce in interior Alaska, Wolff, et. al. (1977) noted minimum xylem pressure potentials in the range of -12 to -15 bars in May which occurred at 0800 hours. Maximum xylem pressure potential values for May were in the range of -4 to -6 bars and occurred between 0200 and 0400 hours. Soils were cold with depth to frost only 3 to 8 cm. The maximum diurnal amplitude of xylem pressure potential was measured in May at 9.4 bars.

Tranquillini (1976) reported that small P. cembra trees at timberline had needle water content of only 80% dry weight (a loss of 36% from Autumn) and osmotic potentials below -40 bars. This dessication occurred during a severe drought in February.

Pressure bomb measurements of base xylem pressure potential of P. contorta during the winter in Wyoming indicated that the trees were under considerable water stress. During the period of March and April base xylem water potentials were usually less than -13 bars, yet there
were no consistent differences in measurements made on wet or dry sites. Even when soils were saturated, trees showed decreasing xylem pressure potentials (-2.7 bars) on warm days. This increased water stress was attributed to cold soils limiting the water uptake (Fahey, 1979).

Yet, Running (1980) found that dormant Pinus_contortae seedlings at a root temperature of 0 degrees C had leaf water potentials of -11 bars during the day, but could recover to -2.0 bars at night.

Xylem pressure potential measurements of Engelmann spruce during snowmelt showed two distinct patterns of water stress. Depending on the year and site, predawn xylem pressure potential measurements were either fairly low (-10 bars) or fairly high (-5 bars). The minimum xylem pressure potential measurements usually were severely low (-20 bars) in early snowmelt and moved to higher levels (-10 bars) by the time the snow pack melted. Minimum xylem pressure potential was highly correlated to the average temperature of the soil during the snowmelt period. The average temperature of the soil was best estimated by percent of snow cover rather than point measurements within the soil. During the snowmelt period the temperature of the soil had much greater influence on the minimum xylem pressure potential values than did any other variable including atmospheric parameters (Evans and Reid, 1976).

Conifer leaf water potentials in the Medicine Bow
Mountains of Wyoming decreased to the annual minimum values by June or July. The severe timberline site reached values of -30 bars in both *Picea engelmannii* and *Abies lasiocarpa* while the forested site only reached -18 bars for the same two species. The spring recovery was a month earlier in the forested site with water potentials at -12 bars. The timberline site recovered by mid July to -15 bars. Due to a lack of snow pack by November, both sites had frozen soils to a depth of 20 cm. The soils remained frozen throughout the winter (Lindsay, 1971).

Krummholz needles of *Picea engelmannii* near timberline in Utah have reached minimum values of water potential at -90 bars in March and April (Hansen and Klikoff, 1972). Attempts to correlate the very low water potential values with changes in sugar content of the leaves were unsuccessful. It was suggested that frozen soils were the most important factor related to low water potentials in the winter and spring.

Studying the timberline of Australia, Slatyer (1976) found water potentials of *Eucalyptus pauciflora* to be not less than -14 bars in the winter and not less than -10 bars in the spring. No severe water deficits were observed during winter or spring. The measurements of water potential showed very little diurnal change in the winter or spring. As light increase from predawn measurements was apparent in the sun exposed trees during the winter day and
a slight decrease in water potential during the spring day was noted (Slatyer, 1976).

The osmotic pressure of leaves of eastern hemlock was determined using pressure volume curves over the course of two years. The osmotic pressure of the leaves was maximum in January just prior to the coldest average temperatures. The percent water in the shoots was 58% plus or minus 3% throughout the winter and showed no correlation to changes in the osmotic pressure. This suggests some correlation between osmotic pressure and frost hardiness (Tyree, et. al., 1978).

Tranquillini (1976) found that evergreens near timberline in Austria had significant seasonal changes in leaf water content. Both young and mature trees had a decrease in water content through the winter reaching the minimum in February. The young trees showed greater water loss due to smaller reserves of water in stem and branches and shallow rooting.

Small trees on exposed slopes with frozen soil showed greater dessication than small trees within the forest and on unfrozen soil. In addition the Krummholz zone trees demonstrated a greater rate of cuticular transpiration than the forest zone trees (Tranquillini, 1976).

The relative water content of black spruce and balsam fir needles at tree line in New Hampshire showed considerable seasonal fluctuation yet similar patterns for
two consecutive winters. The lowest values were recorded in late February for both years. The low values of relative water content for the two winters were 82.4% plus or minus 6.9% s.d. for spruce and 84.7% plus or minus 3.2% s.d. for firs with corresponding water potentials of -28.0 bars and -17.5 bars respectively. The lower values were recorded in late December, late February and again in April with recovery periods in between these lows. These recovery times occurred during cold periods as well as warm periods which made correlation with weather patterns difficult (Marchand and Chabot, 1978).

Winter water potential measurements at four different elevations in the mountains of New Hampshire showed 51% of the total variation was accounted for among trees, 33% by altitudinal zones and 11% by date (Kincaid and Lyons, 1981). Winter water potentials were not found to be exceptionally low with an overall mean of -11.4 bars. The spring values were generally lower than the winter values with the minimum values recorded at all elevations during March. The coldest days did not correspond to the lowest water potentials, in fact low temperature days corresponded to high water potentials (x = -4.6 bars). Significant winter water deficits were not recorded.

Frost drought or frost dessication are terms used to describe the increased water stress trees undergo during the cold winter months (Tranquillini, 1982). It is generally
accepted that cold temperatures restrict water movement in trees. Therefore any water lost due to transpiration in the winter months is difficult for the trees to replace.

In areas with extreme winter conditions the amount of water stress to trees can be considerable, but usually will not exceed the available water reserves (Tranquillini, 1982). Thus physical damage due to winter dessication is not usually the case for most trees in the temperate zone.

Conifers in the temperate zone have been shown to have significant water reserves. It has been estimated that an Oregon Douglas fir forest is capable of storing 267 M3 ha⁻¹, 75% of this in the stemwood (Waring and Running, 1978). Running (1980) noted similar results in *Pinus contorta* in degrees Colorado. The bole provided 73% of the water reserves and the branches provided 14%.

These internal water reserves can provide a long term source of water for the needles. After removing the root system of *Pinus contorta* and subjecting the trees to a dry down period, it was four weeks before dessication damage was observed. After 33 days of dry down the needle water content only dropped from 109% to 107% while the sapwood water content dropped from 66.2% to 21.8%. The leaf water potential dropped from -15.6 bars to -23.1 bars, however most of this drop in water potential occurred within hours of the removal of the water supply and remained nearly constant for up to 33 days. No diurnal change in leaf water
potential occurred during the dry down (Running, 1980).

The soil - plant - atmosphere continuum (SPAC) cannot be described fully using the analogy of Ohm’s law. The capacitance or water storage within the plant must also be considered. The relative water content of the sapwood of *Pinus contorta* was reduced to 60 - 70% regardless of the soil water status (Running, 1980b).

In summary, during the winter periods when water uptake and conductance are either limited or prohibited by cold temperatures within the rooting zone and xylem tissue, leaf water potential will decrease to a certain level and remain relatively constant (Running, 1980). With stomates closed, any change in water status will be a slow rate of increased water stress due to cuticular transpiration. The amount of water lost to cuticular transpiration will depend upon the cuticular resistance of the species, and the vapor pressure gradient between the leaf surface and the air (Tranquillini, 1982).

At the decreased rate of water loss due to cuticular transpiration only, the amount of water stress depends on the water reserves in the shoots, branches and stem (Tranquillini, 1982). During long periods of subzero temperatures the amount of water available to leaves from the adjoining reserves will be limited by the conductance rates within frozen tissue (Hygen, 1965; Sakai, 1968).

During periods of above freezing air temperatures, the
xylem will conduct water immediately upon thawing (Hygen, 1965; Sakai, 1968; Sucoff, 1969). Regardless of the water uptake by roots, the leaves will be rehydrated at the expense of the water reserves within the tree (Running, 1980; Tranquillini, 1982). As long as the water reserves of the tree are not depleted and are available, severe winter dessication of conifers will not be apparent.
CHAPTER III

HYPOTHESIS

Due to topographic influence of microclimate, conifers on a south site will thaw earlier and for longer periods on warm spring days than conifers on a north site. This will result in earlier and greater rehydration (higher predawn leaf water potentials) from internal water reserves, but also earlier and greater dessication (lower minimum leaf water potentials) due to increased transpirational losses for conifers on the south site.
Experimental Sites

The study was conducted at the Lubrecht Experimental Forest about 56 km northeast of Missoula, Montana, during winter/spring of 1982. The Lubrecht Experimental Forest is within the Blackfoot River drainage of the Garnet Range. Located in Western Montana and under the influence of both maritime and continental air masses, the climate of the area is characterized by cold moist winters and warm dry summers. The average annual average precipitation is 45 cm. About 50% is snow (November - April) and another 25% spring rains (April - June). The average annual temperature is 3.8 degrees C with the monthly average temperature below freezing from November through March. The annual average number of days with freezing temperatures is 241 with frost free nights becoming common during May. The snow pack is usually maximum in February (average depth 39 cm, water content 9.4 cm) with snow melt completed by the end of April (Steele, 1983).

Two study sites were located 200 m apart on opposing north and south aspects of a small ridge at an elevation of 1250 m. The south site (azimuth 180°) was on a 6% slope and the north site (azimuth 330°) was on a 39% slope.

The two sites, although in close proximity to each
other, had distinct differences in vegetational composition. The south site supported a stand of predominantly *Pinus ponderosa* (77%) and *Pseudotsuga menziesii* (22%) with an occasional *Juniperus scopulorum*. The north site consisted of a stand of *Pinus contorta* (43%), *Pinus ponderosa* (37%), *Pseudotsuga menziesii* (18%) with an occasional *Larix occidentalis* (less than 2%).

Stand structure was also different for the two sites. (Table I) The south site had an open canopy of a few larger *Pinus ponderosa*, while the north site had a closed canopy dominated by numerous larger *Pinus contorta*. Both stands were young seral stages of the habitat type *Pseudotsuga menziesii/Vaccinium caespitosum* (Pfister, et al., 1977) with a large percentage of sapling size trees.

**Meteorological Measurements**

Comparable meteorological measurements were made for both sites using standard instrument shelters mounted 1.4 m above the ground at the center of each .08 hectare plot for the period of November to June. Air temperature, relative humidity and incoming shortwave radiation were measured at each instrument shelter. Soil temperature was measured at depths of 5 cm and 50 cm. Snow depth and density measurements were made with a Mount Rose snow sampler at random points, but restricted to areas not directly under a tree crown. The percent of snow cover was obtained from the
average of two independent occular estimates similar to the method used by Pfister, et al. (1977) for estimating canopy coverage.

Temperature measurements were made with 1/4" long temperature probes consisting of bare thermistors (Atkins Tech. Inc.) mounted in 1/8" stainless steel tubing with silicon rubber. All thermistors were calibrated at 0 degrees C and 40 degrees C. Incoming radiation was measured with pyranometers (Li-Cor, Inc.) and calibrated against a pyrheliometer (Kipp). Relative humidity was measured with a commercially available (Omnidata, Inc.) humidity sensor.

**Tree Temperature Measurements**

In order to determine when internal water was unfrozen and readily available to the tree, thermistor probes were inserted into the xylem tissue. These probes were inserted and sealed in small holes drilled 2 cm deep from the cambium layer into the north and south sides of the bole at 1.4 m above the ground and into a 4 cm branch on the south side at a mid-crown position.

On each site, a small (dbh < 15 cm) and a large (dbh > 15 cm) tree of both _Pseudotsuga menziesii_ and _Pinus ponderosa_ species were inserted with temperature probes. All four trees on a site were within a 15 m radius of the meteorological station.

Air temperatures, soil temperatures, tree temperatures
and radiation were measured at one hour intervals. All data were then recorded on a digital data logger.

**Tree Water Status**

In order to assess seasonal changes in water status, water potential measurements of selected trees on both sites were made throughout the winter / spring period using a pressure chamber (Ritchie and Hinckley, 1975). Four trees (2 > 15 cm dbh, 2 < 15 cm dbh) of *Pseudotsuga menziesii* and *Pinus ponderosa* were monitored on both sites. In addition, four *Pinus contorta* were monitored on the north site. Predawn water potentials were measured monthly through February months and increased to semi-monthly after February. Since measuring water potentials of frozen twigs may introduce errors (Evans and Reid, 1974), samples collected at below freezing air temperatures were allowed to thaw in the dark in moist plastic bags before measurement (Karlic and Richter, 1979).

Diurnal water potential measurements were taken on the same sample trees on above freezing days throughout the spring. These diurnal measurements were made on at least two week intervals to determine if there was daily fluctuation in the tree water status during periods that would be favorable to physiological activity. Diurnal water potential measurements were taken within the hour for both sites and at about 3 hour intervals throughout the day.
## TABLE I

**STAND CHARACTERISTICS FOR NORTH AND SOUTH STUDY SITES**

<table>
<thead>
<tr>
<th></th>
<th>SOUTH SITE</th>
<th>NORTH SITE</th>
</tr>
</thead>
<tbody>
<tr>
<td>density (trees hectare⁻¹)</td>
<td>655</td>
<td>630</td>
</tr>
<tr>
<td>basal area (M² hectare⁻¹)</td>
<td>7.99</td>
<td>17.03</td>
</tr>
<tr>
<td>mean dbh (cm.)</td>
<td>8.89</td>
<td>14.73</td>
</tr>
<tr>
<td>mean height (m.)</td>
<td>4.57</td>
<td>7.59</td>
</tr>
<tr>
<td>% large trees (&gt;25.4 cm dbh)</td>
<td>7.5</td>
<td>25.5</td>
</tr>
</tbody>
</table>
CHAPTER IV

RESULTS

Site Microclimate Comparisons

The south site was consistently warmer than the north site during winter and spring. The maximum air temperatures showed the greatest differences between sites over the season while the minimum temperatures usually occurred at night and were nearly the same.

The coldest temperatures recorded were during a 10 day period in early February. Minimum temperatures of -30 degrees C with maximum temperatures of -15 degrees C were followed by a week of mild weather with temperatures above freezing during the day and barely freezing at night.

During March the south site had 28 above freezing days while the north site was above 0 degrees C only 21 days. Except for 2 days on the north site, both sites had above freezing days from April 1 to June 6. Above freezing nights began to occur regularly in mid May on both sites.

Figure 1 shows the relationship between the north and south sites based on a 5 day mean temperature calculated from daily maximum and minimum temperatures. The temperature relationship is linear and nearly parallel to the line of equal response at a distance of 1.27 degrees C.
Figure 1. The relationship between north site air temperature and south site air temperature (Jan. 29 - June 6, 1982). The dashed line represents the hypothetical line of equal response, the data points represent the 5 day mean temperature calculated from daily max-min temperatures; $y=1.03x-1.27$, $r^2=0.99$. 
This suggests that the north site is significantly cooler than the south site. Using the two-tailed T-test, hourly temperature comparisons were made between the two sites. The temperature comparisons showed a significant difference in the mean air temperature of the two sites for the full 24 hour day and the daytime (800h - 1800h), but no difference in the night time (1900h - 700h) temperatures. The difference in the mean temperatures was greatest during the daytime with the north site .4 degrees C cooler through the period.

For the winter/spring period there was a significant daytime temperature difference of only .4 degrees C on the average between the two sites. Although the overall temperature difference seems minimal for the period, considerable temperature differences between sites were observed on a number of days. For example on a sunny late winter day the south site was above freezing from 1100h to 1700h, while the north site barely reached above-freezing for an hour (Fig. 2). Given that the potential for physiological activity in trees is greater when air temperatures are above freezing, a number of days similar to the one shown in Fig. 2 would provide favorable conditions for trees on the south site but not on the north site.

The seasonal differences in above freezing air temperatures between the two sites are shown in Figure 3. By calculating the number of degree days above 0 degrees C
Figure 2. Comparison of environmental conditions on day 3-16-82 for both north (---) and south (----) sites.
Figure 3. Seasonal comparison of heat accumulation (degree days above 0°C) for both north and south sites Julian day 29 - 156.
(Thomson and Moncrieff, 1982) for the period, the amount of heat accumulation for the two sites can be compared. For the total period (Julian day 29 - 157) the south site accumulated 20% more degree days above 0 degrees C than the north site. Before snowmelt was complete (day 110) the south site had accumulated 60% more degree days above 0 degrees C than the north site. Once snowmelt was completed on the south site (Julian day 113) both sites had an increased rate of degree day accumulation (Fig. 3). Comparing degree days above 0 degrees C between the two sites for one winter / spring period only, it appears that the south site trees do have a greater potential for physiological activity than the north site trees. The difference in heat accumulation between the two sites is greatest, however, during the pre-snowmelt period when soil temperatures are near 0 degrees C and water uptake by trees is severely restricted.

A comparison of the snowmelt period (Fig. 4) shows the effect of canopy and aspect differences on the rate of snowmelt and soil warming in the spring. The north site maintained a greater coverage and greater depth of snowpack throughout the snowmelt period. This resulted in a 10 day lag in warming of the soil on the north site. While the north site soil temperatures remained at 0 degrees C (5 cm depth) the south site had daytime soil temperatures that ranged from 3 to 18 degrees C.
Figure 4. Comparison of maximum soil temperature [5 cm depth] and snow cover for both north [-----] and south [- - - - ] sites during the snowmelt period 1982.
Soil temperatures for both sites remained at or near 0 degrees C throughout the winter and early spring. Once snow cover was less than 50%, the soil at 5 cm warmed quickly on both sites. After snowmelt the soil temperature on the south site was consistently warmer than the north site at both the 5 cm and 50 cm depths. With intense surface heating on the south site the soil temperature at 5 cm reached temperatures in the 25 - 30 degrees C range in May, while the north site rarely exceeded 15 degrees C. Minimum soil temperatures seldom fell below 0 degrees C on either site. During very cold periods (air temperature -25 degrees C) the soil temperature (5 cm) dropped to -1 degrees C on both sites for several hours a day. Once the snowmelt was complete, minimum soil temperatures rarely dropped to 0 degrees C.

The soil temperature at 50 cm on the south site reached 5 degrees C by April 22nd and remained above 5 degrees C for the remainder of the study period. The soil at 50 cm on the north site did not attain temperatures greater than or equal to 5 degrees C until May 14.

The south site showed above freezing soil temperatures 10 days earlier than the north site at a depth of 5 cm and 22 days earlier at the 50 cm depth. With soils saturated by snowmelt, the potential for water uptake by trees comes earlier in the spring on the south site. During spring days when air temperature and radiation levels are favorable for
tree physiological activity, water uptake on the north site is still restricted by cold soil temperatures (Fig. 5).

The differences in microclimate observed between the north and south sites during the winter / spring period are the result of differences in radiation loads for the two sites. Air temperature differences (especially prior to snowmelt), snowmelt rates and soil temperatures are all influenced by incoming radiation on the sites.

Due to aspect and slope differences it was expected that the two sites would receive different amounts of incoming shortwave radiation. In addition to aspect and slope, it was expected that the amount of canopy coverage would affect the amount of radiation received beneath the canopy.

Figures 2 and 5 illustrate common diurnal differences in radiation received by the two sites. Total measured amounts of radiation received on the two sites for the spring (day 64-155) are shown in Figure 6. By day 155 the north site had received only 43% of the amount of radiation received by the south site.

Based on a computer program for calculating potential incoming radiation for a given site (Swift, 1976), a comparison of north and south sites for the same period is shown in Figure 7b. Considering aspect and slope differences only, the north site should receive 74% of the amount received by the south site. The difference between the slopes of the lines in Figures 7a and 7b can be
Figure 5. Comparison of environmental conditions on day 4-22-82 for both north [---] and south [-----] sites.
Figure 6. Seasonal comparison of accumulated short wave radiation for both north and south sites.
Figure 7. Seasonal comparison of accumulated radiation on the north vs. south sites. 7(a) shows actual measured radiation between day 63 - 155. 7(b) shows maximum potential radiation for the same period.
attributed to the canopy differences between the two sites.

Comparing differences in magnitude between Figures 7a and 7b, the south site received 47% of the maximum potential radiation. Thus canopy closure combined with cloudy conditions reduced incoming radiation for the north and south sites by 73% and 53% respectively. Assuming similar cloud cover for both sites the 20% difference represents the difference in canopy closure for the two sites.

**Potential Physiological Activity**

The results of monitoring air temperatures, soil temperatures and radiation indicate that the potential for physiological activity is greater and earlier for trees on the south site during the winter / spring period due to more favorable environmental conditions. But favorable environmental conditions are not enough if the trees themselves remain frozen. The potential for physiological activity in trees is also determined by the temperature of the xylem tissue. Frozen xylem tissue results in blockage or severe reduction in the movement of water within trees (Sakai, 1968; Hygen, 1965).

Except for several days in January the bole (stem) and canopy branches of all trees on both sites remained below 0 degrees C from mid November to mid February. Significant thawing of trees occurred during a warm period in February and the trees experienced numerous freeze thaw cycles from
mid February to April 20th. By this time all tree boles were thawed and freezing nights reduced canopy branch temperatures to below 0 degrees C but rarely the boles themselves. Below 0 degrees C temperatures in the canopy branches occurred as late in the season as May 30th for some trees. The coldest day recorded for this study brought tree temperatures down to -31 degrees C on both the north and south sites.

Yet during short midwinter warming periods the canopy branches of trees on both sites rose to above 0 degrees C during the day. The canopy branches on the south site were consistently warmer than the branches on the north site and were generally very close to the air temperature for the site. While the branch temperatures were often well above 0 degrees C for a number of hours per day, the south side of stems barely thawed on either site. The north side of the stems did not thaw during these brief warm periods.

The stems of smaller trees were able to respond more quickly to changes in air temperature than were the stems of larger trees. During brief warm periods the canopy branches of all trees on both sites thawed first followed by the south sides of the boles of small trees.

Figures 8 and 9 compare the temperatures of various trees for both sites during the major February thaw. While the branches and stems of small trees thawed on both sites, only the branches of the large tree on the south site were
Figure 8. Comparison of various tree temperatures to air temperature on day 2-15-82 on the south site.

- canopy temp = temperature of branch within the south side of the canopy
- s. stem temp = temperature of south side of stem
Figure 9. Comparison of various tree temperatures to air temperature on day 2-15-82 on the north site.

- canopy temp = temperature of branch within the south side of the canopy
- s. stem temp = temperature of south side of stem
above 0 degrees C. The stem of the large tree remained at 0 degrees C despite being on the south site.

Due to radiation loads, surface heating and storage, it was common for the canopy branch temperatures to exceed air temperatures. The effect of radiation loads on tree temperatures is demonstrated in Figures 10 and 11. Day 3-7-82 was a low radiation day and day 3-8-82 was a high radiation day. On the high radiation day, the south site had much higher branch and stem temperatures than the north site for trees of comparable size.

Figure 12 illustrates the effects of site aspect on the warming of larger *Pinus ponderosa* stems during the spring. Although both sites have above freezing air temperature, the low level of radiation on the north site is reflected in the cooler stem temperatures. The south side of the stem on the north site pine rose above 0 degrees C for only two hours during the day, while the complete stem of the south site pine was above 0 degrees C during the P.M. hours.

Based on hourly temperature data for all trees over the period January 29 to June 6, the canopy branches on the south site averaged above 0 degrees C for 145 hours more than the canopy branches on the north site. The south side of the stems on the south site averaged above 0 degrees C for 213 hours more than the south side of stems on the north site.

Comparing hours above 0 degrees C for the winter /
Figure 10. Comparison of radiation and air temperature effects on temperatures of small trees (dbh=3cm) on north and south sites on day 3-7-82.

- canopy temp = temperature of branch within the south side of the canopy
- s. stem temp = temperature of south side of stem
Figure 11. Comparison of radiation and air temperature effects on temperatures of small trees (dbh=3cm) on north and south sites on day 3-8-82.

canopy temp = temperature of branch within the south side of the canopy
s. stem temp = temperature of south side of stem
Figure 12. Comparison of radiation and air temperature effects on temperatures of large trees (dbh=30cm) on north and south sites on day 3-8-82.

s. stem = south stem temperature
n. stem = north stem temperature
spring period showed the greatest difference in stem thawing to be site related. While the south side of stems on the south site trees maintained above 0 degrees C for 53% of the time, those on the north site averaged 46%. Comparing the number of hours above 0 degrees C for branches and stems of large and small trees on the same site, the small trees averaged 2% more than the large trees. A similar comparison of north and south sides of tree boles showed 3% more hours above 0 degrees C for the south side of the bole.

In conclusion, the temperature of the xylem tissue of the canopy branches very closely mimics the ambient temperature of the site. During periods of high radiation, branch temperatures may exceed ambient temperatures. Therefore above freezing air temperatures usually mean above freezing canopy branch temperatures.

The temperature of the xylem tissue within the stem is dependent on the air temperature, size of the bole, position within the bole and the amount of exposure to direct/indirect radiation.

Generally, the canopy branch thaws first, followed by the stems of small trees, south sides of stems of larger trees and finally the north sides of stems of larger trees. This pattern is strongly influenced by the site and highly variable due to the complexity of radiation within the forest stand.
Potential Physiological Activity - Tree Water Potentials

Winter / spring predawn water potential measurements for the three common species found on the two sites are shown in Figures 13 and 14. All three species show a significant recovery from low mid winter water potentials on day 50 which coincides with a major mid winter thaw. Other than a few above freezing days in January, this was the first major period of above freezing temperatures since late November.

After the major recovery in February all three species followed similar patterns throughout the spring period. Generally periods of cold air temperatures were followed by decreased water potentials while periods of warm air temperatures were followed by increased water potentials. After snowmelt was complete on both sites and air temperatures were consistently warm, the predawn water potentials for all species stabilized in the range of -.6 to -.8 MPa.

Except for the February recovery, Pseudotsuga menziesii maintained lower predawn water potentials than the other two species throughout winter and spring. This species also showed the greatest seasonal fluctuation in predawn water potentials whereas Pinus contorta was much more stable (Fig. 14).

Since Pseudotsuga menziesii appeared the most sensitive to environmental conditions, site comparisons of predawn
Figure 13. Seasonal course of predawn water potential (MPa) for *Pinus ponderosa* (——) and *Pseudotsuga menziesii* (-----) on the south site. Each point is the mean of four pressure chamber readings; vertical bars are one standard error.
Figure 14. Seasonal course of predawn water potential [-MPa] for Pinus ponderosa (---) and Pseudotsuga menziesii (--.--.) and Pinus contorta (——.—) on the north site. Each point is the mean of four pressure bomb readings; vertical bars are one standard error.
water potentials are shown in Figure 15. Early winter measurements show greater dessication on the south site, however after the February recovery the north site tends to show greater dessication. When major recoveries occur (days 50, 88), and during the warmer days of late spring, both sites have very similar predawn water potentials.

The minimum water potentials for *Pseudotsuga menziesii* showing the greatest daily water stress throughout the spring are shown in Figure 16. The greatest difference in minimum water potentials between sites occurs during the period when snowmelt is complete on the south site but not on the north site (days 111, 113, 116). The north site has consistently lower minimum leaf water potentials during this period.

Both sites show increasing diurnal water stress throughout the spring. By early May some trees on both sites have water potentials less than -1.6 MPa in warm soils that are still saturated from snowmelt. Although the warm saturated soils allow for overnight recovery to -0.8 MPa, the decrease to less than -1.6 MPa by 1400 hours suggests an increase in water use by the trees.

Figures 17 and 18 illustrate the difference in water use by the two species on the south site on similar winter and spring days. Although both days show similar ambient conditions (Table II) the diurnal water potential curves are considerably different. Both species show greater diurnal
Figure 15. Comparison of seasonal course of predawn water potentials for Pseudotsuga menziesii on north [---] and south [-----] sites. Each point is the mean of four pressure chamber readings; vertical bars are one standard error.
Figure 16. Comparison of minimum spring water potential measurements for *Pseudotsuga menziesii* on both north [---] and south [----] sites. Each point is the mean of four pressure chamber readings; vertical bars are one standard error.
Figure 17. Comparison of diurnal water potentials for two different days with similar ambient conditions on the south site (see Table II). Each point is the mean of four pressure chamber readings of the same four trees (*Pseudotsuga menziesii*) for both days. Vertical bars are one standard error.
Figure 18. Comparison of diurnal water potentials for two different days with similar ambient conditions on the south site [see Table II]. Each point is the mean of four pressure chamber readings of the same four trees (Pinus ponderosa) for both days; vertical bars are standard error.
TABLE II

<table>
<thead>
<tr>
<th>DAY</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
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<tr>
<td>3-9-82</td>
<td>2°C</td>
<td>10°C</td>
<td>8.6</td>
<td>2585</td>
<td>0°C</td>
<td>1°C</td>
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<tr>
<td>5-3-82</td>
<td>3°C</td>
<td>9°C</td>
<td>6.1</td>
<td>2169</td>
<td>12°C</td>
<td>8°C</td>
</tr>
</tbody>
</table>

A: Previous night minimum air temperature
B: Maximum daytime temperature (1400 h)
C: VPD (mb) at 1400 h
D: Total daily incoming radiation (wm$^{-2}$)
E: Soil temperature -5cm.
F: Soil temperature -50 cm.

TWO COMPARABLE ABOVE FREEZING DAYS/NIGHTS - SOUTH SITE

The two days referred to in Figures 17 and 18 show similar ambient conditions; the pre-snowmelt day and post-snowmelt day show considerable differences in soil temperature.
water stress development in late spring when water uptake is not limited by low soil temperatures.

The diurnal curves shown in Figures 17 and 18 represent typical winter and spring measurements. Generally the winter days showed only small diurnal changes in water potential but by late April all three species showed significant diurnal changes in water potentials. This pattern was similar for the three species on both sites.
CHAPTER V

DISCUSSION

It is generally accepted that soil temperatures near 0 degrees C greatly reduce the uptake of water by conifers (Anderson and McNaughton, 1973; Kaufmann, 1977; Evans and Reid, 1976; Running and Reid, 1980). Therefore during winter and spring when snow pack is present, water uptake by conifers is severely restricted. Water lost by trees during this period cannot be easily replaced by uptake from the cold soil.

From November to January *Pseudotsuga menziesii* showed increasing dessication while *Pinus ponderosa* and *Pinus contorta* did not (Figures 13 and 14). Since transpiration rates are very low during the winter due to stomatal closure (Kozlowski, 1943; Parker, 1961, 1963; Neilson and Jarvis, 1976) water loss during this period is attributed to cuticular transpiration (Tranquillini, 1982). The greater water loss by *Pseudotsuga menziesii* suggests greater cuticular transpiration by this species.

Since thawing of frozen xylem allows for almost immediate water movement (Hygen, 1965; Sucoff, 1969; Hammel, 1967), even the thawing of a small portion of sapwood conducting area will allow for significant amounts of water to be conducted (MacKay and Weatherly, 1973). Regardless of
the water uptake by roots, the leaves will be rehydrated at the expense of the water reserves within the tree (Running, 1980; Tranquillini, 1982).

Once environmental conditions allowed branches and portions of stems to thaw (day 50), all three species rehydrated as indicated by much higher leaf water potentials. Since water uptake by the roots is limited by cold soils, this major recovery and probably other minor recoveries observed throughout the winter/spring are the result of water movement from reserves within the trees themselves.

By comparing maximum potential radiation for the two sites with actual radiation received beneath the canopy, it becomes apparent that canopy coverage is an important variable to consider when comparing micro sites. In this study the amount of radiation received on the site was an important factor in whether large tree stems thawed or not. This supports Sakai's (1966, 1970) and Derby and Gates' (1966) conclusions that incoming radiation is a significant factor influencing stem temperatures.

Since the south side of stems of trees on the south site averaged above 0 degrees C for 213 hours more than the north site trees, trees on southern exposures should be able to maintain higher leaf water potentials by utilizing tree reserves. After the major recovery of day 50, the *Pseudotsuga menziesii* on the south site were often able to
maintain leaf water potentials greater than the north site trees. When recoveries occurred, both sites returned to equal levels of higher water potentials.

Since the north site received less radiation, it had cooler air, tree and soil temperatures than the south slope. When comparing the daytime temperature regimes of the two sites over winter/spring, the average hourly difference of .4 degrees C seems minimal. Yet, this difference accumulated 60% more degree days above 0 degrees C for the south site prior to snowmelt. The result was a 5 day lag in snowmelt and a subsequent lag in soil warming on the north site.

When soil moisture on the south site was readily available to the trees at a depth of 5 cm with maximum temperatures ranging from 3 to 18 degrees C, the north site soil temperature remained at 0 degrees C for another 10 days. Assuming that water uptake by conifers is substantially limited by soil temperatures below 5 degrees C (Kaufmann, 1977) the differences between sites at a soil depth of 50 cm is even greater. The soil temperature at the 50 cm depth on the north site reached 5 degrees C twenty two days later than the south site. Thus a large part of the rooting zone of the north site trees was restricted in water uptake during this time due to cold soil temperatures.

Once snowmelt was nearly complete on the south site, both sites had an increased rate of degree-day accumulation
above 0 degrees C. Despite the fact that the north site still had almost 50% snow cover, the ambient temperatures increased. This suggests that due to convective heat transfer, heat buildup on the bare southern exposures was strongly influencing ambient conditions on the northern exposure.

Warmer daytime temperatures and increased evaporative demand are present on both sites. Yet the north site was still experiencing cold soils from the remaining snowpack. The result was greater water stress for the north site trees for the period day 111 – day 116.

After snowmelt the warmer soils and air temperatures allowed for recovery of predawn water potentials to about -8 bars for all three species on both sites. Significant midday decreases in leaf water potential during this period suggests increased physiological activity by the trees. Although transpiration measurements were not taken, comparison of similar winter and spring days provides evidence of increased physiological activity by May 3rd.

Although there is evidence that freezing nights greatly reduce transpiration in *Pinus contorta* (Fahey, 1979), other researchers have found that lower transpiration rates are the result of stomatal closure which occurs during the normal transition of winter dormancy and frost hardening (Christersson, 1972; Turner and Jarvis, 1975; Tranquillini, 1982). Christersson (1972) found that *Picea abies* reached
maximum transpiration after 4 days of dehardening while
*Pinus_sylvestris* required 14 days.

Since the responses shown in Figures 17 and 18 are for
two days with above freezing nights, it appears the
differences are related more to the dehardening process
rather than the night temperature. This is supported by
results of Graham (1983) who found spring leaf conductances
of *Pinus_contorta* near this study site to be related to both
night temperature and seasonal heat accumulation
(dehardening).

Throughout the winter, *Pseudotsuga_menziesii* showed
greater dessication as indicated by more negative tree water
potentials. *Pinus_contorta* showed the least dessication
while *Pinusponderosa* was somewhere in between. This
suggests a difference in strategies for the species. Using
the terms frost drought or frost dessication to describe the
increased water stress trees normally undergo during the
cold winter (Tranquillini, 1982), it appears that
*Pseudotsuga_menziesii* is frost drought tolerant while *Pinus
contorta* is frost drought avoidant.
LITERATURE CITED


