

AN ABSTRACT OF THE THESIS OF

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Significant post planting mortality of young conifer seedlings often occurs on drought prone sites because seedlings fail to either establish, or maintain favourable water relations. Survival is contingent upon growth which occurs when turgor pressure is above a threshold level. Since growth after planting is influenced by nursery cultural practices, it was hypothesized that survival may be enhanced by the effect of irrigation and nutrient conditioning on seedling water relations.

Principal water relation parameters estimated by traditional and pressure-volume methods were evaluated in conditioned Douglas-fir and jack pine container seedlings during imposed drought stress in a growth room and outside in raised cold frames containing two soil types. Seedling morphology and ion concentrations in the roots were also determined. Initially, declines in plant water potential (ψ) were paralleled by decreases in osmotic potential (ψ_{π}), but as stress increased, differential declines resulted in turgor pressure (ψ_p) being variously maintained depending upon irrigation and level of applied KCl. Estimates of tissue elasticity during drought stress suggested that turgor maintenance was the result of solute concentration through tissue dehydration, not

osmotic adjustment. During a second drought stress, declines in ψ and ψ_{π} lead to marked increases in ψ_p in some treatments. In jack pine, this continued to be the result of dehydration and concentration of solutes, but in Douglas-fir, osmotic adjustment was a factor in turgor maintenance. Variable water relations in either species could not be attributed to the accumulation of any particular ion.

Only root area exhibited an increase during drought stress. Mortality during recovery was significantly higher in daily than weekly irrigated seedlings and was not influenced by the level of applied KCl. Post drought evaluation of growth potential of surviving seedlings revealed that neither conditioning treatment nor successive drought stress precluded growth.

Under field conditions the progressions of water relation parameters were similar to those recorded in growth room conditions, but the rapidity of the responses were affected by soil type. Results suggested the occurrence of osmotic adjustment in Douglas-fir; restrained decline in turgor pressure in jack pine was clearly the result of concentration of solutes through dehydration. Mortality was confined entirely to Douglas-fir in the clay loam soil, but in the sandy soil both species, regardless of conditioning treatment, experienced mortality at low soil water availability.

Water Relations and Associated Morphology of
Conditioned Douglas-fir and Jack Pine Seedlings
Subjected to Periods of Drought Stress

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Subjected to Periods of Drought Stress

1. INTRODUCTION

Silviculturists have recognized the relationship between physiology of seedlings and plantation performance for some time (Wakeley, 1948) and have promoted research to identify particular plant parameters that would adequately characterize its preparedness for outplanting (Duryea and Landis, 1984). Many factors have been identified that, if severe enough, or act over a long period of time, can preclude successful seedling establishment. One of these factors, soil drought, often has a widespread impact on reforestation programs. Below the 50th parallel in northern Ontario, spring periods of soil water deficits are common. When planting occurs during this same period seedling losses have occasionally been high, particularly on sandy till sites. Moreover, losses of containerized seedlings typically planted in the summer have often been high as well. In Southwestern Oregon the period of soil water deficit is extended and more severe than in northern Ontario. Sites in southwestern Oregon that present the greatest problem are generally shallow rocky skeletal soils with a surface mantel of loose ravelly material. Water holding capacity of these soils is extremely low (Hobbs et al., 1980) and when coupled with relatively low rainfall (April to September: < 460 mm) (McNabb et al., 1982) can result in significant soil water deficits.

Seedling water status is governed by a series of energy gradients and resistances from the soil through the plant and finally, to the atmosphere. Although the forest manager can reduce transpiration loss by weeding, he can do little to alter the water storage capacity of the soil; therefore, during rain-free periods water in the soil might be considered a finite resource for the seedling. If continuously drawn upon, soil water will reach a potential below which its movement will cease to keep pace with the demands of the environment leading to severe stress within the

seedling. Any modification to the micro-environment to lessen the evaporative demands made on newly planted seedlings may prolong the period of water availability and increase the chances of the seedling to survive. If the planting environment can not be effectively altered, the last opportunity the silviculturist has to improve reforestation success lies with the seedling itself.

Seedlings destined for planting on droughty sites must possess response mechanisms to drought stress if they are to survive. Nursery cultural practices, such as irrigation and fertilization appear to be important in conditioning seedling response after planting (Duryea and McClain, 1984). However, there is scant information on the specific manner in which irrigation and fertilization affect the water relations and associated morphology of seedlings subjected to drought stress.

It was, therefore, the intention of the present research to broaden our knowledge on the manner and extent to which conditioning practices (irrigation, nutrients) affect the water relations and associated morphology during drought stress of jack pine (*Pinus banksiana* Lamb.) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco.), typical species of northern Ontario and southwestern Oregon, respectively. The specific objectives of the research were as follows:

1. to evaluate the effect of irrigation and nutrient conditioning on morphology and nutrition of container grown seedlings of Douglas-fir and jack pine;
2. to evaluate the progression of seedling morphology, root nutrition, and tissue water relations of conditioned seedlings, firstly, during two successive drought stress periods in a growth room and secondly, during an extended drought stress period on two soil types under protected nursery field-like conditions,
3. to determine the efficacy of irrigation and nutrient conditioning treatments to alter tissue water parameters and elucidate, where possible, specific mechanisms exhibited by Douglas-fir and jack pine for the maintenance of turgor

- pressure during periods of drought stress;
4. to compare the relationships amongst relative water content, total water potential and osmotic potential between each species during the drought stress;
 5. to determine the impact of conditioning treatments on the ability of seedlings to recover from drought stress, and
 6. to determine the effect of conditioning practices on survival and growth of successively drought stressed seedlings.

The above objectives were pursued through the implementation of two independent, but related experiments. The first was carried out in a growth room where conditions of lighting and temperature were closely controlled, and the second experiment was conducted outside in raised planting beds. In both experiments jack pine and Douglas-fir seedlings which were previously conditioned by applying combinations of water stress and levels of potassium chloride were exposed to prolonged periods of increasing soil water deficit. Seedling response parameters pertinent to water relations, morphology, and nutrition were continuously evaluated.

2. REVIEW OF THE LITERATURE

2.1. Plant water relations.

2.1.1 General considerations. Maximov (1929) stated that "the physiological significance of water in the life of a plant is exceedingly great". Since water constitutes 80 to 90 percent of the fresh weight of actively growing plant tissue and is the medium in which all biochemical actions occur (Kramer and Kozlowski, 1979), the validity of this statement is overwhelming. Maximov's treatise of 1929 stands as an important early review of plants in relation to water. Many of the basic principles we now accept are apparent in this review. Modern consideration of plant water relations has benefited significantly by the introduction of thermodynamics to describe the state water (Slatyer, 1967; Taylor, 1968). With water considered in terms of free energy van der Honert's 1948 classic analysis of various plants resistance to waterflow has allowed for a clearer understanding of water movement through plants in response to energy gradients. Models have been proposed to describe the components involved in the transfer of soil water to the atmosphere through the plant. Philip (1966) proposed the "soil-plant-atmosphere continuum" or SPAC to describe this system, and it has proven very useful in the study of specific components of the continuum (Wenkert, 1983).

Within the context of the SPAC model the plant or seedling acts as a pipeline joining the reservoir of soil water to the atmosphere. The flow of water from the soil encounters a number of resistances in series (analogous to an electrical resistance network) with the primary plant resistances being located in the root, mesophyll and across the stomatal openings (Cowan, 1965; Weatherley, 1976). The relatively open tube-like conducting tissue of the xylem offers comparatively little resistance to water flow except during the development of severe water deficits which will be discussed later.

The transpiration stream of a plant begins by the loss of water from the mesophyll cells and escape of water vapour to the atmosphere through the stomata. Loss of foliage water lowers the

water potential of the mesophyll cells and thus sets up a series of potential differences amongst the components of the transport system that within a short time reaches the roots and initiates flow of water from the soil into the root. In a simplified form the flow or flux of water is equated to the potential gradient divided by the sum of the resistance across which the water flows, e.g.:

$$F = \frac{\psi_s - \psi_a}{r_p + r_a}, \quad [2.1.1]$$

where F represents the transpirational flux of water and ψ_s , the water potential of soil water, ψ_a , the water potential of the air surrounding the leaf, r_p and r_a , resistances to water flow attributed to the plant and atmosphere, respectively (Weatherley, 1976; Hinckley et al., 1978).

Indeed, the above formulation is an uncomplicated expression of water flow from the soil, through the plant to the atmosphere. It lacks, for example, consideration of capacitance of woody tissues (Hinckley et al., 1978) a factor that is important in the consideration of drought resistance. Moreover, it does not include any dynamic aspect of control over transpirational losses, e.g. by stomata; in other words, the model is static, not dynamic (Passioura, 1982). It also ignores modifying influences of plant anatomy, morphology, physiology, biochemistry, and cultural history (Ritchie, 1978).

Despite the apparent weakness of the general form of the SPAC model it does emphasize the importance of gradients in water potential for flow and the significance of resistance. To study any aspect of plant water relations it is important to know the energy status of the water as well as the components that make up total water potential at any point within the plant and soil.

Various factors influence water to alter its energy status from that of pure free water, e.g. temperature. According to Slatyer and Taylor (1960), Taylor (1968) and Boyer (1969) the energy status of

water in a system can be expressed thermodynamically in terms of the chemical potential of the water in the system. Simply, the water potential of a system (ψ) is defined as:

$$\psi = \frac{\mu_w - \mu_w^0}{\bar{V}_w}, \quad [2.1.2]$$

where μ_w is the chemical potential of water in the system. μ_w^0 is the chemical potential of pure free water and \bar{V}_w is the partial molal volume of water ($18.05 \text{ cm}^3 \text{ mol}^{-1}$ at 20° C). As defined, water potential provides a measure of the capacity of the water at a point within a system to do work relative to the work capacity of pure free water (μ_w^0), which is taken arbitrarily as zero (Nobel, 1983). ψ is expressed as energy per unit volume.

In plant studies, water potential is often divided into its components which then can be evaluated separately. The salient components of total water potential are: osmotic, pressure, matrix and gravitational (Boyer, 1969) and may be expressed as:

$$\psi = \psi_\pi + \psi_p + \psi_m + \psi_g \quad [2.1.3]$$

where ψ represents total plant water potential and ψ_π , ψ_p , ψ_m , and ψ_g are the osmotic, pressure, matrix, and gravitational effects, respectively. The osmotic component represents the forces due to osmotically active solutes such as sugars, ions, and organic acids which are, in terms of concentration, higher in the vacuole than in cytoplasm (Nobel, 1983). The pressure potential is the result of changes in cell volume. As water enters the cell the vacuolar volume increases and concomitantly exerts an outward pressure (turgor pressure) on the cell walls. At some point, further

expansion of the vacuolar volume ceases because back pressure of the cell walls equals turgor pressure and the inward flow of water ceases. Turgor pressure serves to increase the water potential. Matric potential arises from the presences of macromolecules and colloids in the cytoplasm. Matric potential tends to lower water potential, but at high cellular water contents the contribution of matric potential is negligible and is frequently disregarded in plant water studies. The impact of the gravity component is dependent upon the gravitational position with respect to a point of reference. Effects due to gravity are important in studies that deal with water columns of great vertical extent (Tobiessen et al., 1971), but in laboratory studies the contribution of the gravitational component to total water potential is not considered. Thus, with matric and gravitational potentials deleted from the expression of total water potential (Brown, 1977; Tyree and Jarvis, 1982), equation [2.1.3] in many plant studies reduces to:

$$\psi = \psi_{\pi} + \psi_p \quad [2.1.4]$$

2.1.2 Water relations of single plant cells. Estimations of important water relation parameters are frequently determined on tissue samples of whole plants. These parameters are then ascribed to characterize parameters at the cellular level, but Tyree and Hammel (1972) make the distinction that tissue derived parameters must be considered as bulk estimates.

The nature and limits of the components of plant water potentials as described above [2.1.4] are determined by cellular characteristics. A living plant cell consists of three distinct components: cell wall, cytoplasm and the vacuole. The relative size of these components varies with degree of maturity. Regardless of the degree of maturity, a living cell maintains two important membranes: the plasmalemma and the tonoplast. Both membranes are semipermeable. The plasmalemma encloses the cytoplasm and the tonoplast envelopes the vacuole. In a mature living cell the vacuole occupies approximately 80 to 90% of the cell volume and is

said to dominate cellular water relations (Karamanos, 1981). The vacuolar membrane, the tonoplast, is a differentially permeable membrane allowing the flow of relatively pure water (potential near zero, but closer to -0.1 to -0.2 MPa) to flow into the vacuole. This inward flow is due entirely to the potential gradient that exists between water outside the plasmalemma (apoplast) and water inside the plasmalemma (symplast). The osmometer-like action of the vacuole causes the water potential to rise due to dilution of osmotically active substances and increase the water potential and decrease the potential gradient. Concomitantly, with absorption of water there is an increase in the osmotic volume which exerts an outward pressure on the cell wall. This pressure, referred to as turgor pressure, increases to a point where the inward pressure exerted by the cell wall equals the osmotic pressure. At equilibrium, there is no net flow of water because the potential gradient has been eliminated.

Water potential and its components can be plotted in relation to relative water content in a Höfler diagram to represent the static water relations of a single plant cell (Fig. 1). The water potential curve represents the water potential of the vacuole and where osmotic potential just equals water potential the point of incipient plasmolysis or zero turgor occurs. Reports have been made indicating the occurrence of negative turgor pressures (Slatyer, 1957; Turner and Jones, 1980), but this phenomenon has been challenged by Tyree (1976, 1981). Presumably, errors in determining osmotic potential by the sap extraction method lead to the turgor component being incorrectly deduced (Markhart *et al.*, 1981). In any case, the point of zero turgor in relation to relative water content is considered to be an important ecophysiological parameter (Tyree, 1976; Chueng *et al.*, 1975).

Maximov (1929) gave early recognition to the importance of cell size in the water relations of plants and Cutler *et al.* (1977) have provided clear evidence of the importance of cell size on solute and turgor potentials. As cell size decreases, as it might be expected when the plant is subjected to soil water deficits during growth,

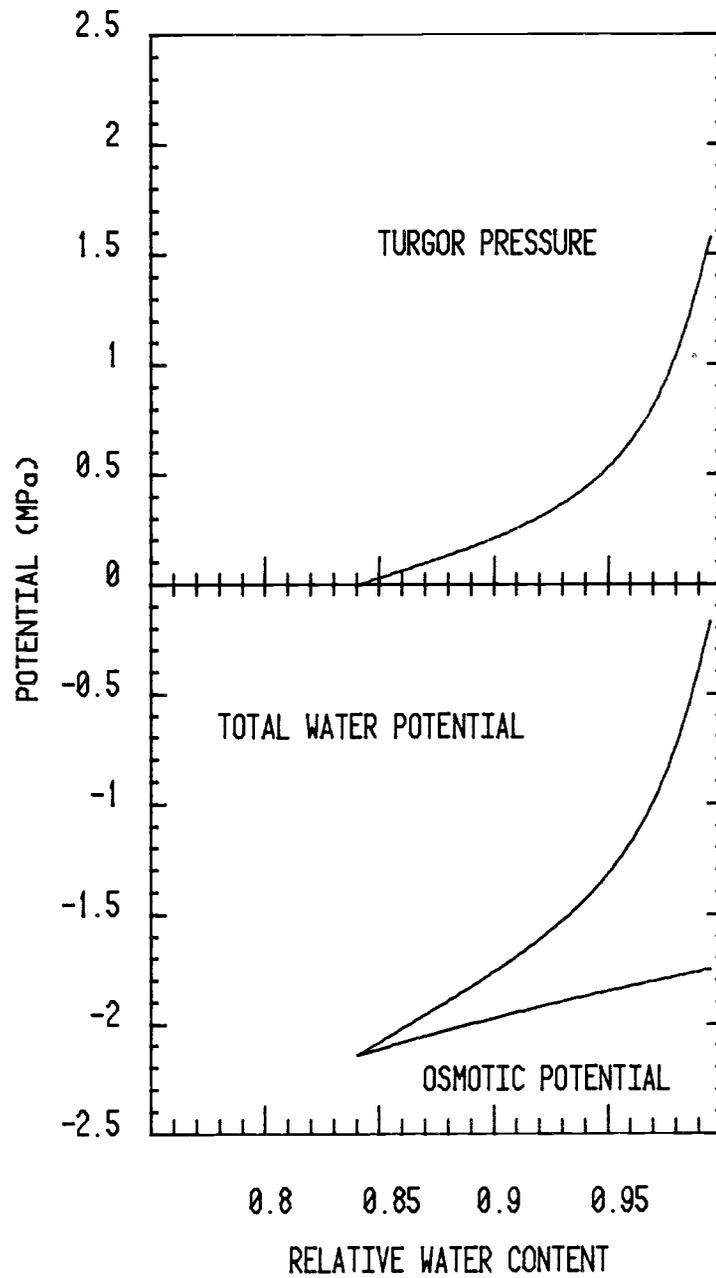


Figure 1. Höfler diagram derived from experimental results.

the proportion of cell wall volume increases relative to cell volume. With equal molar content of vacuolar sap osmotic potentials within a small cell will be lower than in a larger cell. The capability of the cell to maintain turgor pressures at lower water potentials is therefore increased. Moreover, thicker cell walls may also provide a buffer against rapid movement of water out of the protoplast during situations of plant water deficits. Gaff and Carr (1961) estimate that dry preparation of cell wall material can achieve a hydration level of approximately 150% on a dry weight basis. Teoh et al. (1967) lend support to the findings of Gaff and Carr through their determination of sorption-desorption isotherms of various cell wall materials. They conclude that an important factor enabling a drought resistant species to sustain itself through water stress is by the water held in the cell wall and the tenacity with which it is held.

Cell wall elasticity is another important factor that affects cellular water relations (Dainty, 1972). The elastic nature of the cell wall allows for it to swell as water enters the cell and for it to shrink as water leaves the cell. The importance of elasticity is underlined during periods of plant water stress. With water movement out of the cell in response to a potential gradient an elastic cell wall allows for a decrease in cell volume and a decrease in the osmotic potential (Cutler et al., 1977). Lowering of the osmotic potential mediates the loss of water and decreases the rate of turgor loss (Turner, 1979; Passioura, 1982). Evidently, smaller cells have higher elastic properties than larger cells (Zimmermann and Steudle, 1975). Given that thick and elastic cell walls are favorable traits for plants to possess in a drought environment it would be desirable to promote these characteristics in conifer seedlings before planting.

2.1.3 Development of plant water deficits. A review of the literature reveals that "water deficit" is variously defined. Kramer (1983) states that water deficit or water stress (his alternate term) refers to situations in which plant water potential and turgor are reduced enough to interfere with normal functioning

of the plant. In this instance, Kramer (1983) defines water deficit with respect to physiological and metabolic processes. Hsiao's (1973) notable review is aligned with this definition. On the other hand, water stress is often defined from a thermodynamic standpoint. For example, Karamanos (1981) considers that water stress exists when water potential is below zero, but suggests that it is not a very realistic definition. It seems that a logical approach in defining water deficit would be after Kramer (1983) with the realization that quantitatively (in terms of water potential) this is perhaps a unique range of potentials for a plant at a given stage of development in a particular environment. Regardless of how it is defined, the manner in which plant water deficits occur is widely agreed upon.

The plant, as alluded to before, acts as a conduit which allows for the transfer of energy from the soil volume to the atmosphere. Water enters the plant from the soil through the roots, crosses the endodermis to reach the root xylem, whereupon it enters and moves within the xylem to the mesophyll and evaporation sites (Jarvis, 1975). The driving force to move water against the gravitational component of total water potential and frictional resistances is derived from the evaporation of water from the leaf. Traditionally, water stress was considered to occur when evaporation of water from the leaves exceeded the absorption of water by the roots (Weatherley, 1970). This, of course, is numerically true, but is now considered to be an extreme oversimplification of the development of water stress (Jarvis, 1975; Begg and Turner, 1976; Brown, 1977). The model which is now generally accepted to describe the process of development of plant water deficits was first proposed by H.H. Dixon in 1938 (Weatherley, 1970; Jarvis, 1975; Karamanos, 1981).

Initially, when a turgid plant is subjected to evaporative demands of its environment water from all sources within the plant will tend to move simultaneously to the evaporating surfaces. Water from the mesophyll will be lost first followed by water located in the more distal portions of the hydraulic system of the plant. The

loss of water within the xylem places the system under tension at a lower potential. The decrease in potential initiates a potential gradient between the xylem (transpiration stream) and adjacent cells. In response to this gradient, cellular water moves down the energy gradient toward the xylem in an attempt to equilibrate and eliminate the potential difference.

Continued evaporation from the leaf maintains the gradient and the flow of water out of the cell. Since the amount of tissue water is finite the potential of individual cells declines and tends to equilibrate with xylem water potential. Once equilibration occurs and water continues to evaporate a steady state condition is achieved and evaporation equals absorption.

The withdrawal of symplasmic water from individual cells may be buffered by the initial loss of apoplasmic water from cell walls as suggested by Gaff and Carr (1961). However, the inevitable consequence of continued decline in cell water potential is a decline in turgor pressure and osmotic potential as predicted by the Hofler diagram. Should the cell not be able to equilibrate with the xylem water potential with the movement of water out of the cell it would experience incipient wilting as turgor pressure declines. At this stage, most, if not all physiological functions of the plant are impaired (Hsiao, 1973; Kramer, 1983).

Soil water is an important determinant of plant water status. As water within the plant moves in response to gradients of potential energy so does water within the soil. The low xylem water potential in the root initiates the flow of water into the root from the soil, as long as the potential of the soil water is higher than in the root. The movement of water toward the root causes depletion of soil water in the immediate vicinity of the root, decreasing the hydraulic conductivity (Gardner, 1960; McCoy *et al.*, 1984). A greater potential gradient between the root and the soil is, therefore, required to maintain the flow of water. This would necessitate a further decline in plant water potential through continued loss of cellular water (Kaufmann, 1981). If the flow of water from the soil to the plant is not sufficient to satisfy the

evaporative demand, the plant would die from physiological impairment emanating from low plant water potential.

Alleviation of water deficits before plant death variously restores plant function (Kramer and Kozlowski, 1979). Restoration of favorable internal water relations begins as gradients within the plant decline, usually at night when stomata are closed. This requires that the evaporative stress or transpiration decrease (evening) and soil water be replenished adjacent to the root. When both soil water potential and hydraulic conductivities are high, plant water deficits are quickly eliminated, usually by early morning. When soil water potentials are low, hydraulic conductivities prevent complete elimination of the plant water deficit within a similar period of time.

To the silviculturist who is faced with the prospect of reforesting droughty sites the development of plant water deficits is a major concern, not only on a daily basis, but also over an extended period of time. On these sites water potential typically exhibits a continual decline because of progressive drying of the soil profile (Slatyer, 1967). Diurnally, the plant develops water deficits as described above, but because of diminishing soil water supplies the plant is unable to alleviate the entire water deficits previously acquired. During successive days, characterized by high evaporative demand, plant water deficits increase as xylem water potential decreases. The consequences of extended periods without full recovery is equilibration of plant and atmospheric water potentials (see Slatyer, 1967: p. 276) and finally, plant death. Without recovery there is successive impairment of all physiological and metabolic processes (Hsiao *et al.*, 1976).

2.2 Growth response to water stress.

If a planted seedling was to survive, it must grow. Growth is defined as increase in size. Although simple in definition the process of growth is governed by a multitude of diversified physiological processes which are, in some intricate way, orchestrated to provide material and energy substrates and internal conditions for growth to proceed. Based on a review of water

relations research Hsiao (1973) ranked physiological processes in a hierarchial order that reflected their sensitivity to water stress. Cell growth is most sensitive to initial declines in water potential followed by other processes, such as protein sythesis, stomatal function, photosynthesis, transpiration, respiration and substrate conversions.

In new plantations seedlings often fail to burst bud and initiate leader extension which can result in the demise of the plantation. The development of low water potentials in seedlings at the time of planting is often considered the principal factor limiting growth (Hsiao et al., 1976; Wenkert et al., 1978). Strictly speaking, this is not correct. It is well established that cell growth is a turgor mediated process. Direct evidence linking the importance of turgor pressure to expansive growth has been reviewed by Bradford and Hsiao (1982). Apparently, work with giant internodal cells of Nitella has shown that when turgor pressures were monitored directly using a pressure probe, stepwise fluctuations in turgor pressure resulted in corresponding increases or decreases in growth. Research with maize by Acevedo et al. (1971) showed that rewatering after subjecting plants to mild water stress allowed for growth to resume. During acclimation studies of sunflowers in a controlled environment, Matthews et al. (1984) found that after rewatering, growth of leaves resumed at rates that were dependent upon turgor pressure.

Direct examples of turgor dependent growth processes in conifers are scarce. Although the turgor pressure-growth relation was not specifically defined, Glerum and Pierpoint (1968) followed the leader elongation of three Ontario conifers subjected to degrees of soil dryness. Differences existed amongst species, and at the level of greatest soil dryness elongation was reduced relative to the control level of moisture. Thus, it might be presumed that with diminishing soil water seedlings experienced declines in water potential and turgor pressure which affected rate of leader elongation.

The mechanism of expansive growth may be examined from a

physical standpoint. Hsiao and Bradford (1983) suggested that in a non-expanding cell in equilibrium with its surroundings, the difference between the osmotic potential (ψ_{π}) inside the cell and outside the cell is exactly balanced by the turgor pressure (ψ_p). At this point, internal water potential equals outside water potential and no flow of water results. With the advent of growth the cell wall loosens (see Cleland, 1971 and Taiz, 1984) and there is an immediate decline in turgor pressure. In accordance with equation [2.1.4] total water potential inside the cell declines and water flows into the cell in response to the potential gradient. This continues until the backward forces of the cell wall increases turgor pressure to the point where the potential gradient is eliminated and there is no movement of water. This process is repeated throughout the period of elongation. Hsiao and Bradford (1983) emphasize that this process does not continue without the concomitant accumulation of internally generated solutes to compensate for the dilution effect of osmotically active solutes during expansive growth.

Expansive growth has been modelled in terms of only the physical factors that are presumed to affect expansive growth (Lockhart, 1965). The form of the model is:

$$dv/Vdt = E_g (\psi_p - \psi_{p,th}) \quad [2.2.1]$$

where V is the cell volume, dv/Vdt is the rate of growth relative to the original cell volume; E_g is the gross extensibility (a coefficient that is the slope of the curve dv/Vdt vs $(\psi_p - \psi_{p,th})$); $\psi_{p,th}$ is the threshold turgor pressure below which no cell extension occurs. Equation [2.2.1] states that growth does not occur unless turgor pressure is greater than some minimum turgor pressure. Indeed, Boyer (1968) found that during recovery of sunflowers from low water potentials leaf elongation did not occur until turgor pressure had exceeded 6.5 bars (0.64 MPa). Wenkert et al. (1978) showed that even with relatively minor declines in water potential

at values near $\psi_{p,th}$ growth is reduced, and the sensitivity of expanding cells (tissues) is influenced by plant ontogeny.

In sum, expansive cell growth is clearly related to changes in water potential, but primarily to the attending effects of turgor pressure. Favorable internal water relations of stock prior to planting is important and if turgor pressure at the time of planting is less than a threshold level processes of growth may be impeded. Low turgor pressures in roots may significantly limit growth which is governed by similar physical factors described above in equation [2.2.1] (Gracean and Oh, 1972). Lack of root growth would retard the attainment of favorable plant water relations and preclude physiological processes necessary for growth and survival.

2.3 Osmotic adjustment.

Terrestrial plants seldom exist in their environment without experiencing periods of drought stress (Levitt, 1980). Depending upon the degree of stress plants have developed various adaptive capacities for survival and for highly adapted plant growth may occur during high stress periods. The ability of plant species to survive periods of soil water deficits has been termed its drought resistance (Turner, 1979).

The study of drought resistance has lead to a widely accepted classification of drought resistance and is based upon the manner in which plants withstand periods of drought stress (May and Milthorpe, 1962; Turner, 1979; Jones et al., 1981). Drought resistance has been broadly categorized as 1) drought escape, 2) drought tolerance with high tissue water potential, and 3) drought tolerance with low tissue water potential (e.g. Jones et al., 1981). Each category of drought resistance is characterized by mechanisms that are purported to typify plants exhibiting a given form of drought resistance. Conifer seedlings destined for planting on drought prone sites must also possess adaptive characteristics if they are to survive at low water potentials. Since survival is predicated on growth we are concerned principally with that form of drought resistance that permits growth at low tissue water potentials.

Growth from a theoretical and physiological standpoint (see

equation [2.2.1]) depends upon cell wall extensibility and turgor pressure above a given threshold level (Hsiao et al., 1976). Notwithstanding the importance of edaphic factors, unless the roots of planted seedlings maintain turgor pressure above a unique threshold level, growth will cease and survival will be jeopardized. At the time of planting, two alternate strategies are seen for seedlings in response to its microenvironment; first, a plant may respond actively to maintain turgor pressure as water potential declines, or second, a plant may rapidly dehydrate. The latter strategy represents a steady decline in the water content and turgor pressure of the plant to levels below which recovery is not possible.

Plants that are able to resist rapid declines in water content and turgor pressure express an important adaptation to water deficits (Turner, 1979). The relationship presented in equation [2.1.4] indicates that if turgor pressure is to be maintained as water potential declines osmotic potential must also decline. Turgor maintenance has received considerable attention ; e.g. Hellebust, 1976; Zimmermann, 1978; Turner and Jones, 1980; Jefferies, 1981; Wyn Jones and Gorham, 1982; Le Rudulier et al., 1984; Morgan, 1984. The attention that this adaptive mechanism has received is reflected in the diverse and often inappropriate terms that are used to define it (Reed, 1984). Turner and Jones (1980) used the term osmotic adjustment to refer to the lowering of osmotic potential arising from the net accumulation of solutes in response to water deficits. A decrease in the osmotic potential by simple dehydration is not considered osmotic adjustment although turgor pressure may be maintained (Turner, 1979). It is important to distinguish between the two processes by which the osmotic potential decreases. The active accumulation of solutes represents an adaptive mechanism over a range of water potentials before loss of cellular water occurs, whereas increase in solute concentration by dehydration does not. Nevertheless, dehydration of cellular sap decreases osmotic potential and can contribute to the maintenance of turgor and survival of the plant during stress.

Osmotic adjustment has been noted to occur in various species of plants e.g. maize (Hsiao et al., 1976; Fereres et al., 1978; Acevedo et al., 1979), sorghum (Hsiao et al., 1976; Fereres et al., 1978; Jones and Turner, 1978; Turner et al., 1978; Acevedo et al., 1979; Jones and Rawson, 1979), cotton (Ackerson and Hebert, 1981; Cutler and Rains, 1978), wheat (Morgan, 1977), sunflower (Turner et al., 1978; Jones and Turner, 1980), pearl millet (Henson, 1982), apple seedlings (Davies and Lakso, 1978), soybeans (Meyer and Boyer, 1981), and dune grasses (Pavlik, 1984). There is, however, a dearth of specific information as to the capability of conifer species to undergo osmotic adjustment in response to drought stress, although it has been alluded to in several reports (e.g. Cheung et al., 1975; Roberts and Knoerr, 1977; Tyree et al., 1978). Recently, however, Ritchie and Shula (1984) reported seasonal changes in turgor maintenance for Douglas-fir seedlings and attributed it to osmotic adjustment. On the other hand, Joly (1984) provided strong evidence that an osmotic adjustment system does not operate as an adaptive mechanism in this species. Nevertheless, specific organs in other plants have been identified in recent studies to undergo osmotic adjustment in response to water stress e.g. leaves (Jones and Turner, 1980), hypocotyls (Meyer and Boyer, 1972, 1981), spikelets (Morgan, 1979), and roots (Gracean and Oh, 1972; Lawlor, 1973; Osonubi and Davies, 1978; Sharp and Davies, 1979).

The extent to which osmotic adjustment occurs varies and is dependent largely upon the inherent capability of the plant to adjust, rate of stress development, and cultural history, such as irrigation and fertilization regime (Turner and Jones, 1980). Published values of osmotic adjustment are also influenced by the manner of their determination and evaluation of elastic properties of the cell wall over the adjustment period (Radin, 1983). Radin (1983) clearly illustrates that osmotic adjustment occurs when the osmotic potential is decreased at all relative water contents, unlike when osmotic potential increasingly declines because of high cell wall elasticity. The criteria of osmotic adjustment must include evaluation of osmotic potential over the region of relative

water content in the range of positive turgor and of the elastic properties of the cell wall (Radin, 1983; Joly, 1984). Jones and Turner (1978) claim to have shown unequivocal evidence of osmotic adjustment in the leaves of sorghum. Sorghum plants prestressed to pre-dawn water potentials of control, -0.4 MPa, and -1.6 MPa then rapidly dried after rehydration exhibited lower osmotic potentials at all relative water contents and no increase in tissue elasticity. The decrease in osmotic potential was concluded to be from solute accumulation and not from dehydration. The extent of the adjustment was 0.4 MPa and 0.9 MPa lower osmotic potentials at full turgor for the two prestress treatments. Jones and Turner (1980) demonstrated that leaves on sunflower at various stages of ontogeny were capable of osmotic adjustment although, in fully expanded leaves the adjustment was more pronounced than in expanding leaves. Fereres et al (1978) followed the progression of field sorghum and maize under irrigated and non-irrigated treatments and concluded that osmotic adjustment in the latter treatment maintained turgor potentials throughout the test period. Several points must, however, be raised with regard to the techniques employed by Fereres et al. (1978). First, osmotic potentials were determined by the sap extraction method (see Slavik, 1974) and since no correction factor was applied to correct for symplasmic water dilution, it can be assumed osmotic potentials were underestimated (in absolute terms) and second, the elastic properties of the leaf tissues were only inferred. Considering the lack of attention to these details one must look for other data to confirm the occurrence of osmotic adjustment in maize and sorghum. It should be pointed out that turgor was maintained in these species and perhaps it is of little consequence if the mechanism of turgor maintenance is a combination of solute accumulation and cell shrinkage if production is maintained. Morgan (1977) examined the relationship of total water potential and osmotic potential in dehydrating wheat genotypes. Again, neither were determined, nor was a correction factor applied to osmotic potential values determined by the expressed sap technique. In any event, maintenance of turgor was observed as water potential

declined and was attributed to accumulation of solutes.

It is widely accepted that for leaf growth to occur turgor pressure above a threshold level is required. It is logical, therefore, that turgor pressure is important for the growing regions of the root system as well. Nevertheless, turgor maintenance in roots has not received much attention. Grecean and Oh (1972) provided perhaps the first evidence of complete turgor maintenance in root tips (radicals) of Pisum sativum. Osmotic adjustment was believed to have been 100% efficient against soil water potentials down to -1.5 MPa. As soil strength increased, efficiency of osmotic adjustment in maintaining turgor pressure decreased to 70 percent. Working with young seedlings of English oak (Quercus robur L.) and silver birch (Betula verrucosa Ehrl.) Osonubi and Davies (1978) showed that non-irrigated seedlings of oak maintained root turgor, purportedly by osmotic adjustment. As soil water potential dropped by 1.5 MPa root solute potential decreased from around -1.0 MPa to approximately -2.0 MPa and solute potential decreased only slightly. It was determined that when measured against declines in soil water potential oak and birch seedlings exhibited 61 and 13 percent efficiency in osmotic adjustment. Sharp and Davies (1979) withheld water from potted maize plants for a period of seven days. During this period, declines in root water potential were paralleled by declines in root osmotic potential resulting in turgor maintenance and growth of roots as the severity of the stress increased. By the seventh day of the stress, osmotic potential ceased to decline with root water potential. At this point, maize roots had reached their capacity to adjust osmotically and turgor was reduced to zero. The differential capacity of shoots and roots to adjust osmotically to maintain turgor is suggested to provide the basis for lower top:root ratios of drought adapted stock (Hsiao et al, 1976). Evidently, during water stress periods larger proportions of photosynthates are directed toward the root system for a two fold purpose: as substrates for growth and to contribute osmotically for turgor maintenance (Hsiao and Acevedo, 1974; Turner, 1979).

Osmotic adjustment is clearly a drought resistant mechanism, but its occurrence is limited by the rate of stress development and degree of stress. Numerous reports indicate that rapid development of stress diminishes the capacity of the plant to adjust osmotically (Hsiao *et al.*, 1976; Turner and Jones, 1980). Jones and Rawson (1979) studied the effect of rate of stress development on sorghum. At the most rapid rate of stress development of 1.2 MPa per day there was no solute accumulation, but at lower rates of stress development (0.7 and 0.15 MPa per day) solute accumulation occurred to provide reductions in osmotic potentials of 0.6 MPa. Turner and Jones (1980) stated that the rate of stress development is contingent upon soil volume occupied by roots, soil water content, hydraulic conductivities of the soil and plant, stomatal function, leaf area, and atmospheric demand for water. As stress deepens, the capacity to maintain turgor through osmotic adjustment decreases. Morgan (1977) illustrated the pattern of osmotic potential in relation to stress development for non-adjusting and adjusting varieties of wheat plants. In the wheat variety that adjusted, osmotic potentials declined more rapidly than total water potentials to maintain turgor pressures. Turgor remained positive until osmotic and total water potentials equilibrated at -3.5 MPa. The exact limits of osmotic adjustment vary according to plant ontogeny at tissue type (Morgan, 1980).

Finally, considerable attention has been focused upon the species of solutes that accumulate during osmotic adjustment. Morgan (1984) recently reviewed the variety of solutes which have been identified during solute accumulation. The majority of solutes are sugars, amino acids, and certain free cations and anions. The accumulation of sugars has been noted to depend upon photosynthate reserves and accumulation of ions, such as, K^+ and Cl^- in growing regions of the plant may be affected by their concentration in the soil solution during water stress (Borowitzka, 1981). There is some evidence that even suggests that the production of betaine and proline (sometimes referred to as osmoprotectants) is governed by a new class of genes that protect the cell and its constituents

against dehydration (Le Rudulier et al., 1984).

2.4 Enhancement of plant water relations.

Considerable evidence now exists to show that conditioning plants by repeated exposure to moderate water stress can permit certain physiological processes to continue to lower water potentials during a prolonged drought stress period than observed in control plants. The majority of the evidence is derived from research that employed irrigation control as a means of conditioning. Research into conditioning plants by nutrient amendments is scant, but from those reports that exist, results are inconsistent. Nevertheless, consideration of irrigation and nutrition as conditioning procedures is worthwhile because these practices predominate the cultural program of stock production and are easily applied.

2.4.1 Irrigation. The effect of prolonged periods of water stress on plant morphology has been recognized for many years (Pfeffler, 1903; Maximov, 1929). It is unlikely, however, that similar xeromorphic features become well developed in seedlings during short conditioning or hardening periods when frequent episodes of water stress are permitted to occur. Stocker (1960) reviewed literature dealing with the process of hardening and cited Hinckel and Tsvethava's work which indicated that hardened plants possess greater viscosity of the protoplasm. Other cellular changes occur when plants are subjected to the successive development of mild stress and are probably associated with membrane permeability, organization of cytoplasmic constituents (Poljakoff-Mayber, 1981) and de novo synthesis of osmoprotectants (Le Rudulier et al., 1984). Many of the stress induced changes at the molecular level are, however, not well elucidated, but the physiological reaction of plants during prolonged stress development confirm the importance of these changes.

Rook (1972) conditioned radiata pine (Pinus radiata D. Don) by watering daily, weekly and biweekly and evaluated rate of transpiration during a 14 day period following transplanting. Daily watered seedlings exhibited high rates of transpiration which fell to about 10% of the original value after two days. Stomata remained

open despite the development of water stress. When weekly and biweekly irrigated seedlings were transplanted stomata were only partially open, transpiration was less and they developed lower stress than daily irrigated seedlings.

In a greenhouse study, Cutler and Rains (1977) subjected cotton plants to four irrigation regimes in which plants were watered daily (control) and every 4, 6, and 8 days. Once the plants were 55 days old and had attained similar number of leaves water was withheld for a period of five days and water relation parameters evaluated. Dry weight differences were apparent amongst the four conditioning levels, but importantly, threshold response of stomata shifted from -1.8 MPa for control plants to as low as -2.2 to -2.4 MPa for stress conditioned plants. Moreover, stressed plants relative to control plants exhibited a larger decrease in leaf water potential per unit decrease in relative water content. This phenomenon is usually considered to reflect a higher degree of drought tolerance (Jones et al., 1981). Ackerson and Hebert (1981) demonstrated that stress conditioned cotton plants maintained photosynthesis to lower water potentials than control plants and attributed this response to altered stomatal function.

Hennessey and Dougherty (1984) attempted to condition loblolly pine nursery seedlings by implementing two irrigation regimes: control, watered when pre-dawn leaf water potentials reached -0.25 MPa and stressed, watered when leaf water potentials reached -0.75 MPa. Once irrigation treatments ceased, osmotic potentials at full and zero turgor in stressed seedlings were 0.405 MPa lower than control seedlings. It was assumed that the stressed conditioned seedlings had undergone osmotic adjustment. Apart from the obvious advantages offered by osmotic adjustment the conditioning treatment predisposed stressed seedlings to produce nearly three times as many new roots as unstressed seedlings, a factor which is crucial in seedling survival on drought prone sites (Stone, 1955).

2.4.2 Nutrition. Seedling growth is directly affected by its nutrition (Kramer and Kozlowski, 1979). Specific ions are known to affect the water relations and drought resistance of plants. Pharis

and Kramer (1964) investigated the effect of nitrogen supply on the drought resistance of two and a half month old loblolly pine seedlings. Drought resistance (measured in terms of plant ability to survive drought over a specified period of time) was less for seedlings raised at high N levels; least mortality was associated with N deficient seedlings, but growth was poor. Reduced drought resistance was correlated with a marked increase in the shoot:root ratio and an imbalance in the seedling's ability to maintain absorption of water to meet transpirational demands. Similar effects of nitrogen on shoot:root ratios and survival of Douglas-fir has been noted by van den Driessche (1980).

Etter (1969) evaluated the drought resistance of lodgepole pine grown to a different level of nitrate-N in terms of its changes in biochemistry. Although high shoot:root ratios were associated with high N seedlings, there were substantial decreases in soluble carbohydrates and starch components in leaves and roots. When subjected to drought, root mortality was high and the high nitrate-N plants were unable to recover once the drought stress period was relieved. Krueger and Trappe (1967) also noted the importance of carbohydrates to seedling survival and recently, Marshall and Waring (1984) provided evidence that favored the hypothesis that root turnover during drought is contingent upon carbohydrate supply.

Further research has shown that N nutrition alters water relations of sunflower plants (Radin and Boyer, 1982). Osmotic potentials were consistently lower (more negative) in high N plants than in low N plants. Less negative osmotic potentials resulted in lower turgor pressures in low N plants. Low hydraulic conductivities, presumably because of smaller diameter conducting elements, were also associated with low N plants and during periods of high evaporative stress large diurnal variations in leaf water potentials occurred. Osmotic adjustment was unaffected by N nutrition at low water potential. It is possible that N deficiency affects the sensitivity of stomata during periods of stress. Radin and Parker (1979) demonstrated that at 27, 35 and 40^o C threshold potentials for complete stomatal closure were -1.0, -1.5, and -2.6

MPa in N deficient plants and -2.0, -2.0, and -3.0 MPa in high N plants, respectively. The results were for high N plants to transpire longer, develop lower leaf water potentials faster and lose turgor pressure sooner. The effect of N supply on stomata sensitivity may be mediated through ABA (Radin and Ackerson, 1981).

The effect of nutrition on plant water relations may act through changes in cellular dimensions. Atkinson and Davison (1973) subjected seven plant species, which were either sufficient or deficient in P, to drought. P deficient plants were smaller and took 2 to 5 times as long to exhibit signs of drought (flaccidity and drooping leaves) compared to control plants. Interestingly, control plants may have actively responded to water loss because they possessed higher tissue water contents than P deficient plants during the drought stress period and during rehydration. P deficient plants were characterized by cells having thicker cell walls and smaller vacuoles than control plants. These features, which can be induced by stress conditioning, affect cell wall elasticity and distribution of water (symplasmic vs apoplasmic). These properties are determinant factors in tissue water relations (Cleland, 1971; Cutler and Rains, 1977).

Two ions, K^+ and Cl^- , have been shown to be key factors in the regulatory mechanisms of plant water relations (Mengel and Kirkby, 1982). Potassium has been termed the "master-cation" of the plant because of its varied functions (Martin-Prevel, 1981), but only its role in water relations is of immediate interest to us here. Potassium has been shown to be the predominant cation involved with turgor of guard cells in the operation of stomata (Raschke, 1975). Moreover, potassium contributes significantly to the osmotica of cells that adjust osmotically to water stress (Beringer, 1983). Mengel and Arneke (1982) grew dwarf bean in solution culture at two levels of K supply. Water potentials of both groups of plants were nearly identical, but seedlings receiving the higher K supply (4.0 mM) had markedly higher turgor pressures (5.6 vs 8.7 MPa). They concluded that the growth inducing effect of potassium supplement

acts mainly through maintenance of lower osmotic potentials and higher turgor pressures. Jensen (1981a, 1981b) provided evidence suggesting that in both beans and wheat pretreated with KNO_3 , turgor is maintained during exposure to water stress through lowering of osmotic potential by the uptake of inorganic ions. Considering the evidence supporting the valuable role of K in the water economy of plants, as well as other physiological and biochemical processes, it is difficult to explain Wilson and Ludlow's (1983) conclusion that high K supply (KNO_3) did not consistently enhance osmotic adjustment of water stressed leaves of three grasses. It was suggested that other ions counterbalanced the higher K^+ concentrations and lessened the net effect of K^+ for osmotic adjustment. In sorghum and sunflower crops osmotic adjustment was not found to be dependent upon an increase of ions, notably K^+ , but instead, was associated with an increased conversion of starch to soluble sugars (Turner et al., 1978).

Chlorine has recently been confirmed as an element indispensable to plant life (Gouny, 1973), but its purported role in photosynthesis has been questioned (Terry, 1977). Terry (1977) suggested instead, the principal effect of Cl^- deficiency is to reduce cell multiplication rates in leaves, which in turn decreases leaf expansion and growth. Despite this contention there is substantial evidence that to suggest that Cl^- is weakly bound to the cytoplasm, thereby permitting it to behave like a free ion within the cell sap. Excessive applications of Cl^- are noted to affect nitrogen metabolism because of competition with NO_3^- during absorption; furthermore, carbohydrates may also be reduced at high Cl^- levels (Gouny, 1973). Von Uexkull (1984) implicates Cl^- in stomatal function in palm trees. Apparently, mature guard cells lack starch and therefore, rely entirely upon imported osmotica for turgor regulation and Cl^- is absorbed in equal amounts with K^+ . Chloride salts are also known to affect turgor pressure in winter wheat by reducing osmotic potential (Christensen et al., 1981).

In sum, the body of existing evidence confirms the inherent ability of some plants to maintain physiology at the outset of

drought stress by osmotic adjustment. It is also apparent that this ability can be enhanced by subjecting plants to cycles of stress conditioning before the occurrence of a prolonged drought. The modulating effect of nutrient conditioning is not well defined, but deserves increased attention. If the benefits of improved drought physiology can be conferred on conifer seedlings by stress and nutrient conditioning, the silviculturist may realize improved performance if seedlings are planted in the field at a time of increasing soil water deficits.

3. METHODS AND MATERIALS

3.1 Experimental Approach

The research was undertaken in two contrasting environments: growth room and nursery. Under growth room conditions the experimental seedlings were subjected to two successive drought stress/recovery periods. The purpose of this was to investigate the validity of the hypothesis that "conditioning practices (irrigation and nutrient application) influence the water relations of seedlings during drought stress" holds during a second period of drought stress. In the nursery test, seedlings were handled in a near-operational sense by planting in cold frames containing two soil types. In the context of the nursery test the experimental objectives were extended to include consideration of soil type. Techniques of seedling culture, application of treatments, methods of evaluating water relations during drought stress and analysis of data were similar to those used in the growth room experiment. The events of each experiment are diagrammatically represented in Figures 2 and 4 (page 49) for the growth room and field experiments, respectively.

3.2 Phase I: Growth Room

3.2.1 Experimental material. Two conifer species were selected as experimental material: Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) from the vicinity of Butte Falls, Oregon, seed zone 511, elevation 500 m and jack pine (Pinus banksiana Lamb.) from seed zone 3400, north of Thunder Bay, Ontario, Canada. Both sources of seed are from areas which experience frequent periods of soil drought. Although the duration and severity of soil drought in the Ontario seed source zone are less compared to habitat conditions in southern Oregon, both species were expected to possess the ability to adapt during periods of soil water deficits. Adaptive responses were anticipated to be unique to each species.

3.2.2 Seedling culture. Seeds of Douglas-fir only were taken from cold storage (2⁰ C) and nearly equal quantities were placed in three large jars containing room temperature water for 24 hours.

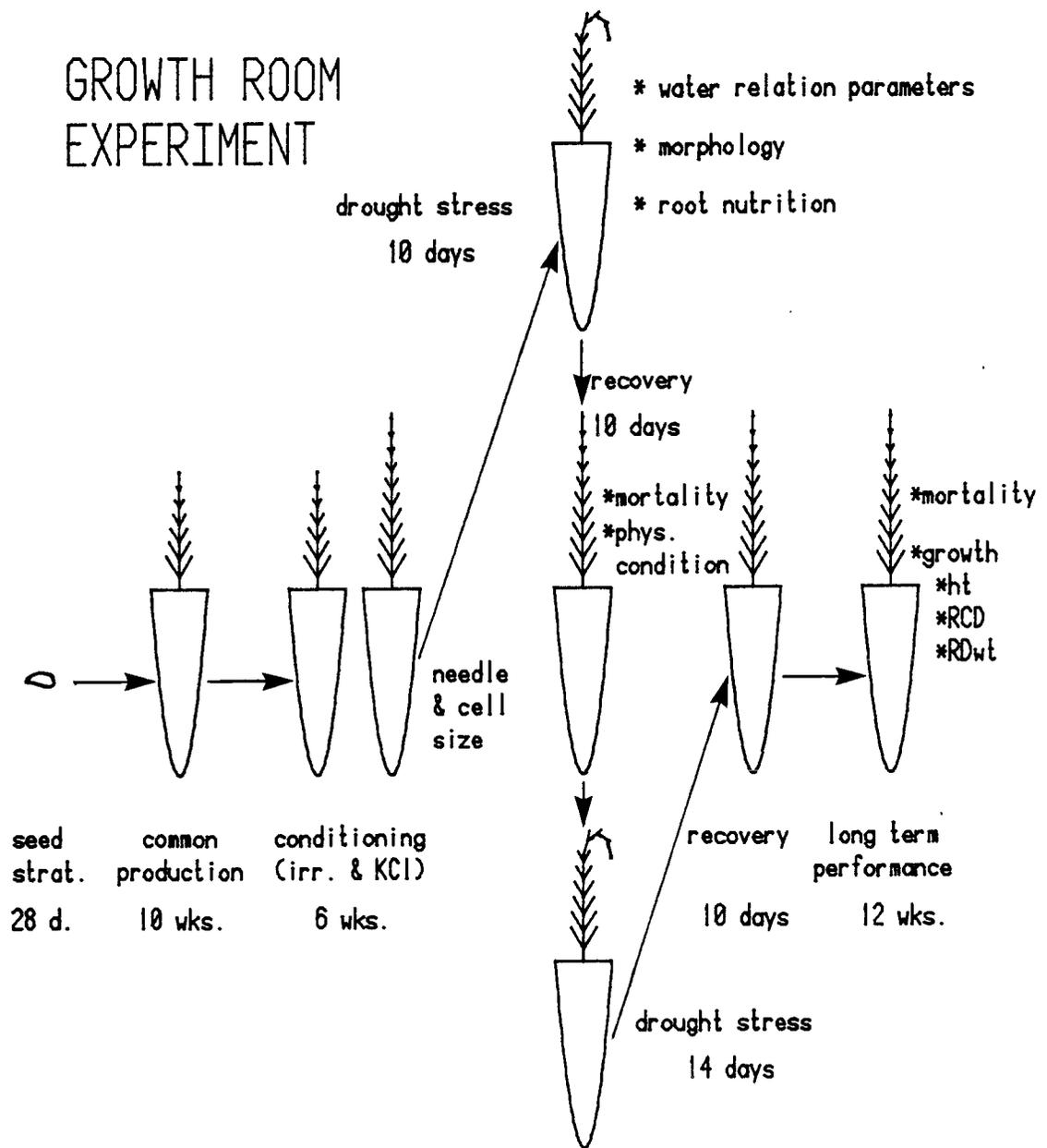


Figure 2. Diagrammatic representation of events during the conduct of the growth room experiment.

The water was changed on three occasions. Seeds were then placed on dry paper towels and excess surface water removed. Seven quantities of approximately 300 seeds were sealed in plastic bags, placed in glass jars and stratified at 2^o C for 28 days. Seed was sown on sterilized peat-vermiculite mix in plastic 12 X 12 X 3 cm germination trays. Jack pine seed, which was not stratified, was sown in the same manner. As the seeds of each species were sown attempts were made to ensure seeds were not in contact with one another so as to retard the spread of mould. Fifteen germination trays of each species were placed into a germination cabinet with controls set to provide a day-night photoperiod of 18/6 hours and corresponding temperatures of 24/18^o C. Relative humidity was kept above 90%.

Seeds were observed and misted daily with distilled water. No visible mould developed.

Seed germination was nearly complete after nine days. From November 2 to 5, 1983, germinants with radicals at least 5 mm in length were carefully transplanted into 165 cc Ray Leach containers containing a moist mixture of peat, vermiculite and medium sand in a ratio by volume of 1:1:1.

Approximately 1,000 germinates of each species were transplanted (96 seedlings per tray) and placed on benches in a fiberglass covered greenhouse. During the following three weeks seedlings were maintained to ensure maximum establishment. Controls of the greenhouse were set to provide a daily photoperiod of 18 hours and day-night temperatures of 25^o C and 18^o C. Frequently, temperatures varied widely, but only for a very short periods of time. Natural daylight was supplemented by overhead high pressure sodium vapor lamps and two 200 watt incandescent lamps. Seedlings were watered with room temperature water, and on one occasion an application of Captan, a fungicide, was made to prevent damping off.

A one cm layer of silica grit was placed on the soil surface to prevent the growth of algae and reduce evaporation. At three weeks, malformed seedlings were culled.

Fertilizer was not applied during the three week establishment

period, but was applied during the following seven weeks (from November 28, 1983 to January 22, 1984). A water soluble fertilizer (Peter's Professional 20-20-20) with iron chelate added to 10 litres of water in a watering can to provide a prescribed concentration of N. When seedlings were small the concentration of N was 50 ppm, but was increased to 150 ppm to coincide with seedling growth. Irrigation water with added fertilizer was applied to the limit of soil saturation at biweekly intervals. The soil medium was leached weekly with deionized water to prevent salt buildup. Variations in temperature and radiation within the greenhouse necessitated systematic rotation of seedling trays to ensure equal exposure of seedlings to environmental gradients.

3.2.3 Seedling growth. At seven day intervals throughout the general cultural period (November 28, 1983 to January 22, 1984) epicotyl lengths of seedlings in randomly selected rows and columns of each tray were measured. Thus, on a weekly basis 20 seedlings per tray were measured for a total of 360 seedlings (i.e. 20 seedlings per tray X 9 trays X 2 species = 360 seedlings). Means and standard errors were determined.

In addition, morphological development of both species at the end of a ten week growth period was determined by randomly selecting 40 seedlings of each species. Once each seedling was selected it was removed from its container and its roots gently washed free of the soil mix. Individual seedlings were then measured for shoot length (± 0.5 cm), root collar diameter (± 0.5 mm), root area index (± 0.1 cm²) (Morrison and Armson, 1968) by use of a LiCor LI-3100 area meter, and top and root dry weight (± 0.01 g) determined. Species differences were determined by t-test.

3.2.4 Seedling nutrition. Once dry weights of seedling components were determined, shoots and roots respectively were bulked, by species, into four groups of ten seedlings. Foliage (stems removed) and roots were then ground in a Wiley mill and analysed for N, P, K, Ca, Mg, and Cl⁻.

Total N was determined by the Kjeldahl method. P, K, Ca, and Mg concentrations were determined by first digesting samples with a

mixture of nitric and perchloric acid. P concentration was determined using a spectrophotometer after color developed with ammonium meta vanadate reagent. K, Ca and Mg concentrations were determined using an atomic absorption spectrophotometer. Chloride concentration was determined first by extracting Cl^- with 0.1 N nitric acid then by potentiometric titration using a chloride specific ion electrode.

3.2.5 Conditioning treatments. For a seven week period from January 22, 1983 to March 10, 1983 1,568 seedlings were subjected to conditioning treatments. Seedlings were randomly arranged in the greenhouse to conform to a multiple split plot experimental design with four replications with main plots as irrigation frequency (daily, weekly), subplots as KCl level (0 ppm, 100 ppm), and 49 seedlings per sub-subplots. Replications and treatments within replications were rotated periodically to lessen the impact of temperature and light gradients on the response of seedlings to treatment.

Seedlings were conditioned by controlling the frequency of irrigation and by applying KCl as follows:

- i) irrigation: two levels of water stress were sought in both species by irrigating half the number of seedlings either on a daily or weekly basis. Daily irrigation maintained seedlings in a low water stress condition, whereas weekly irrigation promoted the development of water stress. Irrigation water was at room temperature and was applied until maximum water holding capacity of the soil was attained.
- ii) KCl: KCl was applied concomitantly with irrigation. Rates of application were set at 0 and 100 ppm.

During the application of the conditioning treatments the cultural level of fertilization (20/20/20) was reduced from 150 to 50 ppm N. Photoperiod and temperature settings were similar to those described under 3.2.2.

Response to the conditioning treatments was evaluated by measuring epicotyl lengths of seedlings at weekly intervals. Rows

and columns of seedlings were randomly selected to provide 13 seedlings at the sub-subplot level (416 seedlings). The efficacy of irrigation frequency to induce water stress during conditioning in the seedlings was determined by using a pressure chamber. For this measurement a minimum of three seedlings were randomly selected for each species X irrigation treatment.

Complete evaluation of seedling morphology was also carried out at the termination of the conditioning period. Ten seedlings at each of the sub-subplot levels were randomly selected and measured as previously described under 3.2.3. Treatment effects were determined by analysis of variance (Snedecor and Cochran, 1980).

An anatomical evaluation of stem and needle cross sections was carried out to determine if treatment effects had influenced dimensions of cell walls and cross-sections of needles. Three seedlings from each sub-subplot level were randomly selected. Needle segments 1 cm in length and 1 cm stem sections above the cotyledon scar were taken and immediately placed in a killing solution of FAA (formaldehyde: acetic acid: alcohol). Procedures according to Saas (1951) were followed for the embedding process. Sample sections of both needles and stems were cut on a rotary microtome at a thickness of 15 μ m, placed on glass slides, stained with safranin and fast green and permanently mounted. Needle and stem sections were observed under a light microscope and specific sections selected for detailed measurement and observation. Needle dimensions (width and height) were recorded using a glass mounted micrometer. Along four radii of stem sections the thickness of tangential and radial cell walls on six cells between the cambium and the pith were recorded. Data were submitted to analysis of variance.

Nutritional status of seedlings selected for morphological assessment was determined on foliage and roots using techniques described under 3.2.4. Treatment effects were determined for each nutrient element by analysis of variance.

3.2.6 Seedling responses to drought stress: first drought.

3.2.6.1 Experiment design and arrangements. After

seedlings had undergone the seven week conditioning period they were all uniformly irrigated over a two day period to leach soil of any possible salt buildup. Limited space within the growth room which was to be used for drought stressing necessitated modification to the experimental design initially employed during the conditioning period. First, the number of replications was reduced to three from four, and second, seedling number was reduced from 98 to 49 seedlings per tray. As before, cull seedlings were removed from further experimental consideration. Within each replication there were eight trays (2 species X 4 treatment combinations of irrigation [2] and KCl [2]). The increase in spacing, provided by the reduction in the number of seedlings per tray, facilitated air circulation. Seedlings were placed on the growth room benches with treatments at the sub-subplot level being randomly located within replications.

3.2.6.2 Growth room conditions. The growth room measured 3 m X 3 m. The light source was provided by 12 banks of high intensity fluorescence lights and eight 200 watt incandescence bulbs. The light intensity at the mid crown of the seedling was $107.3 \pm 2.9 \mu\text{E sec}^{-1}\text{m}^{-2}$. During the drought stress photoperiod was set to provide 18 hour days and day/night temperatures of 25°C and 18°C , respectively. No attempt was made to control humidity at a given level, instead the growth room was set to continually exhaust.

3.2.6.3 Evaluation of seedling water relations. The progression of seedling water relations was followed by the temporal determination of total plant water potential (ψ_T), osmotic potential (ψ_{π}), turgor pressure (ψ_p) and relative water content (RWC). In addition, bulk cellular water parameters were determined by the pressure-volume technique.

3.2.6.3.1 Total water potential: ψ_T . Total water potential was estimated using a pressure chamber (Model 1000, PMS Instrumental Co., Corvallis, Oregon) (Scholander *et al.*, 1965). Selected seedlings were severed to provide a stem sample approximately 12 cm in length. Bark and phloem were removed from 1.5 cm of the basal end of the stem sample which was then inserted

through a rubber bung using a brass insertion tool. Once secured in the pressure chamber which was humidified with a moistened paper towel, the sample was subjected to increasing pressure, the source of which was compressed nitrogen gas (99% N). The pressure was increased slowly, $0.005 \text{ MPa sec}^{-1}$ (Ritchie and Hinckley, 1975) until the end point was reached. This state theoretically occurs when the external pressure just equals the xylem water potential and is identified when the xylem sap reaches the cut surface of the stem. A 10X power hand lens was used to facilitate the identification of this point and to assist in avoiding a false end point.

Preliminary development of methods indicated that for Douglas-fir darkening of the cut surface occurred just prior to the attainment of the end point. For jack pine, however, extreme care had to be exercised in determining the end point because resin would first appear giving the impression that the end point had been reached. Differences in viscosity and coloration between resin and xylem sap were used as distinguishing features in determining the end point. Resin exudation ceased to be a problem at higher applied pressures.

3.2.6.3.2 Osmotic potential: ψ_{π} . Osmotic potential was determined by the expressed sap method (Tyree and Jarvis, 1982; Slavik, 1974). This method involved selecting sufficient number of needles from the stem sample previously used to evaluate ψ_T . Needles were placed in a 10 cm length of 8 mm i.d. tygon tubing, corked with rubber bungs at both ends and placed upon a sheet of dry ice and fast-frozen. After all samples were collected they were transferred to an ultra-cold unit for storage at -80° C until processed.

Osmotic potentials were determined after the experiment was terminated. Samples were removed from frozen storage and allowed to thaw for a minimum of 30 minutes while placed upon a wire support stand. This was to facilitate equal thawing of the sample. After thawing, the foliage was forced to one end of the tygon tubing using a glass rod as a plunger. The tubing was then directed between the rollers of a mechanical press. The compression

of the sample caused crushing of the foliage and release of apoplasmic and symplasmic water which was forced to the upper portion of the tubing. While still in the roller press the cell sap was allowed to stand to permit precipitation of particulate matter. A cover was placed over the open end of the tubing to eliminate evaporation and concentration of the cell sap.

Once the liquid appeared clear (after approximately 30 to 45 seconds) a 10 μ l sample was extracted using a micro pipette. The sample was then ejected onto a 7 mm filter paper disc and secured in the sample chamber of a vapor pressure osmometer (Model No. 5100CX, Wescor Inc.). The reading that was obtained at that temperature (read from an adjacent hygromograph) indicated the number of milli-moles per kilogram of solute in the liquid sample. This value was then converted to -MPa using the following equation:

$$\psi_{\pi} = (\text{mmoles/kg}) (0.08319 \text{ l-bars/mole } K^{\circ}) \times K^{\circ} \times [3.2.1] \\ (1 \text{ mole}/1000 \text{ mmoles}) \times (-\text{MPa}/10 \text{ bars})$$

This particular method for the determination of osmotic potential is frequently employed in plant water relations research. It has, however, one notable drawback. Freezing and crushing tissue samples allows for the mixing of apoplasmic water with the symplasmic water. Since it is the osmotic potential of the symplasm that is desired a correction factor must be employed to account for dilution and avoid overestimating turgor pressure from equation [2.1.4] (Markhart et al., 1981; Wenkert, 1980; Tyree, 1976; Brown and Tanner, 1983).

Originally, it was intended that a series of pressure-volume (P-V) curves (Tyree and Hammel, 1972) be run during the drought stress period to provide an estimate of the apoplasmic water fraction to correct ψ_{π} values from [3.2.1]. However, as discussed below estimates of the apoplasmic water fraction were such that unrealistic values of corrected osmotic potential were

derived leading to obvious overestimates of turgor pressure relative to plant condition. Subsequent discussions regarding this point with notable scientists (Drs. M. Tyree and J. Dainty, University of Toronto, Ontario, Canada; Dr. C. Glerum, Ontario Ministry of Natural Resources, Ontario, Canada; Dr. P. Webb, Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario, and Dr. G. Ritchie, Weyerhaeuser, Centralia, Washington) lead me to employ as part of the correction factor an apoplastic water fraction of 0.1. It was reasoned that the P-V curve conducted on seedling samples (stems and needles) did not accurately reflect the apoplastic fraction of needles alone.

Cheung et al. (1975) noted that ideally, water relation parameters should be representative of those of a sample leaf. While most shoot and leaf water parameters in their study were similar, the apoplastic water fraction of the shoot was determined to be larger in shoots than in individual leaves. Recently, Beeson et al. (1986) provided evidence by direct measurement of needles to confirm the results of Cheung et al. (1975). Since the Douglas-fir sample tissues used by Beeson et al. (1986) were obtained from large trees, not seedlings, their values of apoplastic water fraction in needles did not support the apoplastic water value of 0.1 used in this study. Water relations data pertaining to jack pine seedlings were not found.

Consideration of agronomic literature indicated that for species, such as soybean (Glycine max), snap bean (Phaseolis vulgaris) and sunflower (Helianthus annuus L) the apoplastic water fraction of leaves ranged from 0.07 and 0.13. It was, therefore, deemed that the value of 0.10 for the apoplastic water fraction was indeed a realistic value to employ in the correction factor.

The correction factor was applied to make the calculated osmotic potential more negative because dilution of the symplasmic water decreases the concentration of the solutes to underestimate the osmotic potential (Tyree, 1976). Moreover, it was reasoned that the correction factor must not be applied directly, but incorporate a term to account for the decreasing

water content of the plant cells as the plant decreases in relative water content. Thus, relative water content described below was incorporated into the correction factor (CF) which then had the following form:

$$CF = \frac{RWC}{RWC - Ra} , \quad [3.2.2]$$

where RWC represents the relative water content of the foliage and Ra represents the relative apoplasmic water content of the foliage and in this paper its value was taken as 0.1. Although the nature of the correction factor was developed independently, it has been employed in other research with success (Campbell et al., 1979). Each value of osmotic potential determined by the expressed sap method was subsequently adjusted according to the following:

$$\psi_{\pi} \text{ (actual)} = \psi_{\pi} \text{ (measured)} \times \frac{RWC}{RWC - .1} . \quad [3.2.3]$$

3.2.6.3.3 Pressure potential (turgor pressure): ψ_p .

The turgor pressure of plants is difficult to determine directly, necessitating alternate methods (Slavik, 1974). Most commonly, use is made of the relationship:

$$\psi_T = \psi_{\pi} + \psi_p \quad \text{see [2.1.4]}$$

or in its alternate form to provide an estimate of turgor pressure:

$$\psi_p = \psi_T - \psi_{\pi} \quad [3.2.4]$$

3.2.6.3.4 Relative water content: RWC. The relative water content of leaf tissue has been defined by Barrs (1968) as:

$$\text{RWC} = \frac{\text{water content at time of sampling}}{\text{water content at full turgor}} \times 100 \quad [3.2.5]$$

In the present experiment RWC was determined concomitantly with ψ_T and ψ_π . Immediately after ψ_T was estimated approximately 20 needles of Douglas-fir were severed from the stem, weighed to 0.1 mg, then placed between two moistened layers of paper towel contained in 12 cm X 12 cm plastic germination trays. For jack pine, which possessed longer secondary needles than the tray would accommodate, it was necessary to cut 3 cm sections from whole needles for determination of RWC.

Once needles were collected, the trays were covered with black cloth and placed in a refrigerator at 4⁰ C for 24 to 30 hours to regain full turgor. Needles were then removed from the cool environment, blotted dry to remove excess surface moisture and again weighed to 0.1 mg. Needles were dried in a force drafted oven at 70⁰ C for a minimum of 48 hours, removed, allowed to come to room temperature, weighed and RWC determined as follows:

$$\text{RWC (\%)} = \frac{\text{fresh wt.} - \text{dry wt.}}{\text{turgid wt.} - \text{dry wt.}} \times 100 \quad [3.2.6]$$

3.2.6.3.5 Pressure-Volume curves. The method of constructing pressure-volume curves and the theory behind their interpretation can be found in numerous research and review papers. The theory upon which pressure-volume curves is based is described by Tyree and Hammel (1972), Tyree (1976), Roberts and Koerr (1977), Turner (1981) and Tyree and Jarvis (1982).

The procedures used in the construction of pressure volume curves were after Joly (1984) and initially involved the selection of sample tissue approximately 15 cm in length. Once the

sample tissue was severed from the seedling with secateurs it was immediately placed in a beaker of water and taken to the laboratory for further preparation. The sample was trimmed to a maximum length of 12 cm with the needles removed from a 2 cm length of stem base and recut under water with a sharp razor blade. During the next 24 hour period the tissue sample remained with its base in approximately 2.5 cm of water and to facilitate the rehydration process the sample was encased by a plastic bag which was fastened to the beaker; the beaker was then placed in the cool dark environment of a refrigerator until processed the following day.

The technique of constructing a pressure-volume curve began by first standardizing tissue samples such that their length and fresh weight were respectively similar. Preparation of the sample required that the phloem be stripped from 12 mm of the basal end of the sample tissue and recut cleanly with a sharp razor blade. The sample was inspected for surface water on the stem and needles and patted dry, if necessary, with soft paper towelling then quickly weighed (0.1 mg). The sample was then enclosed with a polyethylene sheath measuring 5 cm X 12 cm containing a moistened 1.5 cm X 1.5 cm paper towel to lessen the rate of water loss from the foliage (Leach et al., 1982).

Three samples were prepared in this manner then inserted through a specially prepared cork and pressure head assembly. Three samples were processed simultaneously. Since the tissue samples continually lost water during the preparation period it was imperative that the time involved from removal from the high humidity environment until placed within the pressure chamber be kept to a minimum. On the average, this process was accomplished in 4 minutes. The initial equilibrium pressure was determined and recorded. Despite special attention to the hydration process rarely was the initial balance pressure below 0.07 MPa. The stems of the samples were then fitted with sap collection devices similar to those used by Joly (1984). These devices were constructed of small diameter tygon tubing and loosely stuffed with absorbent fibrous paper towelling. A pressure of approximately .35 MPa above the

previous equilibrium pressure was applied at a rate of $.005 \text{ MPa sec}^{-1}$, and the sap expressed was absorbed by the paper towelling. At low pressures i.e. less than 2 MPa, 10 minutes was allowed for the expression of sap. At higher pressures the equilibrium time was lengthened to 15 minutes.

At the end of the equilibrium period the overpressure was reduced to the midway point to the previously recorded balance pressure. The sap collection devices were removed from the stems, corked and set aside for weighing. The new balance pressure was then determined for each sample.

This process was continued until 11 to 13 paired data points were obtained. Upon determination of the final balance pressure the pressure within the chamber was gradually decreased, samples removed, and the residual fresh weights determined ($\pm 0.1 \text{ mg}$). The samples were placed in small paper bags and dry weights determined after 48 hours at 70° C .

Data thus collected was analysed further using computer programs developed by Joly (1984). The essential aspects of the analysis involved regression techniques for both the curvilinear and linear portions of the pressure-volume curve. From the analysis specific parameters were derived and those used in this research are as follows: (note references to Figure 3).

- i) osmotic potential at full turgor, OPFT. Osmotic potential at full turgor is a value estimated by extrapolating the linear portion of the pressure-volume relationship (where $\psi_T = \psi_{\pi}$) to the ordinate axis at which point the expressed volume ($\sum V_e$) is zero. According to Tyree and Richter (1982) estimate values of OPFT are fairly accurate, but rely on good experimental technique (Fig. 3, point A).
- ii) osmotic potential at zero turgor, OPZT. Osmotic potential at zero turgor is the inverse of the ordinate value corresponding to the point of zero turgor. The approach taken here, as developed by Joly (1984), was to assume that OPZT was equivalent to the balance pressure at the point where the straight line relating $\psi_T = \psi_{\pi}$ deviated from

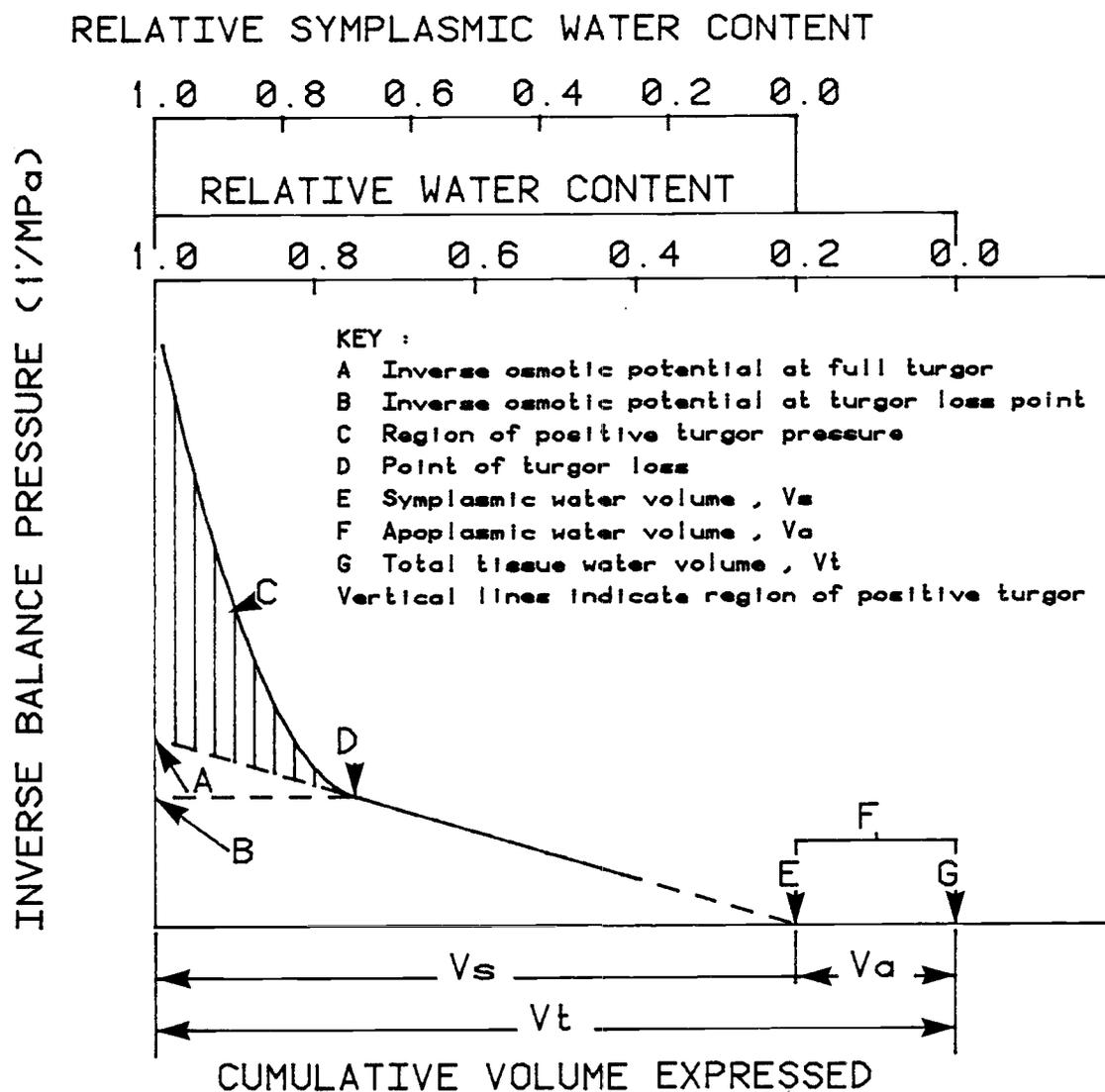


Figure 3. Model pressure-volume curve relating inverse pressure to cumulative volume of expressed sap and relative water content. Important water relation parameters are noted by letters.

linearity. Departures from linearity were reflected in a rapid decrease in the coefficient of determination (r^2) (Fig. 3, point B).

- iii) tissue turgor pressure, ψ_p : This value is determined by taking the difference between the $1/\psi$ on the curvilinear portion of the $1/\psi$ isotherm and $1/\psi_s$ on the linear extrapolation of the same isotherm usually determined at a particular RWC (Fig. 3, point C).
- iv) relative water content at turgor loss point, RWC @ TLP. Pressure volume curves may be plotted as $1/\psi$ versus $\sum V_e$ or as $1/\psi$ versus RWC. Relative water content at turgor loss point is the RWC (noted on x axis) at which $\psi_p = 0$ (Fig. 3, point D).
- v) relative symplasmic water content at turgor loss point, RSWC @ TLP. The relative symplasmic water content is defined by:

$$RSWC = \frac{V_o - V_e}{V_s} \quad [3.2.7]$$

where V_s is the symplasmic water content as determined by extrapolation of the linear portion of the pressure-volume curve to the x-axis (Fig. 3, point E). The RSWC @ TLP therefore is RSWC [3.2.7] at the turgor loss point.

- vi) relative apoplasmic water content, R_a . The apoplasmic water volume is represented by F in Figure 3. The relative apoplasmic water content is determined by:

$$R_a = \frac{V_t - V_s}{V_t} \quad , \quad [3.2.8]$$

where V_t (Fig. 3, point G) is total water volume:

$$V_t = V_s + V_a \quad , \quad [3.2.9]$$

where V_s and V_a are the symplasmic and apoplasmic water volumes, respectively.

- vii) modulus of elasticity at 0.995 RWC, $\bar{\epsilon}$. The form used for the determination of the weight-averaged bulk elastic modulus (i.e. average over sample tissue) was derived by Tyree and Hammel (1972) and later by Tyree and Jarvis (1982):

$$\bar{\epsilon} = \frac{d\bar{P}}{dW} \cdot W \quad [3.2.10]$$

where $\bar{\epsilon}$ is the weight-averaged elastic modulus, \bar{P} is the bulk averaged turgor and W is the weight of symplasmic water at full turgor. Given that the density of the symplasm is 1 g/cc equation [3.2.10] can be rewritten in the form:

$$\bar{\epsilon} = \frac{d\bar{P}}{dRSWC} \quad [3.2.11]$$

Computer computation (Joly, 1984) provided for the calculation of $\bar{\epsilon}$ in RWC decrements of 0.005 from RWC = 1.0 to RWC @ TLP. The value of ϵ near full turgor ($\bar{\epsilon}_{\max}$) was arbitrarily designated as that value of $\bar{\epsilon}$ computed at RWC = 0.995.

3.2.6.4 Evaluation of seedling morphology. Seedlings that were selected for determination of water relation parameters as described in section 3.2.6.3 were also evaluated for morphological changes during drought stress. Epicotyl length (± 0.1 cm), root collar diameter (± 0.5 mm), root area index (± 0.5 cm²), and root dry weight (± 0.1 g) were determined using methods described under 3.2.3. Data were submitted to analysis of variance and significant

mean differences determined by Duncan's Multiple Range Test.

3.2.7 Sampling design and procedures. The duration of the first drought period was 10 days. During this period seedling water relations and associated morphology were evaluated on four occasions: days 1, 5, 8, and 10 commencing on March 18, 1984 and terminating March 27, 1984. On each sampling date one seedling from each sub-subplot was randomly selected for evaluation to provide 24 seedlings per sample date.

Selection of seedlings on each sampling day was made repeatedly 2 hours after the start of the photoperiod. Seedlings that appeared dead were excluded from the sample population because estimates of water relation parameters could not be determined. Sample seedlings were transferred to the laboratory for evaluation. Firstly, epicotyl lengths, and root collar diameters were measured, then root area indices and dry weights recorded once the water relation parameters were determined.

Root systems by species for respective treatments were bulked, ground and stored for later analysis by methods described under 3.2.4. Only roots were considered for nutrient analyses since the majority of foliage from the sample seedling was utilized for measurements of relative water content and osmotic potential.

Water content of the soil occupied by each seedling was determined. Values of moisture content were expressed on an oven dry weight basis after soil was dried at 100^o C for 48 hours in a force drafted oven.

Pressure-volume curves were determined at the initiation, mid-point, and termination of the drought period. Sample seedlings were randomly selected the morning prior to laboratory evaluation i.e. Days 1, 6, and 10. Due to time constraints samples were randomly selected from two randomly selected replications and prepared for rehydration as described under 3.2.6.3.4. The data set for Sample Day 1 was incomplete due to equipment failure.

Data were submitted to analysis of variance and significant differences amongst treatments determined by Duncan's Multiple Range Test.

3.2.8 Seedling recovery from first drought stress. After ten days of drought exposure seedlings were removed from the growth chamber and transferred to a fiberglass greenhouse. Once the transfer was completed seedling condition was subjectively evaluated for degree of foliage wilting and coloration. Seedlings were frequently irrigated with room temperature water and maintained under moderate environmental conditions: day/night temperatures of 27^o C and 15^o C, respectively. Lighting remained as described under 3.2.2.

After the soil medium had regained maximum water holding capacity seedlings were individually evaluated and classified as dead, variously wilted (i.e. needles green in color but attainment of turgidity not obvious) or healthy (turgid condition obvious). Dead seedlings were removed to avoid any incidence of disease e.g. Botrysis spp. Evaluation of recovery was undertaken on the second and fourth day of the recovery period. Total water potential was estimated on the seventh recovery day on two randomly selected seedlings from each of the sub-subplots (n = 48). Analysis of mortality in relation to treatment was evaluated by Chi-square analysis.

3.2.9 Seedling responses to drought stress: second drought.

3.2.9.1 Experimental design and arrangement. Upon completion of the 10 day recovery period the remaining population of experimental seedlings was irrigated to saturation, allowed to drain and transferred to the growth room. Seedlings were placed on the growth room benches in conformity with the previously described arrangement 3.2.6.1.

3.2.9.2 Growth room conditions. Growth room conditions were maintained as described under 3.2.6.2.

3.2.9.3 Evaluation of seedling water relations. Methods for the evaluation of seedling water relations were those previously described under 3.2.6.3 and 3.2.6.4.

3.2.9.4 Evaluation of seedling morphology. Morphological parameters were evaluated using methods described under 3.2.6.4.

3.2.9.5 Sampling design and procedures. The length of

exposure of seedlings to drought conditions in the second drought period was 14 days. During this period water relation parameters and seedling morphology were determined every second day thereby providing seven sample days. The procedures employed for selecting seedlings have been described under 3.2.7. Depletion of soil water by evapotranspiration was monitored on a daily basis by weighing designated seedling/containers (24) selected at the sub-subplot level. Analyses of data followed techniques stated in subsections under 3.2.6.4 and 3.2.7.

3.2.10 Seedling recovery from second drought stress. After drought exposure seedlings were removed from the growth room and transferred to the greenhouse for a 10 day recovery period. Refer to section 3.2.8 for description of greenhouse conditions and evaluation procedures to assess seedling condition and water status. In this instance, however, evaluations were conducted on the second and tenth days of the recovery period. Chi-square analysis was employed to test the hypothesis that mortality was independent of the condition treatment.

3.2.11 Response of droughted seedlings to long-term favorable growing conditions. Upon completion of the second drought/recovery test the remaining living seedlings were grouped by treatment level and by species. From this amalgamation, 15 seedlings from each of the four treatment combinations (2 irrigation X 2 KCl levels) were randomly selected from each species to provide 120 test seedlings. Seedlings by species and respective treatments were planted in 11 litre pressed peat pots filled with clay loam soil, five seedlings per pot. This provided 24 pots (3 replications X 2 irrigation X 2 KCl levels X 2 species = 24).

The pots were arranged in the growth room by replication within which pots were randomly located. Conditions within the growth room were maintained to provide a photoperiod of 16 hours and day/night temperatures of 24^o C and 18^o C for a 12 week period. During this period the seedlings were watered frequently to avoid water stress and the pots were kept weed-free.

Immediately after planting, epicotyl lengths (± 0.5 cm) and

root collar diameters were recorded. After 12 weeks seedlings were removed from the pots, root systems washed free of soil then measured for the above morphological parameters as well as root dry weight and shoot dry weight.

The final analysis of seedling performance also included aspects of health condition by interpretation from foliage color and classified as healthy/unhealthy. Bud set was noted and root growth activity was subjectively classified as nil, little or extensive based upon presence of white root tips.

Morphological parameters were submitted to analysis of variance.

3.3 Phase II: Nursery Experiment.

Inasmuch as the nursery experiment was undertaken to provide a measure of validation of seedling response to conditioning treatments as determined under growth room conditions much of the experimental approach was repeated and therefore, will not be reiterated in its entirety here. Differences, where they occurred, will be noted. Figure 4 diagrammatically presents the sequence of events of the nursery experiment.

3.3.1 Seedling culture. Seeds of Douglas-fir and jack pine from the same seedlot as previously used (see 3.2.1) were similarly stratified then placed in a lighted temperature controlled cabinet for germination. On February 5, 1984, nine days after the start of germination germinants with radicals measuring 0.5 cm to 1.0 cm were transplanted into 165 cc Ray Leach cells containing a peat - vermiculite - sand mix (by volume 1:1:1). Approximately 2,000 germinants were transplanted.

Once all germinants were transplanted seedlings were placed in a glass house with supplemental lighting. The photoperiod was set to provide an 18 hour daily photoperiod and temperature was set to provide 25/15⁰ C day/night temperatures. Seedlings were adequately watered during the first three weeks of the growing period to ensure maximum establishment; no damping off was detected. Fertilization commenced according to the prescription set under 3.2.2.

Careful observation of seedling development during the common

NURSERY EXPERIMENT

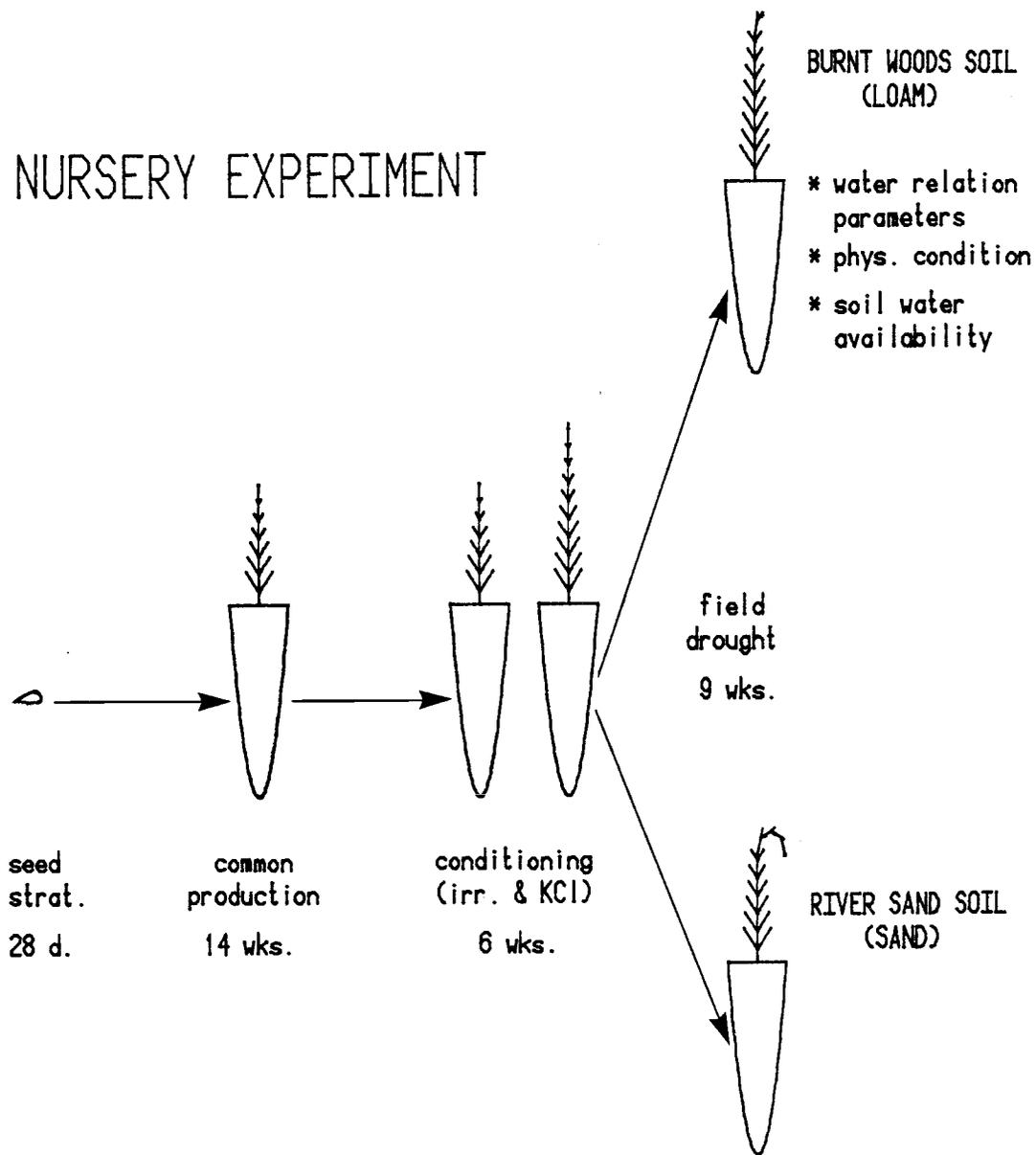


Figure 4. Diagrammatic representation of events during the conduct of the nursery experiment.

production period revealed that although seedlings were healthy and green their rate of growth was markedly below that which was exhibited by the previous crop. Greenhouse controls were found to have malfunctioned resulting in a reduced photoperiod. At this point, when seedlings were 10 weeks old, they were transferred to another greenhouse in which conditions could be better controlled. The 18 hour photoperiod was reestablished and the fertilization frequency was increased to three times per week. These actions initiated growth of seedlings, but increased the common cultural period by five weeks.

3.3.2 Conditioning treatments. When both species of seedlings were 15 weeks old conditioning treatments were commenced. Because seedlings were to be planted outside for drought stressing it was necessary to condition the foliage of the seedlings against damage by solarization. Hence, the conditioning process was relegated to a large covered cold frame. Within the cold frame seedlings were arranged in a multiple split plot design in which there were five replications. Within each of the replication treatments were randomized as described under 3.2.5. Cull seedlings were eliminated from further treatment.

Seedlings were conditioned by irrigation and KCl applications as described under 3.2.5. Seedlings were exposed to conditioning treatments for a period of six weeks from May 20, 1984 to July 1, 1984.

3.3.3 Seedling growth and nutrition. During the conditioning period seedling growth was evaluated weekly by measuring epicotyl lengths (± 0.5 cm) of 13 seedlings in randomly located rows and columns of each seedling tray. After measurement, seedlings were rotated within replications which provided varying lengths of exposure to sunlight. Once the conditioning period terminated five seedlings were randomly selected from the sub-subplot level for complete morphological assessment. Seedling root systems were carefully removed and rinsed free of the soil mixture, and the seedlings then measured for shoot length, root collar diameter, and root area index. Roots and shoots were subsequently and

individually dried in a forced draft oven for 48 hours at 70° C, then weighed, ground in a Wiley mill and stored for analysis of N, P, K, Ca, Mg and Cl⁻ as described under 3.2.4.

Morphological and nutritional data were submitted to analysis of variance.

Anatomical observations were made on stem and needle cross-sections of three randomly selected seedlings from each of the sub-subplot levels (3 X 2 irrigation X 2 KCl X 2 species = 24 seedlings). Preparation of sample tissue has been described under 3.2.5.

3.3.4 Seedling responses to nursery drought stress.

3.3.4.1 Preparation for outplanting. Immediately following termination of the six week conditioning period all seedlings were uniformly and repeatedly leached to remove excess fertilizer salts which may have accumulated. Small or excessively large seedlings were culled and excluded from further consideration.

Planting was done into soil contained by two adjacent cold frames measuring 9.1 m X 1.8 m X 0.6 m located in the nursery area at the rear of the Forest Research Laboratory at Oregon State University. The cold frames were divided by a wooden barrier into two compartments, each approximately 4.5 m in length to accommodate two soil types. The soils were, by mechanical analysis: a sandy clay loam (sand 47%, silt 30%, clay 23%) and a loamy sand (sand 89%, silt 5%, clay 6%). The sandy clay loam was originally obtained from a forest site in the vicinity of Burnt Woods, Oregon, 36 km west of Corvallis, and the loamy sand was obtained from a local gravel supply company. The soils were selected because of their widely different textural properties. The intent was to provide soil conditions in which soil water deficits developed at different rates.

Both Douglas-fir and jack pine seedlings are known to rapidly extend their roots vertically after planting to access large volumes of soil for water. To ensure that only a finite volume of water was available for absorption a barrier of 6 ml polyethylene plastic sheeting was placed over the subsoil at a profile depth of

25 cm. Once the plastic barrier was in place the two soil types were randomly allocated to the compartments. The function of the barrier was to restrict the vertical growth of roots and to prevent the upward movement of water from the subsoil by capillary action. Examination of some seedling root systems at the termination of the experiment revealed that growth of roots was not restricted by the plastic barrier. The principal function of the barrier, therefore, was to prevent the capillary flow of water into the rooting zone.

To further limit the amount of soil water available to the seedlings during the development of drought conditions shelters were constructed above the cold frames. The shelter framing was covered with light transmitting fiberglass sheeting. Although these shelters were maintained throughout the experimental period seedlings received a minimum of 75% of full sunlight exposure on a daily basis.

Soil water was monitored throughout the experimental period. Sixteen stations (four per compartment) were randomly located; each station consisted of three cylindrical gypsum units (Delmhorst Instrument Co., Boonton, New Jersey), one each at 5 cm, 15, and 25 cm depths. Readings of resistance, taken every second day during the experimental period, were translated into estimates of soil water potential and water content by developing calibration curves using a pressure plate apparatus.

3.3.4.2 Planting and experimental design. Seedlings were planted at 12 cm centers using a wooden dibble to first create a hole into which the soil root mass of the seedling was firmly placed by hand. Planting began on July 2, 1984 and was completed July 3, 1984.

The experimental layout used for planting was similar to that employed during the application of the conditioning treatments i.e. a multiple split plot design. Several modifications had to be implemented however. Due to limited space the number of replications was set at two, each cold frame representing a replication and as mentioned above soil type was added as an additional test treatment. Within each of the four compartments the

original eight sub-subplots (i.e 2 irrigation X 2 KCl levels X 2 species) were randomly located. The area occupied by each treatment designation was approximately 0.9 m X 1.2 m within which there were 56 planting spots. In total 1,792 seedlings were planted (2 irrigation X 2 KCl levels X 2 species X 2 soil types X 2 replications X 56 seedlings per plot = 1,792 seedlings).

Survival plots were located within each treatment and consisted of 16 seedlings in a 4 X 4 arrangement. These seedlings were used exclusively for following the occurrence of mortality and were excluded from future sampling consideration.

3.3.4.3 Sampling and analysis procedures. Sampling of seedling water relations and associated morphology was carried out at precisely seven day intervals beginning one week following planting (July 9, 1984) and continued up until August 27, 1984. Over this assessment period eight evaluations were undertaken using the following procedures:

3.3.4.3.1 Morphology. One day prior to assessment of water relation parameters (see below) one seedling from each of the sub-subplots within soil types and replications was randomly selected (survival plot and edge row seedlings excluded) providing 32 seedlings for assessment. Once tagged and marked as to their respective treatment epicotyl length (± 0.5 cm) and root collar stem diameter (± 0.1 mm) below the cotyledon scar were measured. Constraints on time did not permit evaluation of the root system.

3.3.4.3.2 Plant water relations. Evaluations of plant water relations were undertaken between the hours of 2:00 a.m. and 6:00 a.m. In groups of four, selected seedlings were severed at ground level and immediately placed in a plastic bag containing a dampened swath of paper towel and sealed. The bags were then placed in a styrofoam cooler containing a freezer bag. The cool, dark and moist environment provided adequate short-term storage and prevented changes in water relation parameters before actual measurement.

Seedlings were taken quickly to the laboratory whereupon they were individually assessed for total water potential (see 3.2.6.3.1), osmotic potential (see 3.2.6.3.2), turgor pressure

(see 3.2.6.3.3), and relative water content (see 3.2.6.3.4).

3.3.4.3.3 Pressure-volume determinations. Water relations of seedlings were further evaluated employing pressure-volume techniques described under section 3.2.6.3.4. Sampling was carried out on four occasions during the experimental period. For the first assessment, 16 seedlings were selected, two each from the eight sub-subplots (2 irrigation X 2 KCl levels X 2 species). The remaining three assessments were carried out at regular biweekly intervals. On each occasion, 32 seedlings were randomly selected, one from each sub-subplot level within both soil types (2) and replications (2). Complete pressure-volume determinations of 32 seedlings were completed in three and a half 14 hour days.

3.3.4.3.4 Physiological condition during drought stress. Weekly, from July 28, 1984 to August 1984, the population of seedlings remaining in each treatment were subjectively evaluated as to their average physiological or health condition. Stages of diminishing health used for this assessment were described by degree of foliage discoloration (i.e. yellowing), degree of turgidity, withering of stem and needles and mortality which was deemed to have occurred when all foliage was brown.

3.3.4.3.5 Methods of analysis. Water relation and morphological parameters were submitted to analysis of variance, first by species then by soil type. Water relation parameters derived from pressure-volume curves were also analysed by analysis of variance. Chi-Square analyses were conducted for each species to test the hypotheses that mortality was independent of conditioning treatment.

4. RESULTS

4.1 Phase I: Growth room experiment

4.1.1 Seedling growth and nutrition during production. During the 10 week common production period mortality was confined to four seedlings suggesting that conditions in the greenhouse were very favorable for growth. Growth progression of Douglas-fir and jack pine in terms of epicotyl length (Fig. 5) indicates that both species grew at near similar rates from the third week of production up until the tenth week. Table 1 presents a summary of morphological parameters of seedlings measured at week 10. Differences between species for all parameters, except total seedling dry weight, were highly significant.

Nutrient concentrations of foliage and roots of both species at week 10 are presented in Table 2. According to critical nutrient values presented by Morrison (1974) none of the nutrient elements (N, P, K Ca, Mg) was deficient. In Douglas-fir, concentrations of N, P, K, and Cl^- were higher in the foliage than in the roots and concentrations of Ca and Mg were highest in the roots. For jack pine, only N concentrations were highest in the foliage. The concentration of Cl^- in the roots of Douglas-fir and jack pine exceeded that in the foliage by factors of 5 and 7, respectively.

4.1.2 Seedling growth and nutrition in response to conditioning treatments.

4.1.2.1 Seedling growth. Analysis of variance by sample time (Table B-1) suggests that there were no differences in epicotyl length due to treatment on either species through week 13 (Fig. 6). By week 14 a significant treatment effect was detected, but was due only to irrigation level and was dependent upon species (significant irrigation X species interaction). At this point, differences in epicotyl length for daily vs weekly irrigated Douglas-fir and jack pine were 19.1 cm vs 16.5 cm and 12.2 cm vs 12.5 cm, respectively. When seedlings reached 17 weeks, differences in epicotyl length due to irrigation were significant (Table 4) and irrigation X species

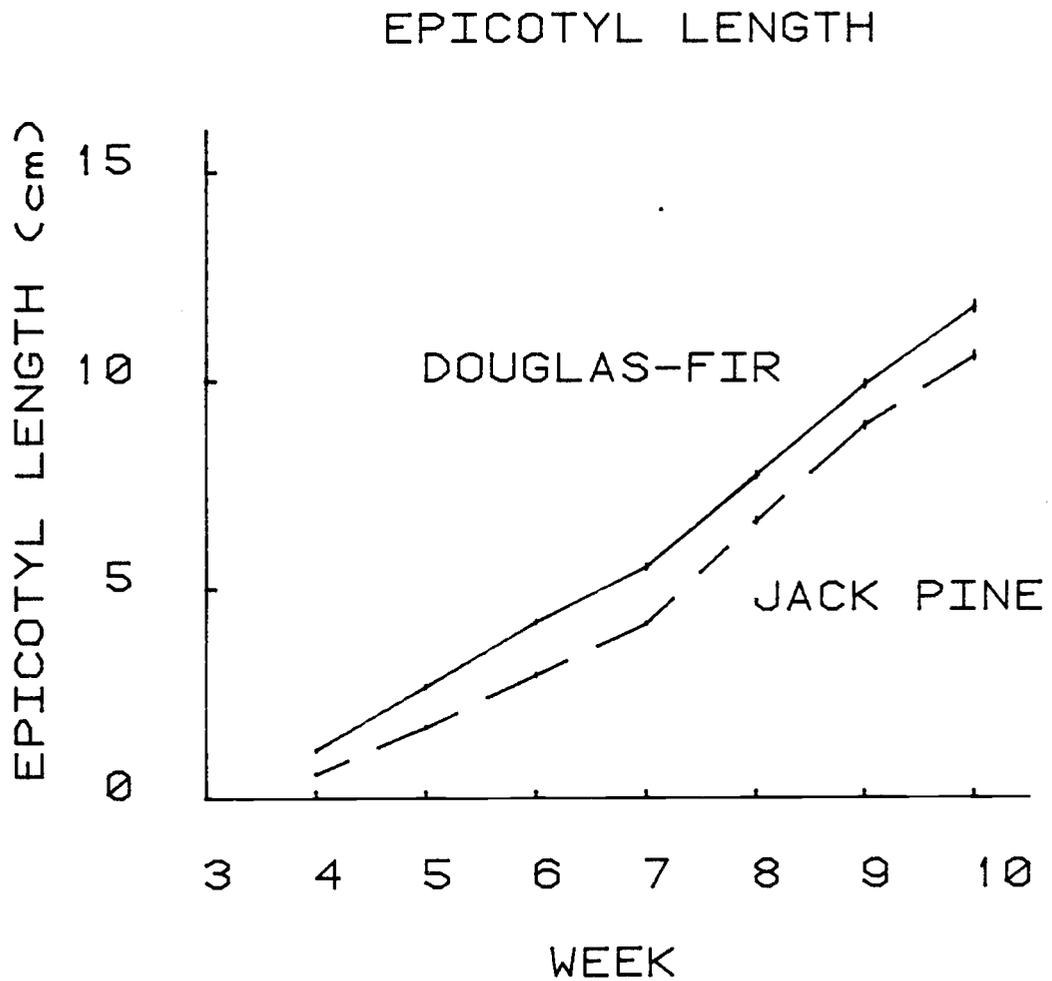


Figure 5. Progression of epicotyl lengths of DOUGLAS-FIR and JACK PINE seedlings during the early greenhouse production period. Vertical bars represent standard errors ($n = 9$).

TABLE 1. Morphological characteristics ($\bar{X} \pm SE$) of 10 week old DOUGLAS-FIR and JACK PINE seedlings. Significant differences between species are appropriately noted¹ (n = 40).

Seedling parameter	Species				Sig.
	Douglas-fir		Jack pine		
	\bar{X}	$\pm SE$	\bar{X}	$\pm SE$	
Shoot length (cm)	15.14	0.27	14.00	0.23	**
Root collar diameter (mm)	1.55	0.03	1.73	0.03	**
Root area index (cm ²)	15.98	0.65	18.36	0.69	**
Shoot dry weight (g)	0.44	0.02	0.53	0.02	**
Root dry weight (g)	0.11	0.01	0.09	0.005	**
Total seedling dry wt. (g)	0.55	0.02	0.62	0.23	NS

¹ ** p < .01
NS Not significant

TABLE 2. Mean nutrient concentrations in foliage and roots of 10 week old unconditioned DOUGLAS-FIR and JACK PINE container seedlings (n = 4).

Species	Plant component	Nutrient					
		N	P	K	Ca	Mg	Cl ⁻
		----- % -----					ppm
Df	Foliage	2.36	0.739	1.527	0.166	0.161	0.426
	Roots	2.10	0.732	1.406	0.259	0.194	2.039
Jp	Foliage	3.06	0.372	1.302	0.187	0.170	0.678
	Roots	2.85	0.824	1.864	0.334	0.253	4.718

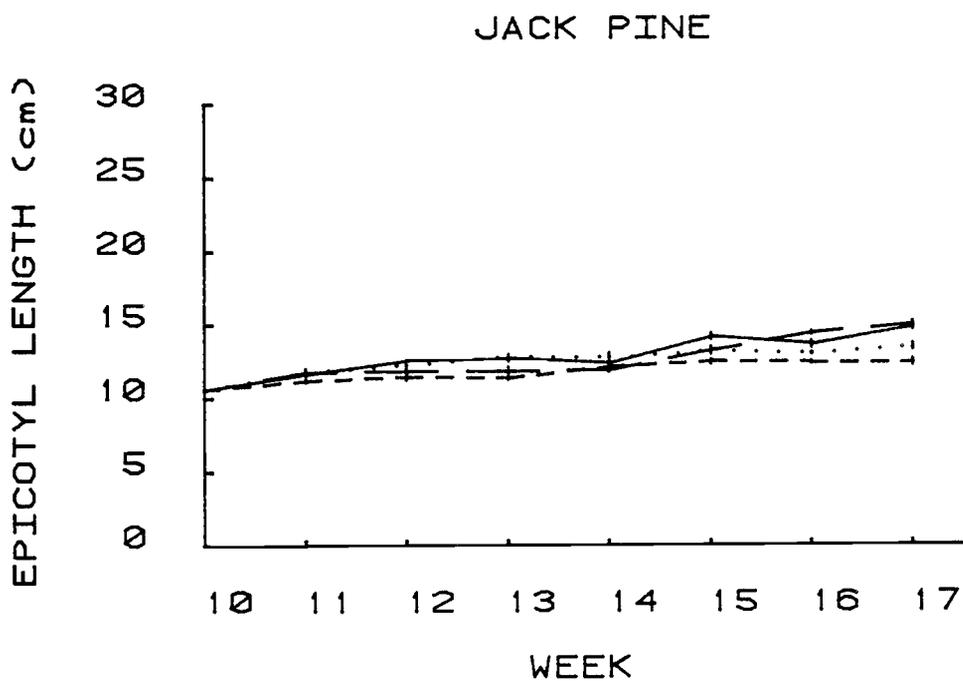
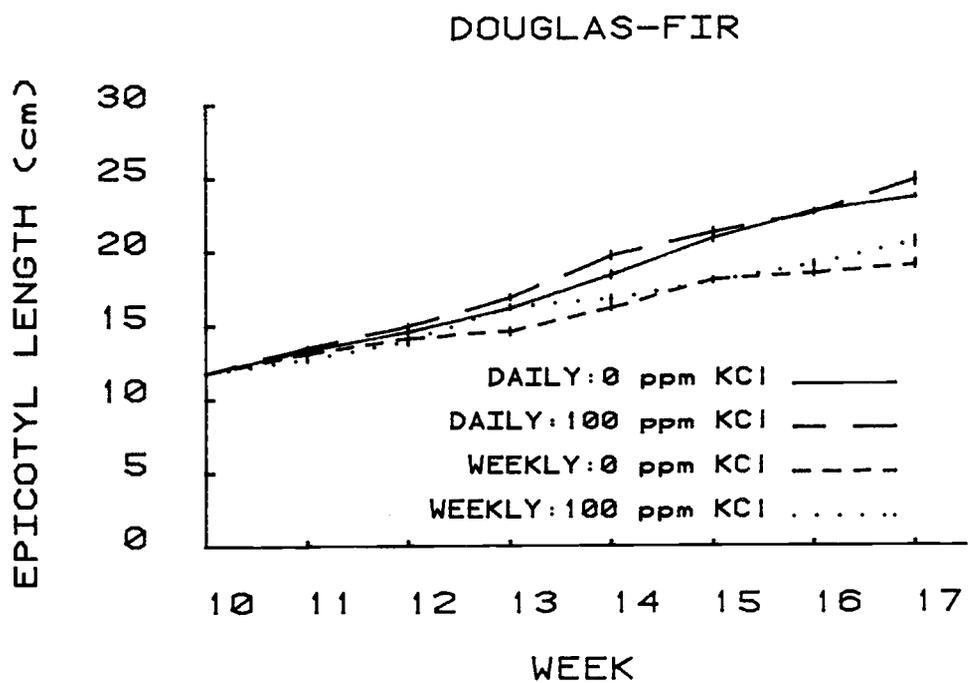


Figure 6. Progression of epicotyl lengths of DOUGLAS-FIR (upper graph) and JACK PINE (lower graph) seedlings during the seven week conditioning period.

interaction remained significant. Since the epicotyl lengths of weekly irrigated Douglas-fir and jack pine were respectively, 18% and 13% less than daily irrigated seedlings it might be assumed that Douglas-fir shoot elongation was more sensitive to periodic water stress than jack pine.

Plant water potential was monitored on five occasions in an attempt to judge the success of irrigation treatment to induce stress. Table 3 indicates the range of plant water potentials reached prior to daily and weekly irrigations. For all sample dates, except two for Douglas-fir, potentials of weekly irrigated seedlings were lower than those of daily irrigated seedlings by more than a factor of two. Thus, based upon differences in epicotyl length and plant water potentials attained by daily and weekly irrigated seedlings it was concluded that irrigation was a successfully applied conditioning treatment. However, attempts to associate conditioning treatments with differences in cell wall thickness and variations in needle morphology failed. Analysis of variance of radial and tangential cell wall thicknesses of stem sections indicated that conditioning treatments were not significant. Similarly, dimensions of needle cross sections were not significantly altered by irrigation or applications of KCl.

A complete morphological assessment of 17 week old seedlings revealed (Table B-2) that the main order effects of irrigation and species were significant for most parameters. Data are presented in Table 4 by species and irrigation level. Irrigation frequency did not significantly affect root area index or root dry weight. Figure 7 exhibits root system development which was typical of Douglas-fir and jack pine at 17 weeks of age. It should be noted, that despite non-significance of dry weight, characteristics of the root systems were distinctly different (Fig. 7). The root system of Douglas-fir was coarse, i.e. it possessed many thickened secondary roots and a very small component of fibrous roots. The root system of jack pine, on the other hand, was fibrous; coarse secondary roots were much less distinct and fibrous tertiary roots predominated.

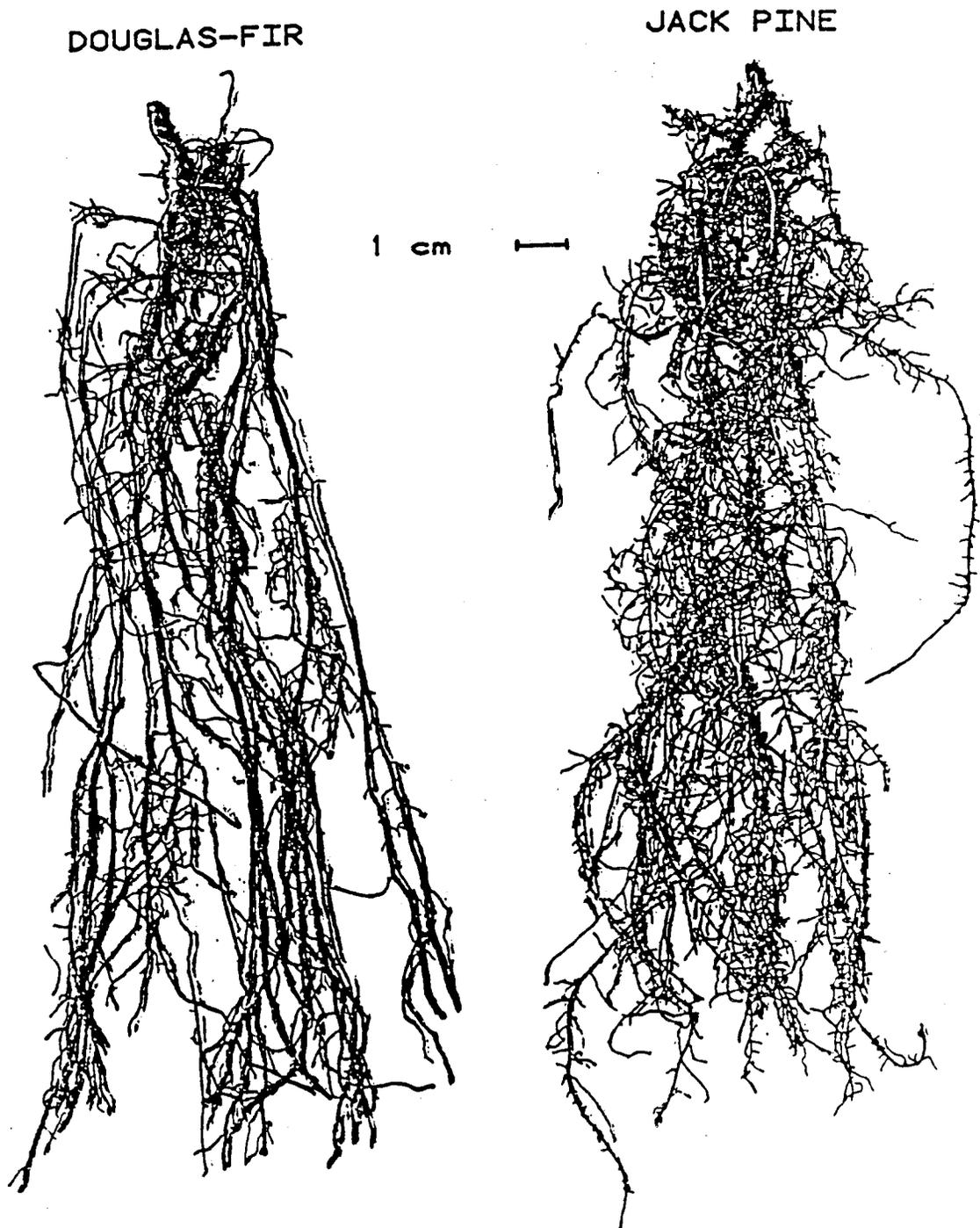


Figure 7. Typical root systems of 17-week-old conditioned DOUGLAS-FIR and JACK PINE seedlings.

TABLE 3. Plant water potentials of DOUGLAS-FIR and JACK PINE seedlings prior to irrigation. Values at each date were based upon a minimum of three seedlings per irrigation regime and species.

Date	Seedling age (weeks)	Species/Irrigation			
		Douglas-fir		Jack pine	
		Daily	Weekly	Daily	Weekly
		----- MPa -----			
Feb. 12	10	-0.48	-1.02	-0.33	-0.67
Feb. 19	11	-0.48	-1.32	-0.38	-1.30
Feb. 26	12	-0.75	-1.50	-0.34	-1.25
Mar. 4	13	-1.01	-1.60	-0.59	-1.52
Mar. 11	14	-0.67	-0.96	-0.34	-1.23

TABLE 4. Morphological parameters of 17 week old conditioned DOUGLAS-FIR and JACK PINE container seedlings. Means and standard errors are determined over replications and KCl levels which were non-significant in the analysis of variance.

Seedling parameter	Species/Irrigation							
	Douglas-fir				Jack pine			
	Daily		Weekly		Daily		Weekly	
	\bar{X}	\pm SE	\bar{X}	\pm SE	\bar{X}	\pm SE	\bar{X}	\pm SE
Root collar diameter (mm)	2.5	0.04*	2.15	0.04	2.83	0.06*	2.32	0.03
Shoot length (cm)	29.78	0.46*	23.54	0.54	19.66	0.37*	16.04	0.35
Root area index (sq. cm)	25.78	0.88*	21.42	0.51	31.41	0.90 ^{NS}	29.08	1.34
Shoot dry weight (g)	1.49	0.07*	1.05	0.03	1.88	0.05*	1.34	0.02
Root dry weight (g)	0.28	0.02 ^{NS}	0.28	0.01	0.28	0.01 ^{NS}	0.25	0.02
Seedling dry weight (g)	1.77	0.09*	1.33	0.04	2.16	0.06*	1.59	0.04
Top:Root ratio	5.49	0.23*	3.82	0.10	6.71	0.23*	5.52	0.27

Significance level

* $P < 0.05$

NS Not significant

Top:root ratios were lower in weekly irrigated treatments of both Douglas-fir and jack pine. Since root dry weights were not significantly affected by irrigation treatment lower values of top:root ratio in the weekly irrigation treatment can be attributed to the significant decrease in shoot dry weight (Table 4).

4.1.2.2 Seedling nutrition. Nutrient concentrations of foliage and roots are presented in Table 5. With only a few exceptions concentrations of nutrient elements in foliage and roots were higher in daily irrigated seedlings rather than in weekly irrigated seedlings. Foliar concentrations of P and K and root concentrations of P, K and Mg were significantly affected by irrigation (Tables B-3 and B-4 respectively). Except for K concentration in the roots, species differences for all elements were significant. K concentrations in foliage and roots were not significantly affected by the level of applied KCl. On the other hand, Cl^- concentration in foliage and roots was significantly affected by level of applied KCl. Concentrations of K in foliage and roots, but not Cl^- concentrations, were significantly influenced by irrigation (Tables B-3 and B-4). For both Douglas-fir and jack pine, at all treatment combinations, K concentrations were higher and Cl^- concentrations lower in the foliage than in the roots.

4.1.3 Seedling responses to drought stress; FIRST DROUGHT.

4.1.3.1 Soil water loss. Soil water contents were determined concomitantly with morphological and water relation parameters. Table 6 summarizes the soil water contents by species and irrigation level throughout the drought stress period. Initially, soil water contents were high, but then dropped precipitously by the fifth sample day then slowly decreased to terminal values.

4.1.3.2 Seedling Morphology. The progression of epicotyl length, root collar diameter, root area index and root dry weight throughout the experimental drought period are presented in Figure 8. Because of a lack of statistical significance of KCl by sample date (Table B-5), means are presented by species and irrigation treatment. Further analysis indicated (Table B-6) that epicotyl

TABLE 5. Nutrient concentrations of foliage and roots of 17 week old conditioned DOUGLAS-FIR and JACK PINE container seedlings.

Treatment				Nutrient					
Irriga- tion	KCl level (ppm)	Sp.	Plant compo- nent	N	P	K	Ca	Mg	Cl ⁻
				----- % -----					
Daily	0	Df	Top	2.188	0.767	1.707	0.245	0.178	0.546
			Root	2.038	0.438	0.717	0.282	0.201	0.942
	Jp	Top	2.583	0.332	1.061	0.197	0.160	0.548	
		Root	2.498	0.504	0.843	0.323	0.239	1.710	
Weekly	100	Df	Top	2.110	0.717	1.781	0.231	0.167	2.039
			Root	2.120	0.479	0.883	0.270	0.200	2.275
	Jp	Top	2.443	0.309	1.062	0.184	0.146	1.258	
		Root	2.365	0.476	0.938	0.313	0.249	3.579	
Weekly	0	Df	Top	2.148	0.585	1.295	0.222	0.165	0.495
			Root	1.760	0.282	0.510	0.292	0.293	0.798
	Jp	Top	2.608	0.301	1.061	0.172	0.152	0.751	
		Root	2.340	0.381	0.559	0.351	0.204	1.051	
100	Df	Top	2.405	0.611	1.435	0.228	0.179	1.454	
		Root	2.045	0.309	0.586	0.297	0.199	2.395	
Jp	Top	2.238	0.301	1.045	0.170	0.151	1.036		
	Root	2.360	0.366	0.529	0.334	0.195	2.403		

TABLE 6. Water content (% oven dry wt.) of rooting medium of sample seedlings by species and irrigation conditioning treatment.

Species	Irriga- tion	Sample time (experimental day)			
		1	5	8	10
		----- % -----			
Douglas-fir	Daily	47.0	10.8	4.0	4.0
	Weekly	50.0	7.2	5.6	5.2
Jack pine	Daily	54.7	4.7	2.8	2.1
	Weekly	51.0	5.5	3.5	2.6

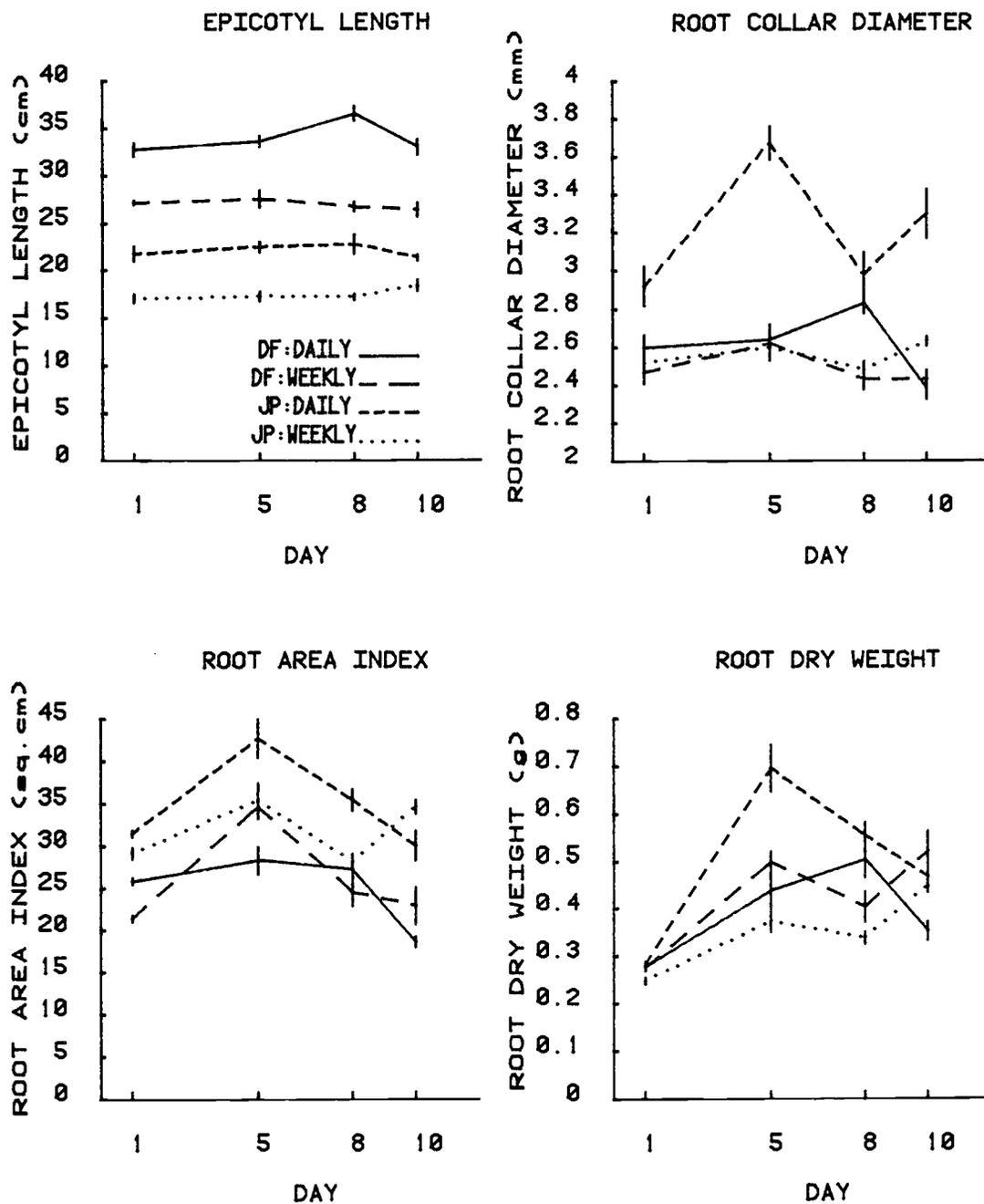


Figure 8. Epicotyl length, root collar diameter, root area index and root dry weight of conditioned DOUGLAS-FIR and JACK PINE seedlings on four sampling occasions during the first growth room drought period. Data presented for irrigation frequency averaged over KCl levels; vertical bars represent standard errors (n = 4).

length and root collar diameters did not vary significantly over time in contrast to root area index and root dry weight.

Differences between initial parameter values and the largest value recorded during the drought period were examined more critically by determining the least significant difference (after Little and Hills, 1978; see Table B-7). A summary of results are presented in Table 7.

Irrigation frequency (averaged over KCl levels) did not significantly affect epicotyl length over time for either species (Tables 7, B-8) as reported earlier. Root collar diameter of daily irrigated jack pine showed a significant increase from 2.92 mm at Day 1 to 3.67 mm at Day 5 after which, there was a significant decrease to 2.98 mm at Day 8 (Tables 7, B-9). Daily irrigated jack pine and weekly irrigated Douglas-fir exhibited similarly significant increases in root area index (Table 7). For jack pine, root area index increased from 31.41 cm² at Day 1 to 42.60 cm² at Day 5 then consistently decreased to 29.94 cm² by Day 10 (Table B-10). Root area index of weekly irrigated Douglas-fir increased significantly from 21.42 cm² at Day 1 to 34.60 cm² at Day 10.

At all irrigation and species levels, root dry weight means exhibited a significant increase as the drought period progressed from Day 1 (Table 7). Although there was some inconsistency amongst treatment levels as to the sample days that were significantly different from Day 1, maximum relative increases in root dry weight ranged from 80% to 145% (Table B-11). Only weekly irrigated Douglas-fir and jack pine seedlings exhibited an increase in root dry weight during the latter stages of the drought period when soil water contents were low (2.6 to 5.6% on a dry weight basis).

4.1.3.3. Seedling water relations. Total water potential and its components, turgor pressure and osmotic potential, are presented graphically by conditioning treatment for Douglas-fir and jack pine in Figures 9 and 10, respectively, for each sampling date throughout the drought stress period. Each component will be presented separately by species.

4.1.3.3.1 Total water potential: ψ_T . With few exceptions, total water potential of Douglas-fir and jack pine

TABLE 7. Summary of significance¹ determined by t-test between pre-drought value of morphological parameter and maximum value recorded for seedlings during exposure to drought.

Irrigation	Species	Parameter			
		Epicotyl length	Root collar diameter	Root area index	Root dry weight
Daily	Df	NS	NS	NS	*
	JP	NS	*	*	*
Weekly	Df	NS	NS	*	*
	Jp	NS	NS	NS	*

¹ Significance level
 *P < 0.05
 NS Not significant

declined steadily as the duration of drought exposure increased (Figs. 9 and 10, respectively; Table B-14). Analysis of variance by individual sample day revealed that both irrigation and KCl did not significantly affect water potentials except for KCl level at Sample Day 4 (Table B-12). Species differences were inconsistent throughout the drought period. However, when time as a factor was included in the analysis it was clear that the water potential of daily irrigated seedlings declined differently with respect to KCl level than weekly irrigated seedlings (significant irrigation X KCl interaction); differences were dependent upon species (significant irrigation X KCl level X species interaction). The exact nature of this interaction is difficult to discern, but an examination of means (Table B-14) suggests that in both Douglas-fir and jack pine the total water potential of daily irrigated seedlings fell more rapidly than weekly irrigated seedlings and that within each irrigation level the rate of decline was mediated by the level of KCl.

4.1.3.3.2 Osmotic potential: ψ_{π} . The progressions of osmotic potential throughout the drought period by treatment levels for Douglas-fir and jack pine are presented in Figures 9 and 10, respectively and Table B-15. Osmotic potentials generally paralleled the declines in total water potential, but only during the latter stages of the drought period. Initially, osmotic potentials were much lower than total water potentials, but as the drought period progressed the rate of decline depended upon treatment and species (Table B-12). Irrigation conditioning exhibited the most consistent effect throughout the drought period, whereas KCl level was only significant at Sample Day 4. With time incorporated in the analysis (Table B-13) all the main order effects of irrigation, KCl level, species and time were statistically significant. The effects of irrigation and differences between species depended upon time.

It is significant to note that initial osmotic potentials of weekly irrigated seedlings were lower than those of daily irrigated seedlings (Table B-15), but because of a more rapid

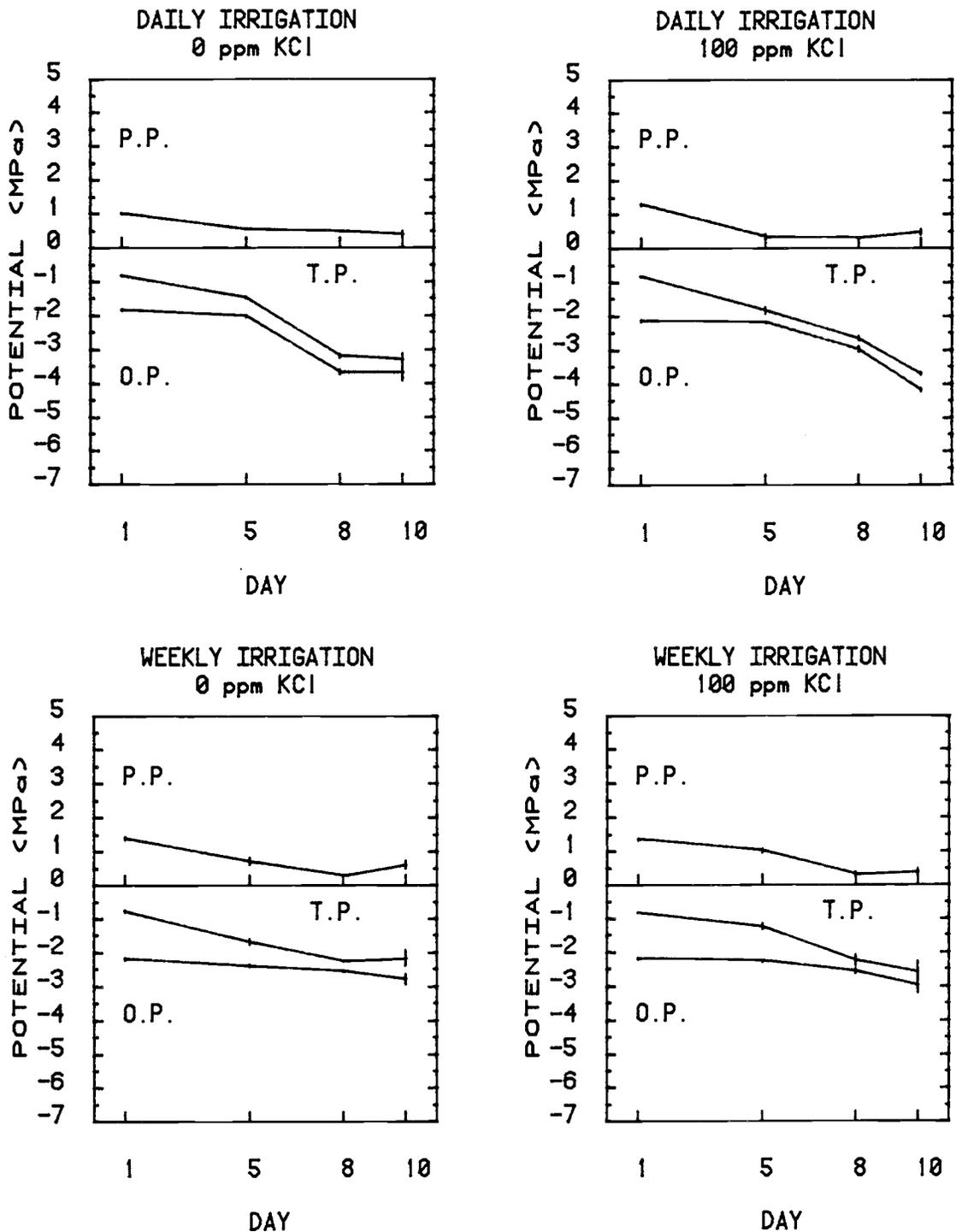


Figure 9. Progression of total water potential (T.P.), osmotic potential (O.P.), and pressure potential (P.P.) or turgor pressure of conditioned DOUGLAS-FIR seedlings during the first growth room drought period (10 days). Specific conditioning treatments are noted at top of each graph; vertical bars represent standard errors ($n = 3$).

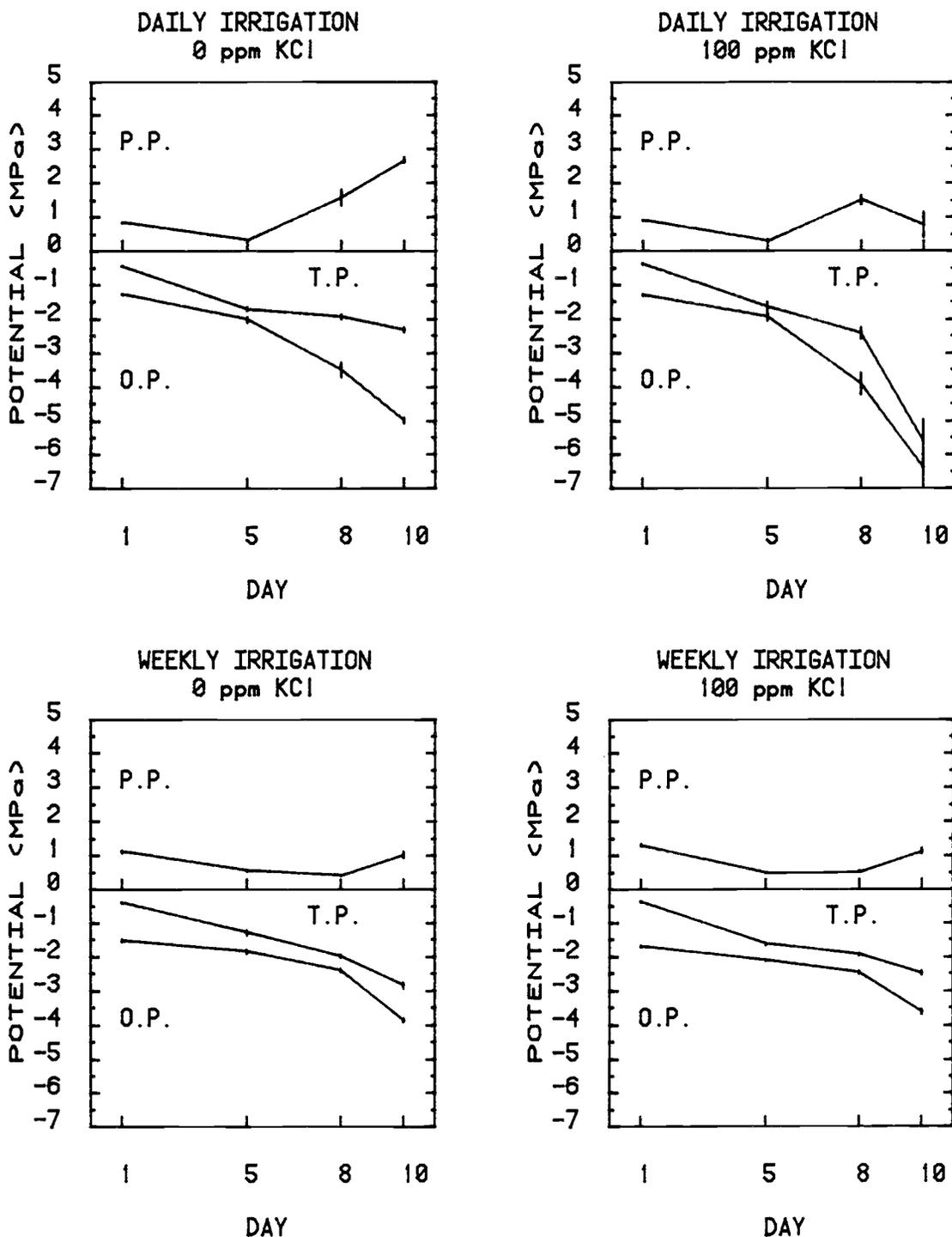


Figure 10. Progression of total water potential (T.P.), osmotic potential (O.P.), and pressure potential (P.P.) or turgor pressure of conditioned JACK PINE seedlings during the first growth room drought period (10 days). Specific conditioning treatments are noted at the top of each graph; vertical bars represent standard errors ($n = 3$).

decline of osmotic potentials in the daily irrigated seedlings, terminal values were much lower by the last sampling time.

4.1.3.3.3 Turgor pressure: ψ_p . During the course of the drought period turgor pressures of Douglas-fir declined gradually, then levelled off, and in one instance, increased (Fig. 9, Table B-16). Turgor pressure in jack pine varied widely (Fig. 10, Table B-16). For example, daily irrigated jack pine at both KCl levels initially declined, then increased substantially. Weekly irrigated jack pine, in contrast, declined steadily to the third sample time then increased significantly. Analysis of variance by individual sample day revealed that turgor pressure in daily irrigated plants differed significantly compared to irrigated plants for the first three sample days (Days 1 through 8), but demonstrated similar responses at the end of the drought period (Table B-12). Species differences were significant throughout the drought period (Tables B-12, B-16), but was dependent upon level of irrigation (significant irrigation X species interaction) With time included in the analysis turgor pressure within species varied similarly regardless of irrigation or level of applied KCl. Species differences were dependent upon time (significant species X time interaction) (Table B-13).

4.1.3.3.4 Relative water content: RWC. Relative water content, like the components of total water potential, is important in the evaluation of plant water relations because it provides an estimate of the water content of needles relative to a turgid condition at various stages of decline in water potential. Figure 11 shows that for each species the rates of decline in relative water content are similar for each KCl level within irrigation levels. Analysis of variance by individual sample date indicated significant main order effects for irrigation and species throughout the drought stress period, with one exception (Table B-12). By the end of the drought period, KCl level was also significant; higher RWC values were associated with 0 ppm KCl. In the fuller analysis (Table B-13) irrigation, species and time were significant, but the differences in relative water content due to

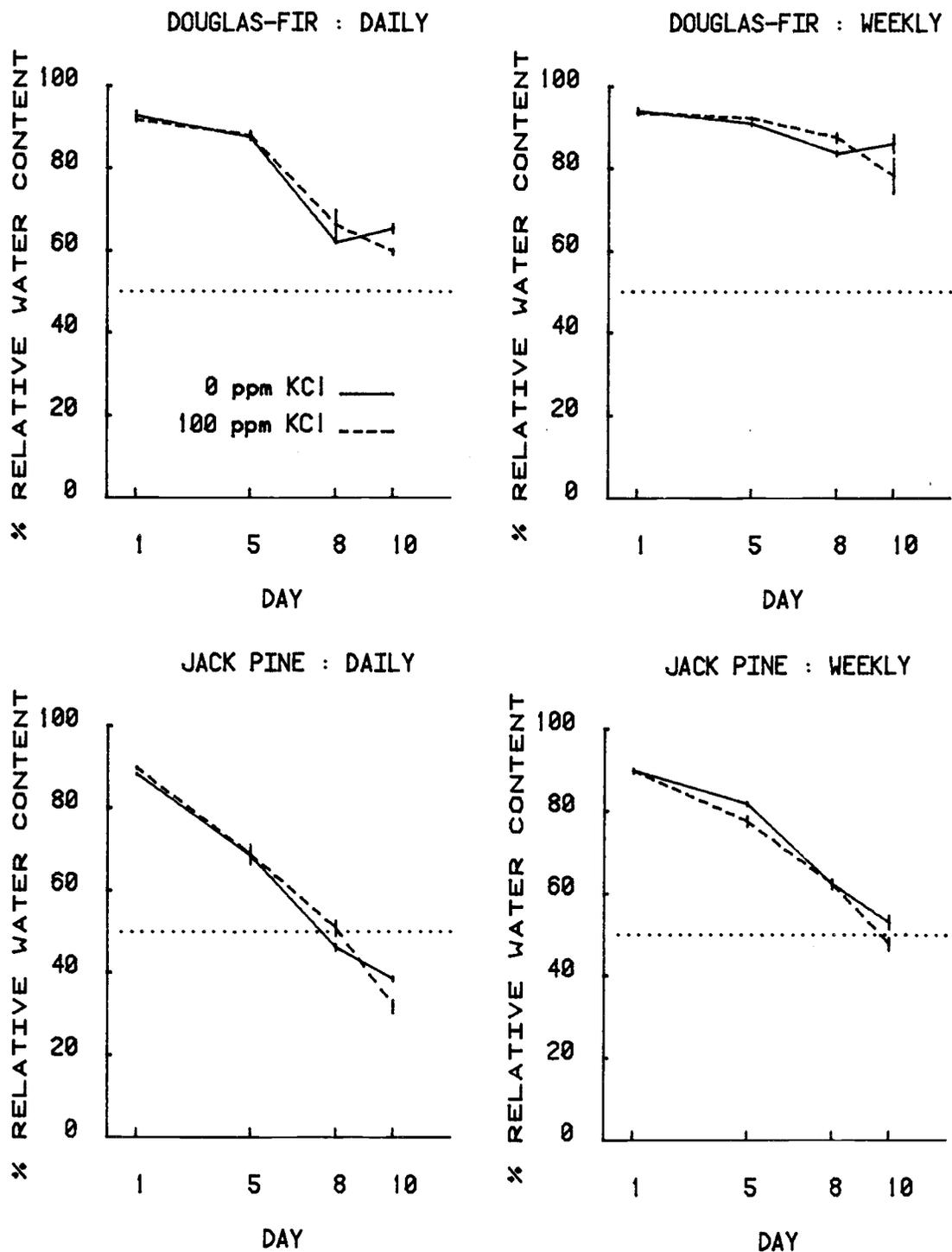


Figure 11. Progression of relative water content of conditioned DOUGLAS-FIR (upper graphs) and JACK PINE (lower graphs) seedlings during the first growth room drought period (10 days). Each graph represents a specific irrigation frequency in combination with levels of applied KCl; vertical bars represent standard errors (n = 3).

irrigation and species depended upon time (significant irrigation X time and species X time interactions).

Further examination of Figure 11 and Table B-17 indicate that the rates of decline in relative water content between species were statistically significant, e.g. as exemplified by overall mean relative water contents of 83.3% vs 67.2% for Douglas-fir and jack pine, respectively. Within species, relative water contents of daily irrigated seedlings were less than for seedlings watered weekly e.g. for Douglas-fir: daily vs weekly, 76.7% vs 88.3% and jack pine: daily vs weekly, 60.3% vs 70.5%.

4.1.3.3.5 Relationships amongst plant water relation parameters. Initial attempts in examining the relationships amongst plant water relationship parameters by treatment level and species did not provide meaningful information because the amount of data by treatment level was too small. Treatments were therefore combined by species. Freehand curves were fitted through the data because the nature of some of the relationships did not permit computer determination of equations by common regression methods.

4.1.3.3.5.1 Relative water content/Plant water potential. The relationships between relative water content and plant water potential for Douglas-fir and jack pine exhibited similar form; both are curvilinear downward (Fig. 12). At any given plant water potential Douglas-fir seedlings throughout the drought period maintained higher relative water contents than jack pine e.g. at -1.0 MPa the relative water content of Douglas-fir and jack pine were 93% and 84%, respectively.

4.1.3.3.5.2 Relative water content/Osmotic potential. For Douglas-fir and jack pine the relationships of relative water content to osmotic potential are similar in that they are both curvilinear downward. At any osmotic potential Douglas-fir maintains a higher relative water content than jack pine (Fig. 13). At near full turgor, a condition that existed prior to placement of the seedlings in the growth room, Douglas-fir exhibited lower osmotic potentials than jack pine (e.g. ca -2.2 MPa vs ca -1.5 MPa), despite similarly high relative water contents greater than 90%. A

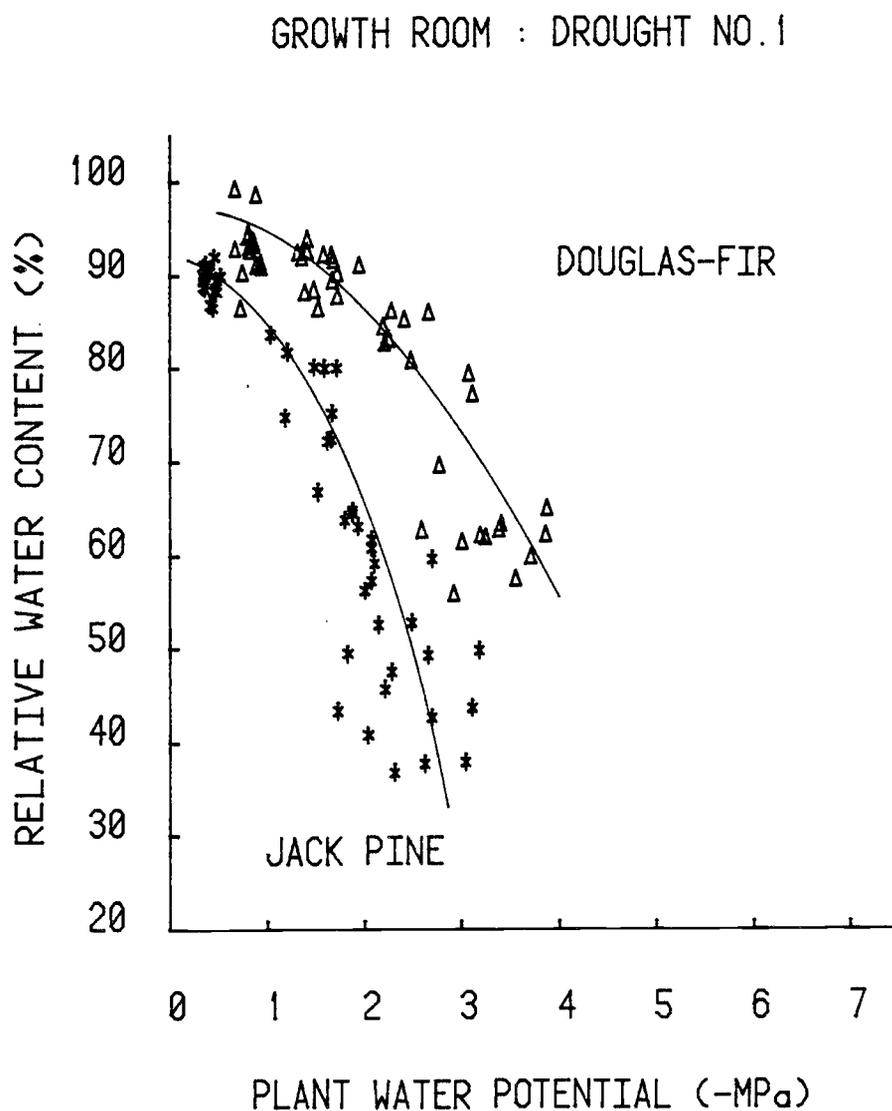


Figure 12. Relationship between relative water content and plant water potential of conditioned DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data combined by species from first growth room drought period and are fitted with free hand curves.

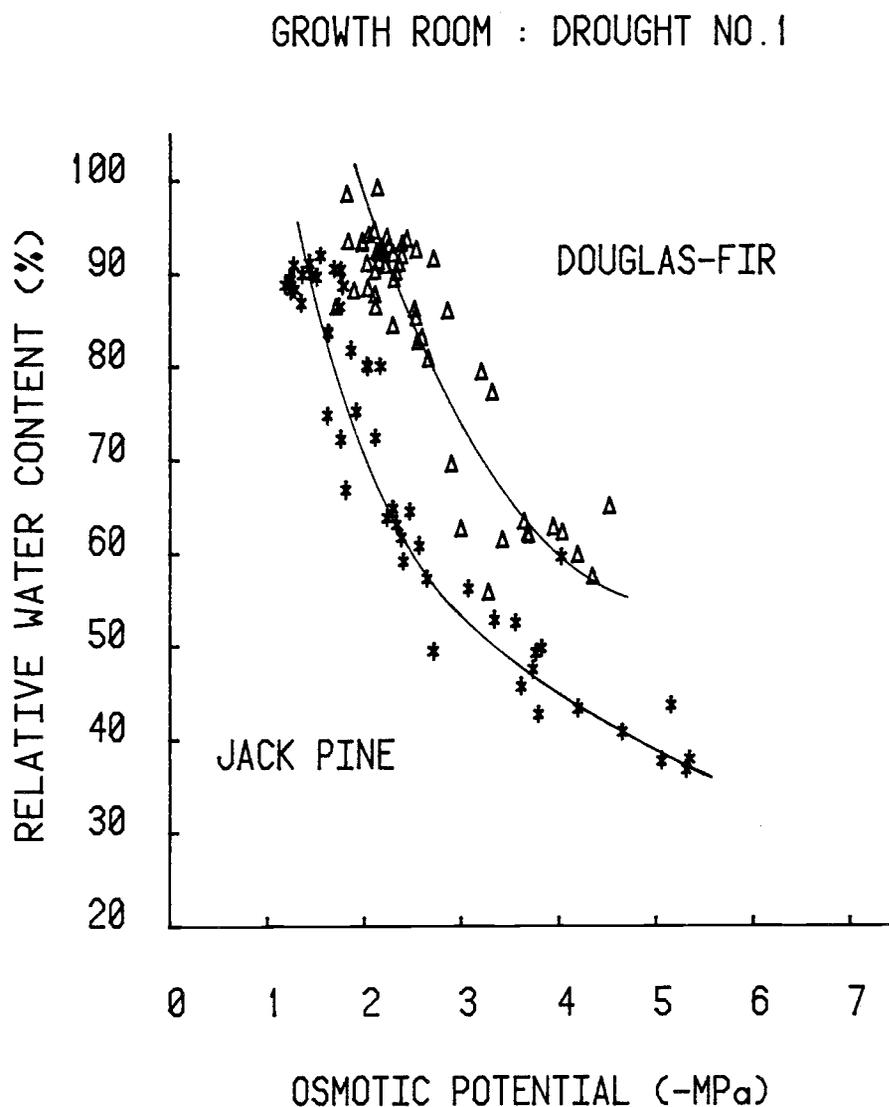


Figure 13. Relationship of relative water content and osmotic potential of conditioned DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined by species from first growth room drought period and are fitted with free hand curves.

drop in relative water content from 90% to 70% is represented by a concomitant decrease in osmotic potential of ca 0.7 MPa and ca 0.9 MPa in jack pine and Douglas fir, respectively. Biologically, this rate of decrease in osmotic potential may, indeed, be important particularly with respect to species' differences in turgor maintenance.

4.1.3.3.5.3 Osmotic potential/Plant water potential.

The relationships of osmotic potential and total water potential for Douglas-fir and jack pine are presented in Figure 14. Although the relationships are not distinctly separated several aspects are worthy of note. First, at high plant water potentials i.e. near 0 MPa, the osmotic potentials of Douglas-fir are lower than for jack pine, hence turgor pressure as determined from the vertical distance above the 1:1 line (i.e. where osmotic and plant water potentials are equal) is greater. Second, at a plant water potential of ca -1.8 MPa, osmotic potentials of both species are similar and so are turgor pressures. Finally, once plant water potentials of both species decrease to ca -1.8 MPa the decline in osmotic potential of jack pine exceeds that of Douglas-fir, resulting in an apparent increase in turgor pressure.

4.1.3.4 Pressure-volume parameters. As mentioned under section 3.2.6 of Methods and Materials, equipment failure prevented obtaining a complete data set for the first set of pressure-volume curves. Because analysis of variance indicated no significant treatment effect, data were summed and averaged over treatments and are presented by assessment date for both species (Table 8).

4.1.3.4.1 Osmotic potential at full turgor, OPFT (-MPa). The OPFT of Douglas-fir decreased consistently from -1.78 MPa to -2.03 MPa as the drought stress period progressed. During the same period of time the OPFT of jack pine exhibited an anomalous change. For example, the OPFT decreased from -1.09 MPa to -1.12 MPa by Day 6 then increased to -0.70 MPa. On a species basis, however, a significant difference was detected ($P = 0.05$). The osmotic potentials at full turgor of Douglas-fir were consistently lower than those of jack pine throughout the drought period, a fact which

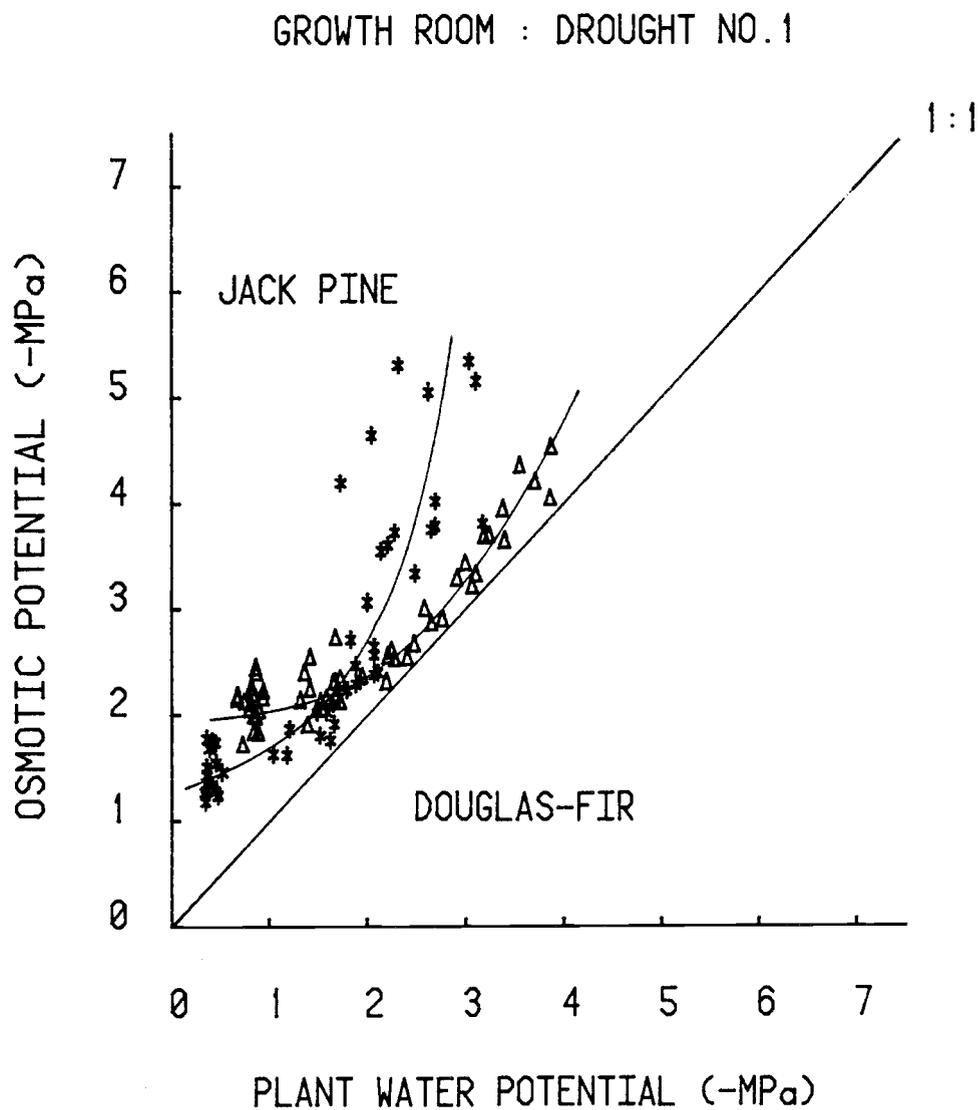


Figure 14. Relationship between osmotic potential and plant water potential of conditioned DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined by species from first growth room drought period and are fitted with free hand curves. The 1:1 line represents a potential state of zero turgor pressure.

TABLE 8. Summary of mean water relations parameters determined by the pressure volume technique on three sampling dates for DOUGLAS-FIR and JACK PINE during the first drought period. Species differences only were evaluated by weighted t-tests and where significance existed means are followed by different letters (P < .05) See text for description of symbols.

Sp.	PV run	Water relations parameter							
		OPFT	OPZT	RWC @ TLP	RSWC @ TLP	Ra	ME@ .995 RWC	Dry wt. Turgid wt.	WSFT Dry wt.
		(-MPa)	(-MPa)	(%)	(%)		(MPa)		
Df	1	1.78	2.21	83.4	80.4	0.15	14.70	0.23	3.01
	2	1.90	2.37	88.6	80.4	0.40	11.37	0.25	1.74
	3	<u>2.03</u>	<u>2.65</u>	<u>83.8</u>	<u>76.7</u>	<u>0.28</u>	<u>4.39</u>	<u>0.26</u>	<u>2.02</u>
	\bar{X}	1.92a	2.44a	84.6a	78.7a	0.26a	9.22a	0.25a	2.30a
Jp	1	1.09	1.67	84.9	65.3	0.56	1.96	0.23	1.50
	2	1.12	1.74	79.6	64.3	0.43	3.14	0.23	1.94
	3	<u>0.70</u>	<u>1.55</u>	<u>73.7</u>	<u>44.8</u>	<u>0.51</u>	<u>1.04</u>	<u>0.23</u>	<u>1.67</u>
	\bar{X}	0.84b	1.61b	76.0b	51.4b	0.49b	1.65b	0.23	1.73b

is in accord with previous data.

4.1.3.4.2 Osmotic potential at zero turgor, OPZT (-MPa). It is not an unexpected occurrence that the osmotic potential decrease from the value attained at full turgor as the point of zero turgor pressure is approached. In both species for each of the three P-V runs, the OPZT decreased by about the same percentage, e.g. for Douglas fir: 24%, 24%, and 30% and for jack pine, percent decreases in osmotic potential were 53%, 55%, and 121%. On a species basis, Douglas-fir reached a significantly lower OPZT (-2.44 MPa) than jack pine (-1.61 MPa).

4.1.3.4.3 Relative water content at turgor loss point, RWC @ TLP. Douglas-fir exhibited a rather variable pattern of RWC @ TLP throughout the drought stress period (Table 8). From an initial value of 83.4% the RWC @ TLP increased to 88.6% by the sixth sample day, then finally decreased to a similar value recorded at the start of the drought period. The mean relative water content at turgor loss point was 84.6% for Douglas-fir. In contrast, the RWC @ TLP for jack pine throughout the drought period decreased consistently from 84.9% to 73.7%. The mean for jack pine was statistically lower than that for Douglas-fir (Table 8).

If the mean values RWC @ TLP for Douglas-fir and jack pine are used to determine the osmotic potential in Figure 13 the results would concur with OPZT for Douglas-fir, but would tend to underestimate (i.e. estimate more negative) the OPZT for jack pine by approximately 13%.

4.1.3.4.4 Relative symplasmic water content at turgor loss point, RSWC @ TLP. At the point of zero turgor symplasmic water loss in Douglas-fir and jack pine was 21.3% and 49.6%, respectively. These differences were significant at $P = 0.05$ (Table 8).

4.1.3.4.5 Relative apoplasmic water content, Ra. The relative apoplasmic water content, i.e. the proportion of water outside the plasmalemma and referred to as non-osmotic water, varied inconsistently in both Douglas-fir and jack pine as the drought stress period progressed (Table 8). In Douglas-fir, Ra increased by

the sixth day (P-V Run 2) to 0.40 from an initial value of 0.15, then decreased to 0.28 at the end of the drought stress. The response pattern in jack pine was the reverse. From an initial high value of 0.56, Ra decreased to 0.43 then increased to 0.51 at the end of the drought period. On a species basis the relative apoplasmic water contents of Douglas-fir and jack pine were 0.26 and 0.49, respectively, a significant difference.

4.1.3.4.6 Modulus of elasticity at near full turgor, ME @ .995 RWC. The modulus of elasticity of Douglas-fir decreased from a high value of 14.70 MPa to a low value of 4.39 MPa as the drought stress period progressed (Table 8). This suggests that the elasticity of cell walls in Douglas-fir become more elastic as water stress in seedlings increased. In jack pine, values for the modulus of elasticity increased initially to 3.14 MPa from 1.96 MPa then declined to 1.01 MPa. This trend suggests that the elastic properties of cell walls in jack pine decreased, then increased with water stress in seedlings. Comparatively, jack pine cell walls were more elastic than Douglas-fir cell walls by more than five fold.

4.1.3.4.7 Ratio of sample dry weight to fresh weight. The ratio of dry weight of tissue sample to its fresh weight in Douglas-fir tended toward slightly higher values (.226 to .261) as the drought stress period progressed (Table 8). In jack pine the ratio did not change. There were no significant species differences.

4.1.3.4.8 Ratio of weight of symplasmic water at full turgor to dry weight of tissue sample. At the start of the drought stress period the symplasmic water/dry weight ratio of Douglas-fir was high (3.01) then decreased by the sixth sample day to 1.74 then increased to 2.02 (Table 8). In jack pine, the trend was the reverse. From an initial value of 1.50 the ratio increased to 1.94 then decreased to 1.67 at the end of the drought period. Species means (Douglas-fir: 2.30, jack pine: 1.73) were significantly different.

4.1.3.5 Root nutrition. As mentioned under section 3.2.7 foliage was not analysed for nutrient concentrations because the

majority of the foliage on each stem was utilized to determine osmotic potential and relative water content. Therefore, nutrient analyses were conducted on roots which were bulked by treatments within species to provide enough plant material for analyses. Bulking samples did not permit analysis of results by statistical methods, but examination of nutrient concentrations suggested trends and differences between species (Table 9).

4.1.3.5.1 Nitrogen N. Without exception, N concentrations were higher in jack pine roots than in Douglas-fir roots at each treatment combination and time of sampling and overall, N concentration of jack pine exceeded those of Douglas-fir by 22% (2.38 % vs 1.95%). There was no apparent relationship between plant water stress and N concentration at any treatment combination for either Douglas-fir or jack pine. Also, none of the conditioning treatments had, either singly or in combination, any effect on N concentration.

4.1.3.5.2 Phosphorus, P. With only two exceptions, the P concentrations in jack pine exceeded those in Douglas-fir; species means were 0.54% vs 0.44% respectively. P concentrations in both species increased from the first sample date to the second sample date, but then depending upon species and conditioning treatment, increased or decreased as the drought period progressed. Based upon irrigation means by species, higher P concentrations were associated with daily irrigated seedlings. There was no apparent relationship between KCl level and P concentration for either species.

4.1.3.5.3 Potassium, K. Potassium concentrations in jack pine exceeded those of Douglas-fir at all treatment levels, except one. In both species, at each treatment level, K concentrations increased dramatically from the first sampling time to the second sampling, then decreased inconsistently up to the last sampling day to values about 50% higher than those recorded on the first sample day. For both Douglas-fir and jack pine, highest K concentrations were associated with seedlings that were conditioned with applications of 100 ppm KCl and daily watering.

TABLE 9. Nutrient concentrations of root systems of conditioning DOUGLAS-FIR and JACK PINE seedlings sampled on four occasions during the first drought period in a growth chamber.

TREATMENT		NUTRIENT / DAY								
Irrigation	KCl	Species	% N				% P			
			1	5	8	10	1	5	8	10
Daily	0	Df	2.04	2.04	1.85	1.89	0.44	0.72	0.44	0.54
		Jp	2.50	2.07	2.55	2.14	0.50	0.71	0.57	0.57
	100	Df	2.12	1.77	1.56	1.98	0.49	0.50	0.41	0.49
		Jp	2.37	2.07	2.00	2.09	0.48	0.64	0.54	0.55
Weekly	0	Df	1.76	2.27	1.82	2.05	0.28	0.47	0.31	0.42
		Jp	2.34	2.78	2.38	2.55	0.38	0.73	0.48	0.57
	100	Df	2.05	2.06	1.90	1.90	0.31	0.49	0.34	0.36
		Jp	2.36	2.65	2.33	2.90	0.37	0.56	0.53	0.53

TREATMENT		% K								
Irrigation	KCl	Species	% K				% Ca			
			1	5	8	10	1	5	8	10
Daily	0	Df	0.72	1.54	1.06	1.08	0.28	0.27	0.30	0.28
		Jp	0.84	1.55	1.11	1.55	0.32	0.30	0.27	0.25
	100	Df	0.88	1.29	1.09	1.14	0.27	0.28	0.28	0.22
		Jp	0.94	1.87	1.41	1.54	0.31	0.34	0.25	0.31
Weekly	0	Df	0.51	1.01	1.03	0.98	0.29	0.26	0.17	0.22
		Jp	0.56	1.65	1.06	1.44	0.35	0.31	0.27	0.28
	100	Df	0.59	1.41	1.00	0.96	0.30	0.25	0.21	0.25
		Jp	0.53	1.48	1.29	1.31	0.33	0.33	0.27	0.28

(continued ...)

TABLE 9. (continued)

TREATMENT			% Mg				Cl ⁻ (ppm X1000)			
Irrigation	KCl	Species	1	5	8	10	1	5	8	10
Daily	0	Df	0.20	0.26	0.25	0.22	0.94	2.14	2.14	2.21
		Jp	0.24	0.24	0.24	0.31	1.71	4.04	2.37	3.53
	100	Df	0.20	0.17	0.22	0.17	2.28	5.29	3.50	3.88
		Jp	0.25	0.23	0.24	0.24	3.58	6.57	4.67	4.45
Weekly	0	Df	0.19	0.15	0.16	0.18	0.80	2.18	1.76	1.87
		Jp	0.20	0.24	0.22	0.20	1.05	3.35	2.72	3.05
	100	Df	0.20	0.18	0.18	0.17	2.40	4.96	3.85	3.83
		Jp	0.20	0.21	0.19	0.23	2.40	6.00	6.13	4.14

4.1.3.5.4 Calcium, Ca. Little variation in Ca concentration occurred in species throughout the drought period, but when treatments were averaged slightly higher concentrations were present in jack pine. No apparent differences in Ca concentration occurred as a result of KCl levels.

4.1.3.5.5 Magnesium, Mg. Magnesium concentrations were higher in jack pine than in Douglas-fir and within each species, higher concentrations were associated with seedlings conditioned by daily irrigation and applications of 100 ppm KCl. No trends in Mg concentration with time of sampling or plant water stress are apparent from the data.

4.1.3.5.6 Chloride, Cl⁻. At all treatment levels across sampling times, Cl⁻ concentrations were substantially greater in roots of both species conditioned with 100 ppm KCl than those that were conditioned by 0 ppm KCl. Differences ranged from 1260 ppm to 3000 ppm. As the drought stress period progressed and as plant water potentials fell, Cl⁻ concentrations in roots of seedlings at all treatment combinations rose dramatically e.g. Cl⁻ concentrations at the first sample day vs those at the second sample day. These increases were most pronounced in seedlings that had not previously received 100 ppm KCl during the conditioning period. With further development of plant water stress Cl⁻ concentrations tended to decline and stabilize at levels above those recorded at the start of the drought period.

4.1.4 Seedling recovery from drought stress. Distinct species differences in mortality were evident by the second day of recovery (Table 10). Mortality in jack pine exceeded mortality in Douglas-fir on an overall basis. Regardless of species, mortality was associated exclusively with daily irrigated seedlings and was higher in those seedlings conditioned at 0 ppm KCl. By the fourth day of recovery, mortality exhibited little increase.

Two hypotheses were tested by Chi-square analysis at $P = 0.05$; they were: that mortality was not dependent upon irrigation conditioning and that mortality was not dependent upon the level of applied KCl. For both Douglas-fir and jack pine the analyses

TABLE 10. Physiological condition¹ of DOUGLAS-FIR and JACK PINE seedlings 2 and 4 days after removal from drought environment.

Treatment			Assessment Day 2			Assessment Day 4		
Irrigation	KCl	Sp.	Dead	Variously wilted or damaged	Turgid	Dead	Variously wilted or damaged	Turgid
Daily	0	Df	13	26	61	15	23	62
		Jp	23	11	66	24	6	70
	100	Df	10	26	74	10	13	77
		Jp	16	13	71	20	6	74
Weekly	0	Df	0	2	98	0	0	100
		Jp	0	1	99	0	0	100
	100	Df	0	0	100	0	0	100
		Jp	0	1	99	0	0	100

¹ Seedling condition after drought stress:

1. Dead: no recovery, foliage discolored, stems brittle.
2. Variously wilted/damaged: some portion of foliage in limp condition and therefore, considered damaged.
3. Turgid: seedlings which regained turgidity, foliage upright, no shrinkage of stem, good foliage color.

provided strong evidence that mortality was dependent upon irrigation conditioning, but not on the level of applied KCl.

Seedlings that were classified as variously wilted or damaged at Day 4 remained in that condition for the remainder of the test. Color of damaged foliage continued to change to a pale yellow-green, then finally to a light brown.

An evaluation of plant water potential on the seventh day indicated that Douglas-fir and jack pine seedlings had attained values of -0.65 MPa and -0.43 MPa, respectively. This difference was significant at $P < 0.01$. Because differences in plant water potential between KCl levels could not be detected, irrigation means were determined over KCl levels for each species. Plant water potentials for Douglas-fir by daily and weekly irrigation were -0.80 MPa and -0.51 MPa, respectively, and those for jack pine were -0.47 MPa and -0.39 MPa, respectively.

4.1.5 Seedling responses to drought stress, SECOND DROUGHT.

4.1.5.1 Soil water loss. Depletion of soil water was determined as a percent of soil dry weight for each species and treatment combination (Figure 15). The rate of water loss at all treatment levels was uniformly high for both Douglas-fir and jack pine up to Day 5 for daily irrigated seedlings at 0 ppm KCl (D0) and up to Day 7 for the remaining treatment levels. Beyond these dates the rates of water loss remained uniformly low (i.e. 1 to 2%). Although no marked species differences were evident, there is some indication that the rate of water loss was greater for jack pine during the early period of rapid water depletion (approximately Day 5 to 7), after which, no species differences occurred.

4.1.5.2 Seedling morphology. The progressions of epicotyl length, root collar diameter, root area index and root dry weight of seedlings during their second exposure to drought stress are presented in Figure 16. Since analysis of variance revealed infrequent occurrence of significance due to KCl level data are presented by irrigation level averaged over KCl levels.

4.1.5.2.1 Epicotyl length. Epicotyl lengths of Douglas-fir and jack pine by irrigation level exhibited little

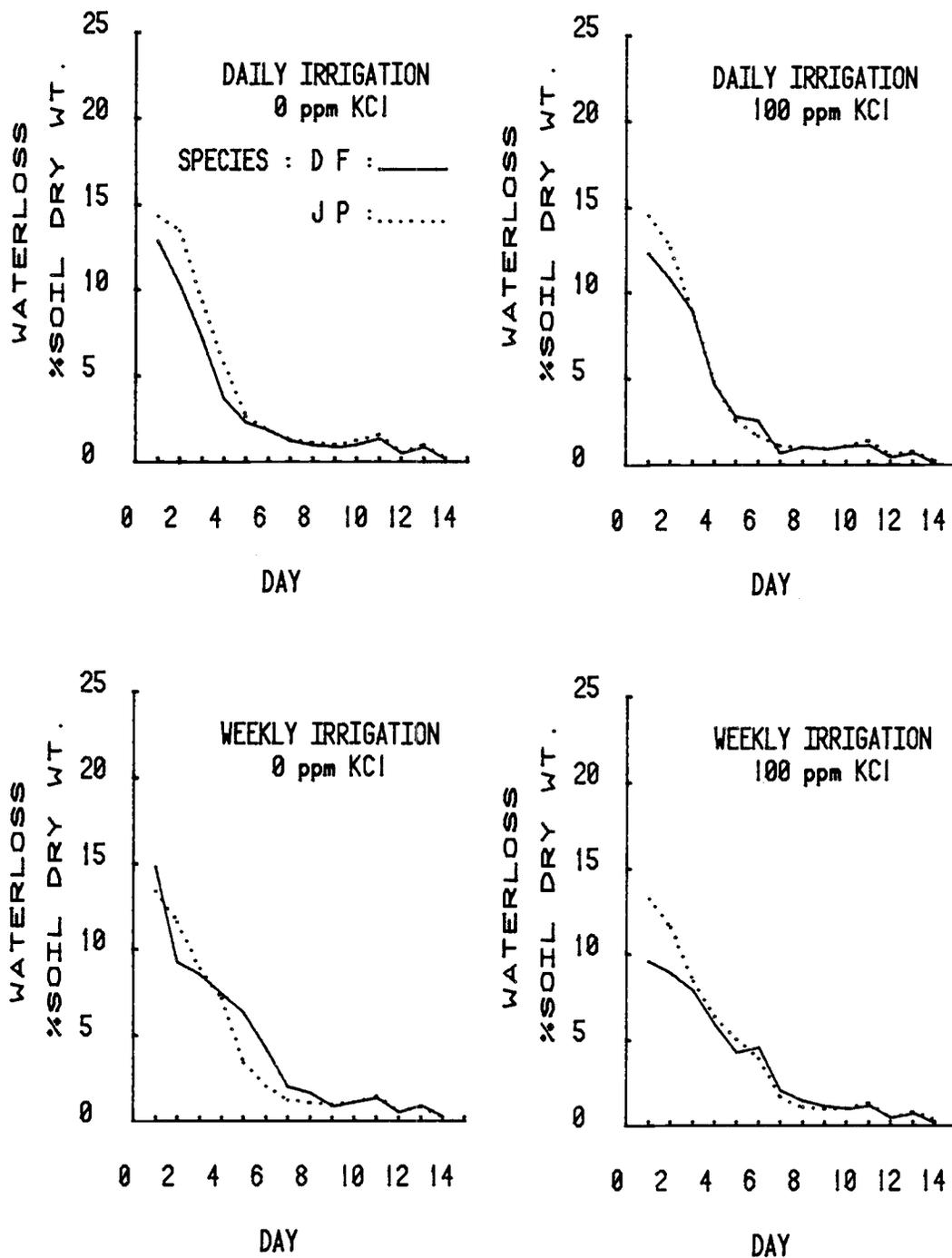


Figure 15. Waterloss by evapotranspiration from rooting medium throughout the second growth room drought period. Data are presented by conditioning treatment for DOUGLAS-FIR and JACK PINE.

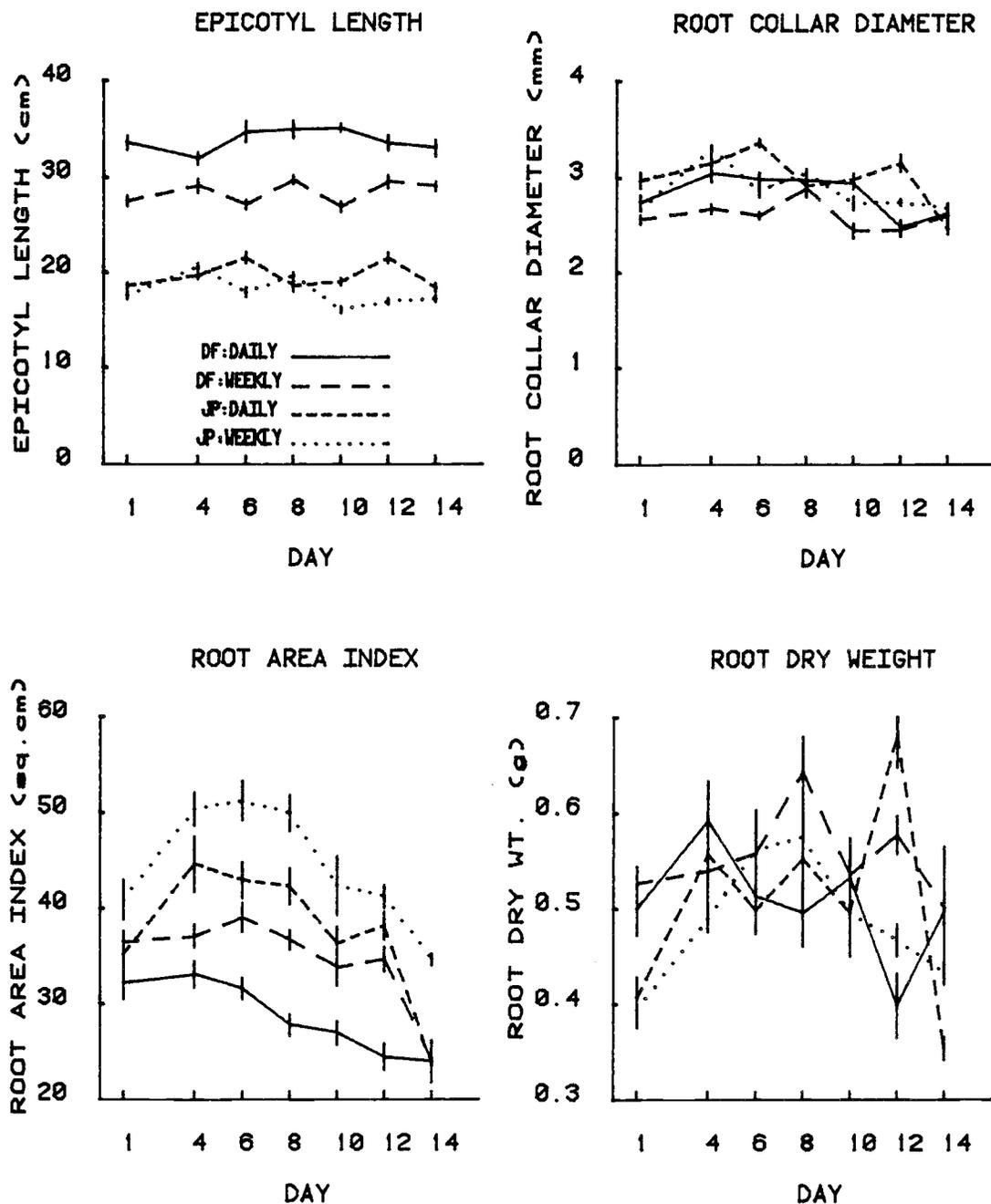


Figure 16. Epicotyl length, root collar diameter, root area index, and root dry weight of conditioned and previously droughted DOUGLAS-FIR and JACK PINE seedlings on seven sampling occasions during the second drought period (14 days). Data presented for irrigation frequency averaged over KCl levels; vertical bars represent standard errors (n = 4).

variation throughout the drought stress period (Fig. 16). Analysis of variance, by sample time, indicated that irrigation level was significant up to Sample Day 5, but not after (Table B-18). A significant difference between species was maintained throughout the drought period (B-18). Weighted t-tests conducted to determine the presence of significant differences between the initial value of epicotyl length and the maximum value recorded during the drought period failed to detect any real differences (Tables 11 and B-20). Therefore, it was concluded that epicotyl length of neither species increased (B-19) as a result of conditioning treatment.

4.1.5.2.2 Root collar diameter. For root collar diameter (Fig. 16) analysis of variance by sample date indicated species and treatment differences were largely insignificant (Table B-18). However, when time was incorporated into the analysis species differences were significant as well as time. Examination of sample time means revealed that for weekly watered jack pine there was a significant increase in root collar diameter from the first sample time to the second sample time followed by a significant decrease (Table B-21). While these differences are significant they do not appear to be part of a clear pattern of growth and therefore, may be a result of random seedling variation.

4.1.5.2.3 Root area index. Root area indices of Douglas-fir and jack pine, by irrigation level, are presented in Figure 16. Consistently, root area indices increased from the initial value at the start of the drought period, then stabilized for approximately four days before decreasing to the end of the experiment. When compared with data presented in Figure 6 several points of difference emerge, for example, in the first drought period root area indices of daily irrigated jack pine exceeded those of weekly irrigated seedlings, but in the second drought period, the reverse was true. In Douglas-fir, root area indices of daily irrigated seedlings frequently exceeded those of weekly irrigated seedlings, but during the second drought period the reverse response occurred.

Analysis of variance by sample day indicated that

TABLE 11. Summary of significance¹ determined by t-tests between pre-drought value of morphological parameter and maximum value recorded for seedlings during drought period.

Irrigation	Species	Parameter			
		Epicotyl length	Root collar diameter	Root area index	Root dry weight
Daily	Df	NS	NS	NS	NS
	JP	NS	NS	NS	*
Weekly	Df	NS	NS	NS	NS
	Jp	NS	*	NS	*

¹ Significance level

* $P < 0.05$

NS Not significant

treatment significance was associated primarily with species, but in one instance (Sample Day 4) it was associated with KCl level (Table B-18). When time was included in the analysis of variance only species and time were significant factors affecting root area index (Table B-19). The question as to whether there were significant increases in root area index from the initial experimental value was examined by t-test. Results of this analysis indicated that real growth differences did not occur in Douglas-fir or in jack pine (Table 11). However, examination of sample time means for weekly irrigated jack pine (Table B-22) reveals that the probability of a real growth difference (between Day 1 [40.86 cm²] and Day 6 [51.21 cm²]) is $P = 0.054$.

4.1.5.2.4 Root dry weight. Root dry weights of Douglas-fir and jack pine at both irrigation levels were highly variable during the drought stress period (Fig. 16). This variability prevented detection of significant differences by analysis of variance (Tables B-18 and B-19).

4.1.5.3 Seedling water relations. Water relation parameters were evaluated in the same manner as previously described under 3.2.6.3. Each parameter was submitted to analysis of variance by sample time (Table B-24) and with time incorporated into the analysis at the sub-sub-subplot level (Table B-25). The progression of total water potential and its components, osmotic potential and turgor pressure, are presented by species and treatment level in relation to sample time in Figures 17 and 18 for Douglas-fir and jack pine, respectively. Relative water content is presented in Figure 19. Treatment means on which the above figures are based are summarized in Tables B-26, B-27, B-28, and B-29.

4.1.5.3.1 Total water potential: ψ_T . In general, the decline in total water potential of Douglas-fir, at all treatment levels, was initially slow up to Day 6. Beyond this point total water potential continued to decline, but at variable rates depending upon conditioning treatment (Fig. 17). During the latter stages of the drought stress period further declines in water potential were intermittent.

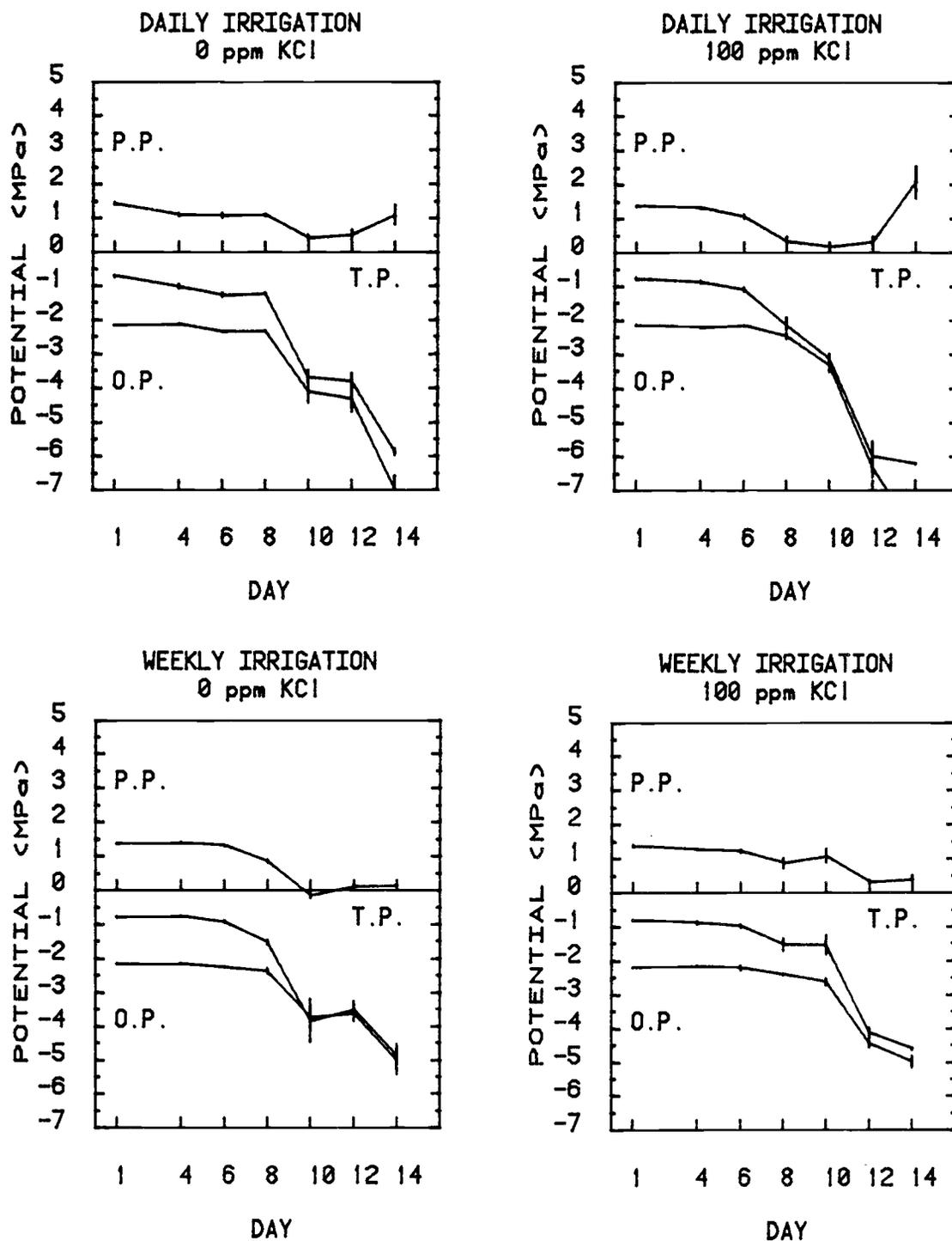


Figure 17. Progression of total water potential (T.P.), osmotic potential (O.P.), and pressure potential (P.P.) or turgor pressure of conditioned DOUGLAS-FIR seedlings during the second growth room drought period (14 days). Specific conditioning treatments are noted at the top of each graph; vertical bars represent standard errors ($n = 3$).

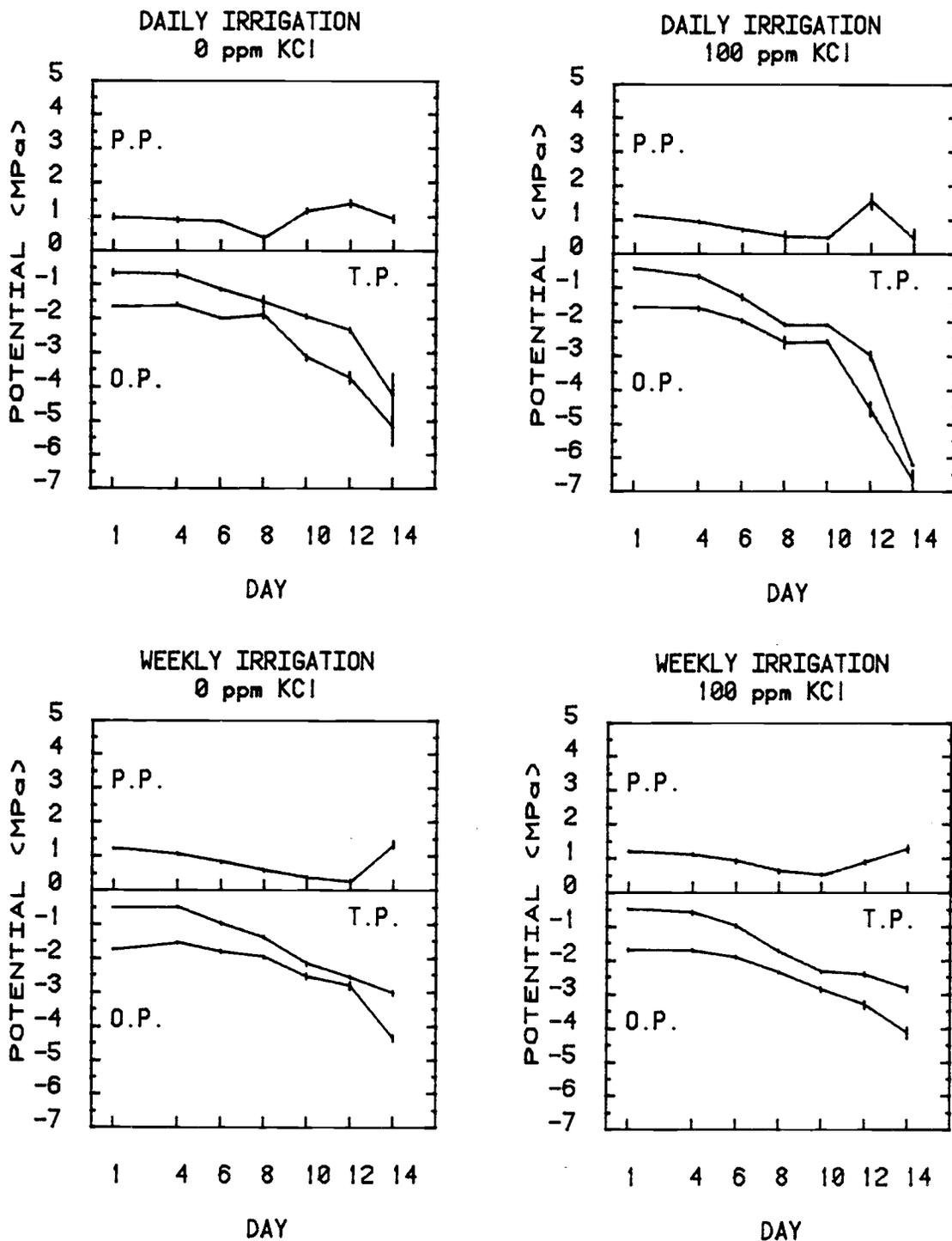


Figure 18. Progression of total water potential (T.P.), osmotic potential (O.P.), and pressure potential (P.P.) or turgor pressure of conditioned JACK PINE seedlings during the second growth room drought period (14 days). Specific conditioning treatments are noted at the top of each graph; vertical bars represent standard errors ($n = 3$).

Rates of decline in water potential in Douglas-fir seedlings conditioned by daily watering were more rapid than for seedlings conditioned by weekly irrigation. This resulted in substantially lower total water potentials in daily irrigated seedlings at the time the drought stress was terminated e.g. daily vs weekly irrigation: -6.03 MPa vs -4.74 MPa, respectively (averaged over KCl levels) (Table B-26).

Rates of decline in total water potential in jack pine were noticeably less than the rate of decline previously noted for Douglas-fir (Fig. 18, Table B-26). From the start of the drought stress period up to Day 10 or 12, rates of decline were similar regardless of treatment. Beyond this point decline in water potentials of daily irrigated seedlings increased dramatically. In contrast, the continued decline in water potential of weekly irrigated seedlings was less rapid. Terminal values of water potential of daily vs weekly irrigated jack pine seedlings averaged over KCl levels are: -5.23 MPa and -2.93 MPa respectively.

Analysis of variance by sample day indicates that treatment effects were not consistent throughout the drought stress period (Table B-24). Significance was infrequently associated with irrigation and only once with KCl level. By the end of the drought period (Day 14) the effects of irrigation and differences between species were significant (Table B-24). With time included in the analysis the main order effects of irrigation, species and time were significant. However, the effects due to irrigation and species were dependent upon time (significant irrigation X time and species X time interactions) (Table B-25).

4.1.5.3.2 Osmotic potential: ψ_{π} . In Douglas-fir the progression of osmotic potential of seedlings at all treatment levels decreased only slightly despite the moderate declines in total water potential (Fig. 17). It wasn't until total water potential fell sharply that noticeable declines in osmotic potential occurred. At all treatment levels, osmotic and total water potentials exhibited no significant differences after approximately 10 days in the drought environment. In two instances (DF/D0,

DF/D100), the decline in total water potential decreased with respect to osmotic potential, thereby resulting in increased turgor pressures (see below).

Osmotic potentials of jack pine appeared to decline in all treatments and in some instances, the decline in osmotic potential exceeded declines in total water potential (Fig. 18). The effect of these differential declines was to increase turgor pressure.

Analysis of variance of osmotic potential revealed that the effects due to irrigation and KCl level were, in all practicality, nonexistent (Table B-24). Differences due to species were significant at all sampling dates except two. With time included in the analysis, the main order effects of irrigation, species, and time were significant, but the effects of irrigation and species were dependent upon time (Table B-25).

Terminal osmotic potentials attained by Douglas-fir seedlings conditioned by daily and weekly irrigation were -7.62 MPa and -5.00 MPa, respectively. For jack pine, they were -5.92 MPa and -4.25 MPa, respectively. It would appear, therefore, that daily irrigated seedlings attained much lower osmotic potentials than weekly irrigated seedlings. These declines must be, however, considered in the context of how total water potential and relative water content varied because the declines in osmotic potential may, in fact, be the result of extreme dehydration and concentration of cell sap.

4.1.5.3.3 Turgor pressure: ψ_p . Turgor pressure in Douglas-fir remained generally above 1.0 MPa for six to eight days (Days 6 and 8) then declined in concert with the declining difference between total water potential and osmotic potential (Fig. 17). At one point, the decline in total water potential exceeded the calculated value of osmotic potential, resulting in an apparent negative value for turgor pressure. Although the differential declines in total water potential and osmotic potential suggest that turgor pressures increased in daily irrigated Douglas-fir (Fig. 17) it cannot be discounted that the increase may be an artifact of the

method used to determine values of osmotic potential. For example, excessive dehydration of sample tissue would lead to very low osmotic potential relative to total water potential and in accordance with equation [2.1.4] positive turgor pressure would be indicated.

Except for daily irrigated jack pine at 0 ppm KCl (JP/D0), turgor pressures gradually and consistently declined. At unique points in the drought stress period seedlings in each treatment exhibited increases in turgor pressure by as much as 1.0 MPa (Fig. 18). A comparison of total water potential and osmotic potential (Fig. 18, Table B-27) shows that increases in turgor were the result of rapid declines in osmotic potential relative to total water potentials.

Analysis of variance reveals that conditioning treatments were essentially ineffective in affecting turgor pressure, but that differences were periodically associated with species (Table B-24). Turgor pressure changed significantly throughout the drought stress period (Table B-25).

4.1.5.3.4 Relative water content: RWC. Relative water contents of Douglas-fir and jack pine with respect to conditioning treatment throughout the drought stress period are presented in Figure 19. For Douglas-fir, the relative water contents, regardless of KCl level, remained relatively high (84% to 86%) up to Day 8, after which, there was a continuous decline to approximately 50% in daily irrigated stock and 65% in weekly irrigated stock. The relative water contents for daily and weekly irrigated jack pine fell almost continuously from the second sample day, reaching terminal values of approximately 41% and 45%, respectively (Table B-29).

Analysis of variance by sample day indicates that significant differences were associated with irrigation and species, and that these effects were significant throughout the drought stress period. There is some evidence that occasionally, the effect of KCl level on relative water contents was also significant (Table B-24). With time included in the analysis the main order effects of

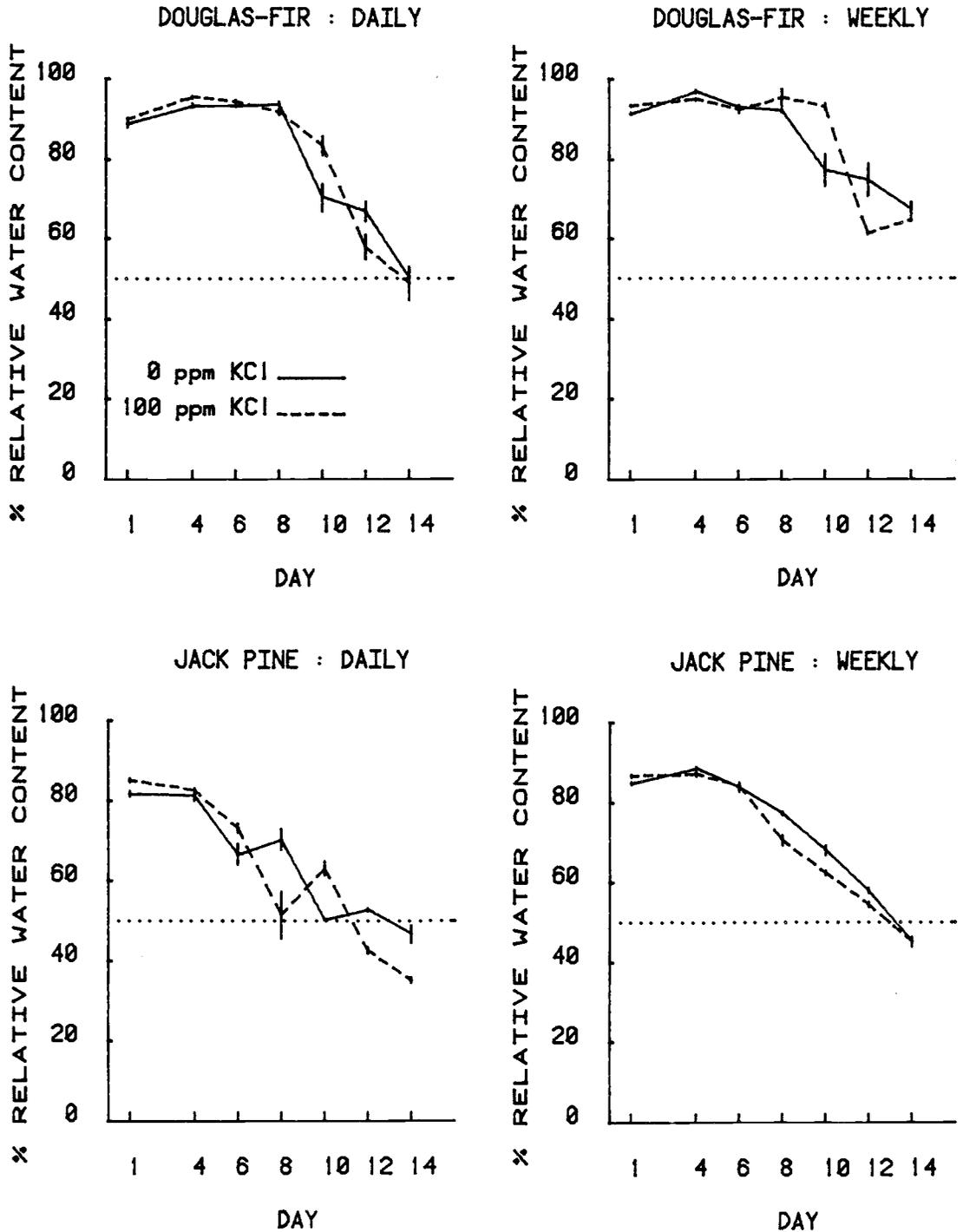


Figure 19. Progression of relative water content of conditioned DOUGLAS-FIR (upper graphs) and JACK PINE (lower graphs) seedlings during the second growth room drought period (14 days). Each graph represents a specific irrigation frequency in combination with levels of applied KCl; vertical bars represent standard errors ($n = 3$).

irrigation, species and time were significant (Table B-25). However, species differences only, were dependent upon time (significant species X time interaction).

Attention is directed to Table B-29 where it is indicated that for both Douglas-fir and jack pine, daily irrigated seedlings possessed lower relative water contents than weekly irrigated seedlings (averaged over KCl levels). The relative water contents of these successively droughted seedlings also exhibited higher average relative water contents than seedlings in the first drought (Fig. 11) after comparable times i.e. 10 days. The relative water contents of seedlings exposed to the second drought period ranged from 15% to 20% higher than for seedlings evaluated during the first drought period except for weekly irrigated Douglas-fir for which the difference was 5%.

4.1.5.3.5 Relationships amongst plant water relation parameters.

4.1.5.3.5.1 Relative water content/Total plant water potential. The relationships between relative water content and total plant water potential for Douglas-fir and jack pine are presented in Figure 20. The relationship is sigmoidal and at any plant water potential relative water contents of Douglas-fir are greater than for jack pine. Initially, relative water content of Douglas-fir decline slowly from approximately 95% to 90% during which plant water potential declines to ca -2.8 MPa from ca -0.5 MPa. The following decline in relative water content to ca 65% is associated with a small decline to -4.0 MPa, a difference of 1.2 MPa. Further declines in relative water content are attended by large changes in plant water potential.

In jack pine the relationship of relative water content to plant water potential is similar to that previously described for Douglas-fir, but with several notable exceptions. Firstly, initial declines in relative water content are rapid and for the same decrement in water potential that represents a decline in relative water content from 95% to 90% in Douglas-fir the decline in relative water content in jack pine is from ca 84% to ca 45%.

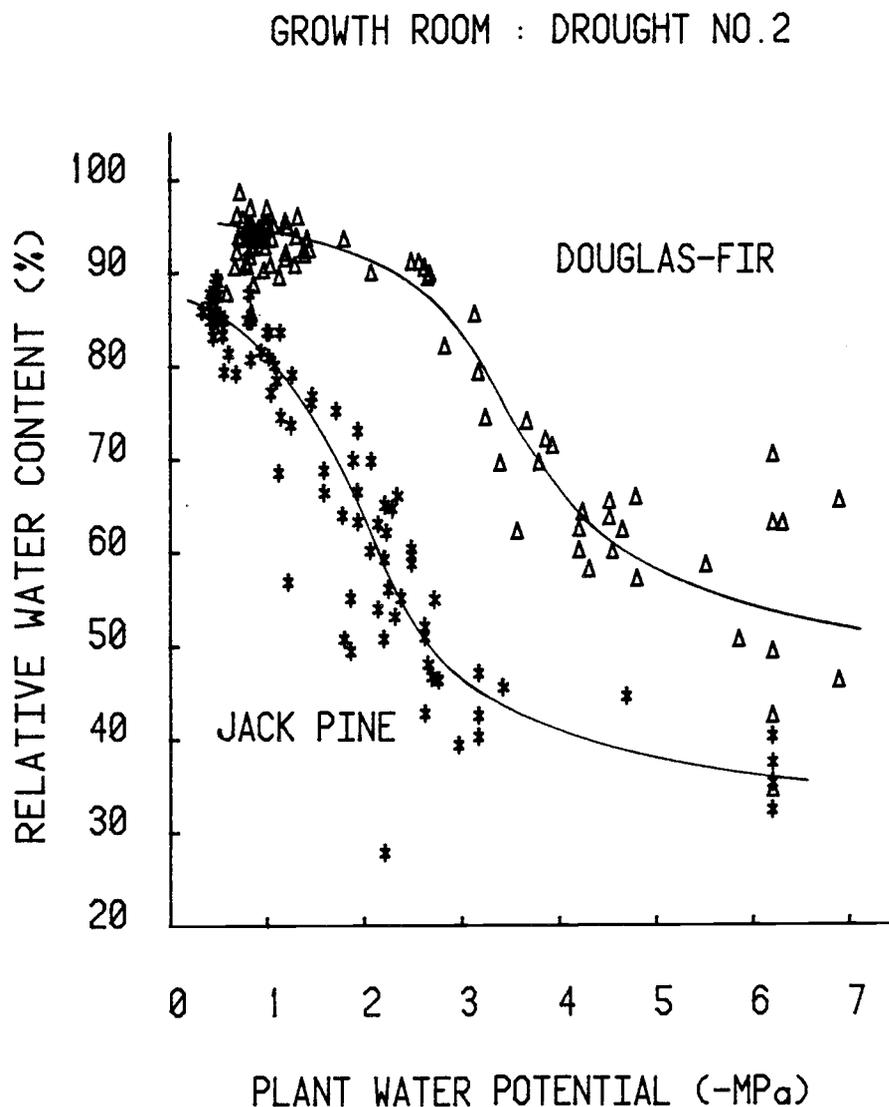


Figure 20. Relationship between relative water content and plant water potential of conditioned and previously droughted DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined by species from the second growth room drought period and are fitted with free hand curves.

This suggests that jack pine is unable to maintain high relative water contents by developing a potential gradient sufficient to absorb water. Secondly, despite higher plant water potentials in jack pine (i.e. -0.4 MPa) relative water contents were approximately 10% below those achieved by Douglas-fir at about -1.0 MPa.

The dramatic difference in form of the relative water content/plant water potential relationship displayed by seedlings of the first (Fig. 12) and second (Fig. 20) drought periods demands comment. The apparent effect of the second drought stress period on Douglas-fir was to increase its capacity to develop a larger potential gradient to maintain high relative water contents during periods of soil water deficits. For example, the equivalent water potential of first drought seedlings at 90% RWC is ca -1.8 MPa whereas, it is ca -2.8 MPa for second drought seedlings, a difference of 1.0 MPa. Jack pine, on the other hand, exhibited no benefit that may have been derived from the first drought; in fact, the relationships are nearly identical at plant water potentials above -2.3 MPa.

4.1.5.3.5.2 Relative water content/osmotic potential. The relationship between relative water content and osmotic potential for Douglas-fir is sigmoidal, whereas, it is essentially curvilinear downward for jack pine (Fig. 21). Regardless of osmotic potential relative water contents of Douglas-fir were 20% to 30% higher than in jack pine. Maximum difference occurred between -1.8 MPa and 2.8 MPa. In this range relative water contents of Douglas-fir remained high as osmotic potentials fell, but in jack pine, relative water contents fell concomitantly with osmotic potentials.

In comparison with first drought seedlings the relative water contents of Douglas-fir are higher and osmotic potentials of second drought seedlings are lower over the entire range of data. For jack pine, the relationships are essentially the same.

4.1.5.3.5.3 Osmotic potential/Total plant water potential. The relationships between osmotic potential and total

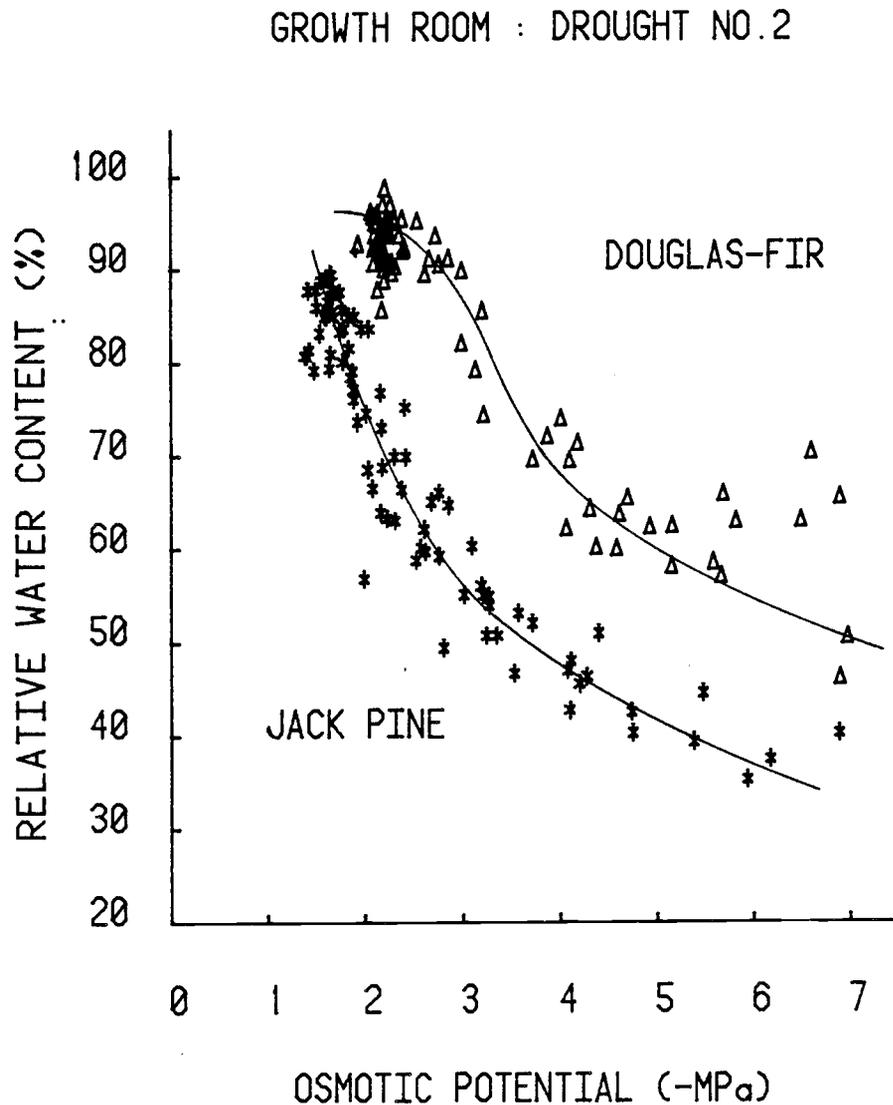


Figure 21. Relationship between relative water content and osmotic potential of conditioned and previously droughted DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined by species from the second growth room drought period and are fitted with free hand curves.

plant water potential for Douglas-fir and jack pine are presented in Figure 22. A 1:1 line is included in Figure 22 and at any point along this line osmotic potential is equal to total plant water, making turgor pressure equal zero. In the region of high plant water potentials i.e. 0 MPa to -2.0 MPa the rate of decline in osmotic potential of Douglas-fir is less than the rate of decline in total water potential. A similar comparison can be made for jack pine. In this same range of total water potentials turgor pressures are higher in Douglas-fir than in jack pine; that is, the differences between total water potential and osmotic potentials are greater for Douglas-fir than they are for jack pine. At a plant water potential of -2.0 MPa osmotic potentials of Douglas-fir and jack pine are equal. From this point, however, turgor pressures of jack pine appear to increase with further decrements in plant water potential. Turgor pressures of Douglas-fir continue to decline. Although turgor pressure does not appear to reach a zero value until values of -5.0 MPa are exceeded, it is unlikely that positive turgor is maintained at these potentials.

4.1.5.4 Pressure-volume parameters. Plant water relation parameters derived from pressure-volume curves were estimated on three occasions during the second drought stress period. Estimated parameters were submitted to analysis of variance which included time as a sub-sub-subplot. The analysis indicates that neither of the conditioning treatments, irrigation or KCl level, had a significant effect (Table B-30). Species difference was consistently significant for all parameters, except one (Table 12), and sample time was significant for osmotic potential at full turgor and osmotic potential at zero turgor (Table B-30).

4.1.5.4.1 Osmotic potential at full turgor, OPFT (-MPa). As the drought stress period progressed OPFT decreased (i.e. became more negative) consistently in Douglas-fir from -1.96 MPa to -2.25 MPa, a 17% decrease. Jack pine exhibited an initial decrease in OPFT followed by an increase. The change in OPFT over the drought stress period represented a 12% decrease. The osmotic potentials of Douglas-fir and jack pine were significantly different

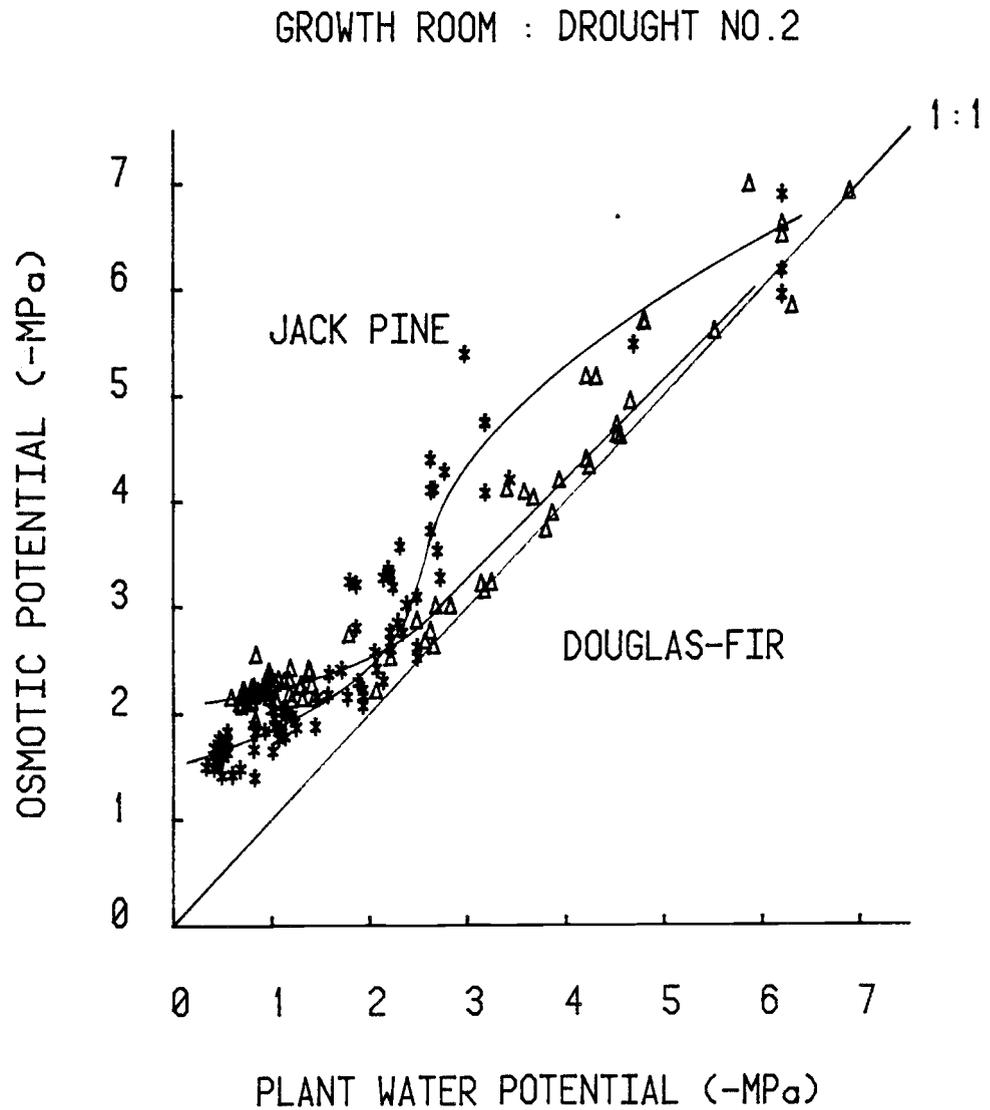


Figure 22. Relationship between osmotic potential and plant water potential of conditioned and previously droughted DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined from the second drought period by species and are fitted with free hand curves. The 1:1 line represents a potential state of zero turgor pressure.

TABLE 12. Summary of mean water relation parameters determined by the pressure volume technique on three sampling dates for conditioned DOUGLAS-FIR and JACK PINE seedlings during the second drought period. Species differences were evaluated by weighted t-tests and where significance existed means are followed by different letters (P < .05). See text for description of symbols.

		Water relations parameter							
Sp.	PV Run	OPFT	OPZT	RWC	RSWC	Ra	ME@	Dry wt.	WSFT
				@ TLP	@ TLP		.995 RWC	Turgid wt.	Dry wt.
		(-MPa)	(-MPa)	(%)	(%)	(MPa)			
Df	1	1.96	2.45	0.87	0.80	0.33	12.36	0.27	1.78
	2	2.04	2.60	0.85	0.78	0.29	13.26	0.27	1.85
	3	<u>2.25</u>	<u>2.88</u>	<u>0.85</u>	<u>0.78</u>	<u>0.32</u>	<u>9.40</u>	<u>0.28</u>	<u>1.71</u>
	\bar{X}	2.08a	2.64a	0.86a	0.79a	0.31a	11.67a	0.27a	1.78a
Jp	1	1.11	1.88	0.80	0.59	0.50	1.74	0.24	1.53
	2	1.32	2.02	0.80	0.65	0.42	2.67	0.24	1.80
	3	<u>1.24</u>	<u>2.14</u>	<u>0.76</u>	<u>0.58</u>	<u>0.43</u>	<u>1.88</u>	<u>0.24</u>	<u>1.72</u>
	\bar{X}	1.23b	2.01b	0.79b	0.61b	0.45b	2.10b	0.24b	1.69a

(Tables 12 and B-30). It is noteworthy that the values of OPFT presented for Douglas-fir and jack pine are similar to the osmotic potentials of the species at maximum relative water content as presented in Figure 19.

4.1.5.4.2 Osmotic potential at zero turgor, OPZT (-MPa). Osmotic potentials at zero turgor pressure in Douglas-fir decreased consistently as the drought stress period progressed (Table 12). This was expected because of decreases in osmotic

potentials at full turgor which were noted above. The differences between the two parameters over time varied between 25 and 28 percent. In jack pine, the decrease in osmotic potential over time was inconsistent, but in contrast to Douglas-fir the differences between osmotic potentials at full and zero turgor ranged from 53 and 73 percent. Jack pine seedlings therefore, appear to be capable of undergoing a proportionately larger decrease in osmotic potential than Douglas-fir during drought stress. However, it must be noted that values of osmotic potential at which zero turgor occur in jack pine are considerably higher than in Douglas-fir.

4.1.5.4.3 Relative water content at turgor loss point, RWC @ TLP. For each species the relative water contents at the turgor loss point did not vary significantly during the course of the drought stress period (Tables 10, B-30). Indeed, they varied between 0.85 to 0.87 for Douglas-fir and 0.76 to 0.80 for jack pine with mean species values of 0.86 and 0.76, respectively. Interestingly, values of RWC @ TLP reported here for the second drought seedlings are higher than those reported for first drought seedlings (Table 8).

4.1.5.4.4 Relative symplasmic water content at the turgor loss point, RSWC @ TLP. The relative symplasmic water content at the turgor loss point did not vary significantly over the duration of the drought stress period in either Douglas-fir or jack pine (Table B-30). The mean species values, which are significantly different (Table 12), are 0.79 and 0.61 for Douglas-fir and jack pine, respectively. This value for Douglas-fir is identical to the

value reported for first droughted seedlings i.e. 0.79 (Table 7), but the RSWC @ TLP of first drought jack pine seedlings was 0.51. The current values of RSWC @ TLP suggest that at the point of turgor loss 21% and 39% of the symplasmic water is lost in Douglas-fir and jack pine, respectively.

4.1.5.4.5 Relative apoplasmic water content, Ra. The apoplasmic water content did not vary significantly during the course of the drought stress period in either Douglas-fir or jack pine with mean species values of 0.31 and 0.45, respectively. These values were significantly different (Table 12) and were only slightly different than those reported for first drought seedlings.

4.1.5.4.6 Modulus of elasticity at near full turgor, ME @ .995 RWC. Modulus of elasticity at near full turgor for both species did not vary significantly during the drought stress period. This point has important implications in determining whether or not plant material adjusts osmotically to development of stress to maintain turgor. It should, however, be noted that modulus of elasticity values for jack pine are in the order of five times less than those recorded for Douglas-fir (Table 10). Species values of $me @ .995 rwc$ attained by Douglas-fir and jack pine during the second drought are lower than values determined during the first drought period e.g. 11.67 vs 9.22 MPa and 2.10 vs 1.65 MPa, respectively.

4.1.5.4.7 Ratio of sample dry weight to fresh weight. The ratio of sample dry weight to fresh weight did not vary significantly over the duration of the drought period for either species (Tables 12 and B-30). Thus, it might be assumed that if changes in dry weight and fresh weight occurred they did so proportionately. Analysis of variance indicates that species difference was significant (Table B-30).

4.1.5.4.8 Ratio of weight of symplasmic water at full turgor to sample dry weight. The weight of symplasmic water relative to tissue dry weight did not vary significantly throughout the drought stress period nor were species differences significant (Tables 12 and B-30). Although this parameter was higher in

Douglas-fir in the first drought compared to the second (i.e. 2.30 vs 1.78) no differences were noted for jack pine.

4.1.5.5 Root nutrition. After seedling shoots were sampled to estimate water relation parameters there was insufficient foliage remaining to analyse for nutrient elements, roots were submitted for analysis of N, P, K, Mg, Ca and Cl^- . Since bulking of samples was necessary to provide sufficient plant material for analysis statistical analyses could not be undertaken. Nevertheless, values of nutrient concentrations provide a basis for evaluating treatment differences in response to drought stress. Nutrient concentrations are presented in Table 13 by conditioning treatment, species and sample time.

4.1.5.5.1 Nitrogen, N. At each treatment level N concentrations of Douglas-fir and jack pine decreased from an initial high value at the start of the drought period to values ranging from 3% to 31% lower than the initial value. Decreases in N concentration throughout the drought period were inconsistent. Greatest declines were associated with jack pine. With few exceptions, N concentrations were higher in root systems of jack pine than in Douglas-fir.

4.1.5.5.2 Phosphorus, P. There is evidence to suggest that as the drought stress period progressed, P concentrations variously decreased. Jack pine appeared to maintain higher P concentrations than Douglas-fir. However, differences are not large or consistent enough to evaluate the impact of irrigation conditioning on P concentrations.

4.1.5.5.3 Potassium, K. The trend in K concentration was variable, but there appeared to be a progression toward a peak during mid-drought (Sample day 3 and 4) then a progression toward lower values. Terminal K values, in all but one instance, were lower than initial concentrations recorded at the start of the drought period. Potassium concentrations in jack pine root systems were markedly greater than in Douglas-fir roots; these differences relative to K concentrations of Douglas-fir were in the order of 33%.

TABLE 13. Nutrient concentrations of root systems of conditioned DOUGLAS-FIR and JACK PINE seedlings sampled on seven occasions during the second drought period in a growth chamber.

		NUTRIENT													
		% N							% P						
		Day							Day						
Irrig.	Spe- KCl cies	1	4	6	8	10	12	14	1	4	6	8	10	12	14
Daily	0 Df	1.93	1.77	1.82	1.58	1.72	1.62	1.62	0.36	0.43	0.34	0.42	0.30	0.32	0.29
	Jp	2.28	2.05	1.98	1.93	1.72	1.34	1.58	0.57	0.58	0.48	0.52	0.42	0.48	0.48
100	Df	1.69	1.61	1.60	1.67	1.53	1.61	1.64	0.44	0.35	0.43	0.39	0.31	0.28	0.29
	Jp	1.91	1.87	1.92	1.73	1.89	1.64	1.62	0.56	0.53	0.49	0.49	0.46	0.44	0.55
Weekly	0 Df	1.66	1.59	1.72	1.59	1.77	1.58	1.63	0.38	0.37	0.31	0.32	0.30	0.29	0.24
	Jp	2.06	2.09	1.88	2.03	1.99	1.57	1.93	0.54	0.54	0.58	0.46	0.45	0.52	0.56
100	Df	1.70	1.67	1.65	1.46	1.45	1.67	1.52	0.35	0.38	0.39	0.32	0.29	0.29	0.30
	Jp	2.13	1.90	1.98	1.79	1.86	1.77	1.71	0.54	0.53	0.49	0.42	0.46	0.45	0.45
		% K							% Ca						
		Day							Day						
Irrig.	Spe- KCl cies	1	4	6	8	10	12	14	1	4	6	8	10	12	14
Daily	0 Df	0.86	1.10	1.02	1.00	0.77	0.91	0.80	0.28	0.23	0.24	0.18	0.23	0.28	0.24
	Jp	1.31	1.40	1.24	1.47	1.28	1.45	1.42	0.26	0.29	0.24	0.26	0.35	0.23	0.22
100	Df	1.06	1.00	1.27	1.00	1.02	0.88	0.88	0.19	0.22	0.21	0.22	0.19	0.23	0.25
	Jp	1.50	1.74	1.47	1.60	1.52	1.30	1.47	0.27	0.31	0.26	0.24	0.28	0.21	0.30
Weekly	0 Df	0.91	0.99	0.88	0.92	0.74	0.76	0.89	0.25	0.21	0.21	0.22	0.30	0.29	0.21
	Jp	1.44	1.38	1.52	1.27	1.27	1.37	1.17	0.32	0.30	0.24	0.33	0.32	0.32	0.30
100	Df	1.00	0.97	1.04	0.74	1.04	0.87	0.86	0.22	0.25	0.23	0.19	0.19	0.30	0.23
	Jp	1.38	1.43	1.48	1.38	1.31	1.45	1.15	0.26	0.26	0.29	0.31	0.27	0.30	0.26

(continued ...)

TABLE 13. (continued)

Irrig.	KCl	Spe- cies	% Mg							Cl ⁻ (ppm X1000)						
			Day							Day						
			1	4	6	8	10	12	14	1	4	6	8	10	12	14
Daily	0	Df	0.19	0.20	0.22	0.18	0.19	0.16	0.16	1.67	1.60	1.69	2.03	1.61	2.07	1.41
		Jp	0.25	0.23	0.20	0.22	0.21	0.19	0.18	2.51	2.66	2.41	2.55	2.83	2.55	2.60
100	0	Df	0.17	0.22	0.22	0.24	0.16	0.15	0.15	2.93	2.34	2.52	2.72	2.63	2.20	2.56
		Jp	0.26	0.26	0.22	0.22	0.19	0.16	0.19	5.18	9.03	3.52	5.95	3.20	4.10	3.17
Weekly	0	Df	0.20	0.22	0.19	0.19	0.19	0.17	0.14	1.83	1.97	1.31	1.76	1.65	1.67	1.94
		Jp	0.26	0.25	0.19	0.24	0.21	0.21	0.20	2.83	3.42	2.67	3.38	2.38	2.91	2.38
100	0	Df	0.17	0.19	0.18	0.15	0.15	0.18	0.17	3.00	2.53	2.26	2.63	2.55	2.69	2.19
		Jp	0.22	0.19	0.19	0.21	0.19	0.19	0.17	5.37	4.72	5.19	4.64	5.03	4.45	4.08

4.1.5.5.4 Calcium, Ca. The concentrations of calcium in both Douglas-fir and jack pine in all treatment levels exhibited inconsistent trends throughout the drought stress period. However, Ca concentrations in jack pine relative to those in Douglas-fir were greater by 8% and 19% for seedlings conditioned by daily and weekly irrigation, respectively.

4.1.5.5.5 Magnesium, Mg. The concentrations of magnesium in both species varied erratically during the drought period, but a maximum value was attained during mid-drought (Sample Day 3 or 4). Beyond this time Mg concentrations decreased to levels at least as low as initial values. Overall, Mg concentrations in jack pine exceeded those in Douglas-fir.

4.1.5.5.6 Chloride, Cl⁻. Changes in Cl⁻ concentration were inconsistent throughout the drought stress period regardless of species and treatment level. Generally, Cl⁻ concentrations at the end of the drought period were lower than initial concentrations. During the decline increases were noted to occur e.g. in daily irrigated jack pine at 100 ppm KCl. Chlorine concentrations were higher in seedlings that were conditioned with 100 ppm KCl compared to 0 ppm and relative to Douglas-fir, Cl⁻ concentrations were consistently higher in jack pine seedlings at all treatment combinations (Table 13).

4.1.5.5.7 Comparable nutrient concentrations between drought periods. The nutrient concentrations averaged over the duration of the drought periods are presented by treatment and species in Table 14. It is clearly apparent, with few exceptions, that lower nutrient concentration occurred in seedlings after exposure to the second drought period. When species are considered individually, the decrease in nutrient concentration of second drought values relative to first drought values ranged from 5% to 22%. There is, however, one exception that should be noted; the concentration of K in jack pine seedlings was higher during the second drought period than in the first drought period: 1.26% vs 1.40%.

4.1.6 Seedling recovery from second drought stress. At the

TABLE 14. Mean nutrient concentration averaged over sample times of root systems of DOUGLAS-FIR and JACK PINE seedlings during the first (D1) and second (D2) drought periods.

TREATMENT		NUTRIENT / DROUGHT PERIOD														
		N		P		K		Ca		Mg		Cl ⁻				
Irrigation	KCl	Species	D1	D2	D1	D2	D1	D2	D1	D2	D1	D2	D1	D2		
			----- % ----- (ppm X1000)													
Daily	0	Df	1.96	1.72	0.53	0.35	1.10	0.92	0.28	0.24	0.23	0.18	1.85	1.73		
		Jp	2.32	1.84	0.59	0.50	1.26	1.37	0.29	0.26	0.26	0.21	2.91	2.59		
	100	Df	1.86	1.62	0.47	0.35	1.10	1.02	0.26	0.22	0.19	0.18	2.28	2.56		
		Jp	2.13	1.80	0.55	0.50	1.44	1.51	0.30	0.27	0.24	0.21	4.82	4.88		
Weekly	0	Df	1.98	1.65	0.37	0.32	0.88	0.87	0.23	0.24	0.17	0.18	1.65	1.73		
		Jp	2.51	1.94	0.54	0.51	1.18	1.34	0.30	0.30	0.21	0.22	3.54	2.85		
	100	Df	1.98	1.59	0.37	0.33	0.99	0.93	0.25	0.23	0.18	0.17	3.76	2.55		
		Jp	2.56	1.88	0.50	0.48	1.15	1.37	0.30	0.28	0.20	0.20	4.67	4.78		
Species Means:		Df	1.94	1.65	0.44	0.34	1.02	0.93	0.26	0.23	0.19	0.18	2.39	2.14		
		Jp	2.38	1.86	0.54	0.50	1.26	1.40	0.30	0.28	0.23	0.21	3.99	3.78		

point the second drought was terminated all seedlings were wilted to various degrees and many seedlings exhibited obvious signs of mortality. Two days after the start of recovery highest overall mortality appeared to be associated with Douglas-fir (Table 15). This is particularly apparent in daily irrigated seedlings where mean mortality over KCl levels for Douglas-fir and jack pine was 75% and 54%, respectively. In weekly irrigated seedlings mortality rates were dramatically lower than observed for daily irrigated seedlings. At 0 ppm KCl mortality of Douglas-fir and jack pine was similar (15% vs 13%), but at 100 ppm KCl Douglas-fir exhibited less mortality than jack pine (i.e. 20% vs 26%). By the tenth day of recovery mortality of daily irrigated Douglas-fir seedlings increased by 5% to 7%, and not in jack pine. Small increases in mortality occurred in weekly irrigated seedlings.

Seedlings classified as variously wilted on Day 2 of the recovery period contributed to the increase in mortality noted on the tenth day of recovery. Seedlings that regained turgor early in the recovery were apparently healthy and did not die at a later date.

Comparatively, species mortality was greater in the second drought stress period than in the first drought period. The second drought period was, however, four days longer.

To investigate the efficacy of conditioning treatments to mitigate the effects of drought, the hypothesis that species mortality was independent of irrigation or KCl level was evaluated for each species separately by Chi-square analysis. In the first instance, there was sufficient evidence to reject the hypothesis and instead, accept the alternative hypothesis that mortality in both Douglas-fir ($\chi^2 = 113.54$) and jack pine ($\chi^2 = 38.04$) was dependent upon irrigation conditioning. In the second instance, the hypothesis that mortality was independent of KCl level was accepted; Chi-square values for Douglas-fir and jack pine were 1.07 and 3.66, respectively.

4.1.7 Long-term performance of droughted seedlings. It is an important consideration that the application of conditioning

TABLE 15. Physiological condition¹ of DOUGLAS-FIR and JACK PINE seedlings averaged over 3 replications, 2 and 10 days after removal from 14-day exposure to second drought stress.

Treatment			Assessment Day 2			Assessment Day 10		
Irriga- tion	KCl	Sp.	Dead	Variously wilted or damaged	Turgid	Dead	Variously wilted or damaged	Tur- gid
			----- % -----			-----		
Daily	0	Df	75	11	14	80	7	13
		Jp	54	9	37	54	8	38
	100	Df	74	8	18	81	0	19
		Jp	54	10	36	54	10	36
Weekly	0	Df	15	12	73	20	6	74
		Jp	13	5	82	15	3	82
	100	Df	20	12	68	28	4	68
		Jp	26	4	70	27	3	70

¹ Seedling condition after drought stress:

1. Dead: no recovery, foliage discolored, stems brittle.
2. Variously wilted/damaged: some portion of foliage in limp condition and therefore considered damaged.
3. Turgid: seedlings which regained turgidity, foliage upright, no shrinkage of stem, good foliage color.

treatments do not ultimately preclude acceptable growth performance should favorable growing conditions prevail either before or after seedlings are subjected to a drought stress situation. To test one aspect it was hypothesized that surviving seedlings previously conditioned and twice droughted would respond if subjected to favorable growing conditions (in a growth room).

After a 12 week growth period seedling performance and physiological conditions were evaluated and are summarized in Table 16. In all treatments epicotyl lengths of seedlings at the end of the 12 week growth period were less than initial values, but not significantly less. During the growth period it was observed that in the majority of seedlings there was slight terminal dessication and, in time, lateral bud activity. However, growth from lateral bud extension was not sufficient to surpass the initial epicotyl length.

Significant increases ($P < 0.01$) in root collar diameter occurred at all treatment levels in both Douglas-fir and jack pine (Table 16), and were 67% and 68%, respectively. Within species, increases for daily and weekly watered seedlings (averaged over KCl levels) were 60% and 73% for Douglas-fir and 64% and 72% for jack pine.

Root dry weights increased significantly ($P < 0.01$) over the 12 week growth period (Table 16). Increases in root dry weight for Douglas-fir and jack pine were 438% and 749%, respectively. Root dry weight increases in daily and weekly irrigated seedlings were 411% and 465%, respectively for Douglas-fir and 698% and 800% for jack pine, respectively. Inspection of root systems after 12 weeks revealed that most seedlings exhibited root growth activity (Table 16).

Classification of seedling health condition indicated that few daily irrigated Douglas-fir seedlings were healthier than weekly irrigated seedlings (57% vs 90%) and that the health condition of jack pine was uniformly high (i.e. greater than 90% at both irrigation levels). Percent terminal bud set was greater for daily irrigated Douglas-fir than weekly irrigated seedlings and regardless

TABLE 16. Changes and significance of morphological parameters and physiological condition of previously droughted DOUGLAS-FIR and JACK PINE seedlings after a 12 week growth period.

		Morphology								
Sp.	Treatment	Epicotyl Length			Root Collar Dia.			Root Dry Wt.		
		Init.	Final	Sig.	Init.	Final	Sig.	Init.	Final	Sig.
Df	D0	31.0	27.8	NS	2.37	4.17	**	0.37	2.41	**
	D100	35.0	24.3	NS	2.90	4.17	**	0.62	2.30	**
	W0	30.2	25.0	NS	2.78	4.43	**	0.55	3.26	**
	W100	27.8	24.4	NS	2.42	4.53	**	0.45	3.32	**
Jp	D0	18.8	15.4	NS	2.50	3.99	**	0.34	2.85	**
	D100	17.8	14.9	NS	2.42	4.05	**	0.37	2.80	**
	W0	17.3	16.9	NS	2.62	4.65	**	0.41	3.53	**
	W100	17.2	16.8	NS	2.72	4.54	**	0.45	4.23	**
		Physiological state								
Sp.	Treatment	Mortality	Healthy	Bud set	Root activity					
					Nil	Little	Ext.			
----- % -----										
Df	D0	23	46	46	8	38	31			
	D100	17	67	50	17	50	16			
	W0	14	80	40	6	47	33			
	W100	0	100	27	0	67	33			
Jp	D0	0	86	0	7	50	43			
	D100	0	100	0	0	33	67			
	W0	0	100	0	0	13	87			
	W100	0	93	0	0	33	67			

of treatment all jack pine seedlings exhibited active terminal shoot growth. Based upon the above evidence it can be concluded that conditioning treatment did not preclude the ability of the surviving seedlings to grow under favourable conditions after exposure to drought.

4.2 Phase II: Nursery Experiment.

4.2.1 Seedling growth and nutrition in response to conditioning.

4.2.1.1 Seedling morphology. The epicotyl growth of Douglas-fir and jack pine seedlings during the six week conditioning period is presented in Figure 22. There was little differentiation amongst treatment levels in both species and none was significantly different regardless of sample week (Table B-31). Species were, however, significantly different. The effectiveness of irrigation frequency in conditioning seedlings was evaluated periodically by estimating the water potential of seedlings in the respective irrigation treatments by species. Water potentials for Douglas-fir subjected to daily and weekly irrigation were -0.69 MPa and -1.04 MPa, respectively and for jack pine, the water potentials were -0.62 MPa and -1.12 MPa, respectively. These differences were, however, not effective in restricting the rate of growth of weekly irrigated seedlings (Figure 23).

Analysis of seedling morphology at the end of the conditioning period revealed that KCl levels had no effect on any morphological parameters except root area index which was only marginally significant (Table B-32). Means of each morphological parameter were, therefore, summarized by species and irrigation level (Table 17). Growth was greater for daily irrigated than weekly irrigated seedlings with one interesting exception. Top:root ratio was not significantly affected by irrigation frequency. Root area index of daily irrigated seedlings was 15% and 17% greater, than weekly irrigated seedlings, in Douglas-fir and jack pine, respectively. Similarly, differences in seedling dry weight were 28% and 25%. Although, not statistically significant top:root

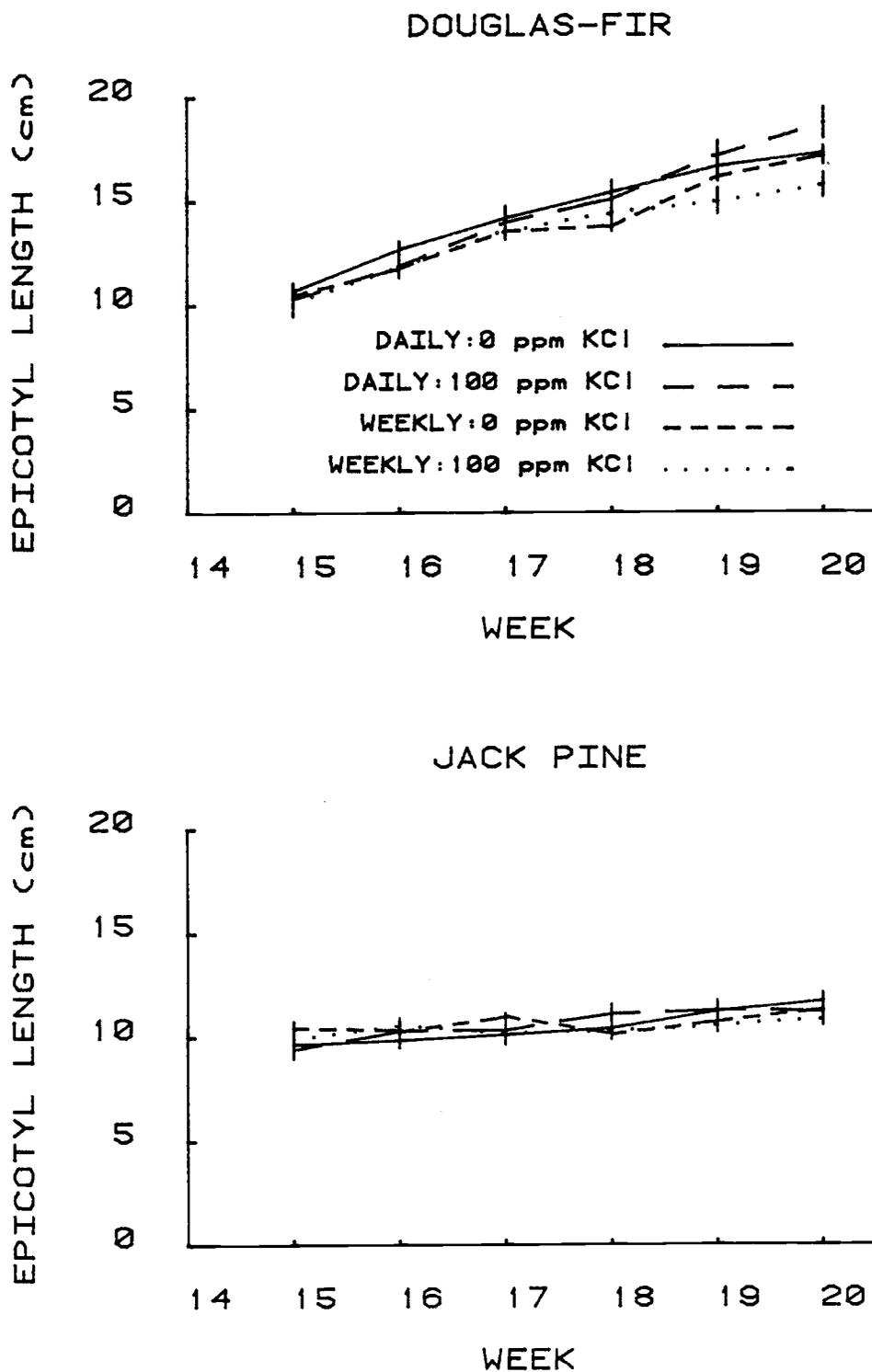


Figure 23. Progression of epicotyl lengths of DOUGLAS-FIR (upper graph) and JACK PINE (lower graph) seedlings during the six week conditioning period.

TABLE 17. Morphological parameters of 21 week old DOUGLAS-FIR and JACK PINE container seedlings. Means and standard errors were determined over replications and KCl levels which were non-significant in the analysis of variance.

Seedling parameter	Species/Irrigation Frequency							
	Douglas-fir				Jack pine			
	Daily		Weekly		Daily		Weekly	
	\bar{X}	\pm SE	\bar{X}	\pm SE	\bar{X}	\pm SE	\bar{X}	\pm SE
Root collar diameter (mm)	2.98	0.07	2.58	0.98	3.18	0.07	2.59	0.03
Shoot length (cm)	24.78	1.36	21.37	1.00	16.74	0.67	13.08	0.40
Root area index (sq. cm)	41.84	1.41	36.41	2.61	57.71	1.60	49.13	1.23
Shoot dry weight (g)	2.02	0.09	1.50	0.09	2.421	0.10	1.93	0.07
Root dry weight (g)	0.55	0.02	0.51	0.03	0.63	0.03	0.51	0.02
Seedling dry weight (g)	2.57	0.11	2.01	0.12	3.05	0.12	2.44	0.08
Top:Root ratio	3.67	0.08	2.99	0.11	3.89	0.13	3.80	0.08

ratios were higher in daily irrigated seedlings than in weekly irrigated seedlings.

Attempts to attribute conditioning effects to differences in anatomical morphology failed. Analysis of tangential and radial cell wall thicknesses amongst treatments lead to the conclusion that neither irrigation frequency or KCl significantly affected these parameters in either Douglas-fir or jack pine. Similarly, significant differences in needle dimensions could not be detected within species.

4.2.1.2 Seedling nutrition. Nutrient concentrations of foliage and roots of Douglas-fir and jack pine are presented in Table 18 and summaries of analysis of variance by element by respective tissue are presented in Tables B-33 and B-34.

4.2.1.2.1 Foliage. Only N, Ca and Cl^- concentrations were significantly affected by level of irrigation and consistently, daily irrigated seedlings had higher concentrations of these nutrients than weekly irrigated seedlings. Potassium chloride levels did not significantly affect concentrations of N, P, Ca, and Mg, but as might be expected, K and Cl^- concentrations were 18% and 151% higher, respectively, at the applied level of 100 ppm KCl relative to concentrations achieved at 0 ppm KCl. Species differences were also significant. When averaged over all treatments concentrations of N, P, and K were higher in Douglas-fir than in jack pine, but concentrations of Ca, Mg and Cl^- were higher in jack pine. For N, P, and Mg species differences were dependent upon irrigation level (significant irrigation X species interaction) (Table B-33).

4.2.1.2.2 Roots. Concentrations of nutrient elements in roots are summarized by treatment level and species in Table 18. Analysis of variance of each element indicated that only P, K and Cl^- concentrations were significantly affected by irrigation (Table B-34). Level of applied KCl significantly affected concentrations of K, Ca, and Cl^- . For all nutrients except N, significant species differences were detected, but for P concentrations species differences were dependent upon irrigation level (significant

TABLE 18. Concentrations of nutrient elements in foliage and roots of 21 week old conditioned (by irrigation and KCl application) DOUGLAS-FIR and JACK PINE.

Treatment				Nutrient					
Irriga- tion	KCl level (ppm)	Sp.	Plant compo- nent	N	P	K	Ca	Mg	Cl ⁻
				----- % -----					
Daily	0	Df	Top	1.602	0.492	1.083	0.137	0.132	0.411
			Root	2.308	0.720	1.459	0.268	0.237	2.475
	Jp	Top	1.846	0.221	0.760	0.174	0.149	0.639	
		Root	1.842	0.742	1.571	0.294	0.263	3.696	
Weekly	100	Df	Top	1.714	0.529	1.245	0.139	0.131	1.044
			Root	2.306	0.662	1.512	0.241	0.223	3.987
	Jp	Top	2.068	0.244	0.938	0.185	0.161	0.986	
		Root	1.898	0.731	1.685	0.294	0.282	5.190	
Weekly	0	Df	Top	1.534	0.493	0.891	0.143	0.130	0.327
			Root	1.908	0.532	1.011	0.271	0.207	1.806
	Jp	Top	1.670	0.192	0.665	0.150	0.141	0.574	
		Root	2.058	0.712	1.205	0.316	0.282	3.143	
100	Df	Top	1.610	0.480	0.099	0.127	0.130	0.810	
		Root	2.004	0.516	1.062	0.233	0.201	2.932	
Jp	Top	1.524	0.186	0.747	0.150	0.149	0.814		
	Root	2.098	0.649	1.298	0.304	0.284	4.447		

irrigation X species interaction).

In Douglas-fir, concentrations of all nutrient elements were highest in seedlings conditioned by daily watering. For jack pine there was no consistent pattern; P, K, and Cl^- were highest in daily irrigated seedlings. At all treatment levels K and Cl^- concentrations were higher at 100 ppm KCl with greater differences in concentrations occurring between 0 ppm and 100 ppm KCl in daily irrigation than with weekly irrigation treatments. In both Douglas-fir and jack pine, K and Cl^- concentrations were comparatively higher in roots than in foliage regardless of treatment.

4.2.2 Development of soil water deficits. The evaluation of seedling morphology and water relationships in a field setting should be related to significant site parameters. Under present experimental conditions soil water contents were monitored over the course of the experimental period in the two contrasting soil types. The progression of soil water depletion should provide a good basic reference against which changes in water relations parameters and morphology can be evaluated.

The two soil types: a sandy clay loam from Burnt Woods and a loamy sand (river sand material) exhibited unique soil water release characteristics (Fig. 24). Maximum water holding capacity at saturation for the Burnt Woods soil is approximately 52%, whereas it is 20% for the River Sand soil. If it is assumed that field capacity is between -0.01 MPa and -0.03 MPa the water content of the two soils at field capacity would range between 27% and 36% and 3% to 4% for Burnt Woods and River Sand soils, respectively. Thus, it might be expected that seedlings planted in River Sand would be subjected to more rapidly mounting soil water deficits than would seedlings planted in the Burnt Woods soil.

The progressions of soil water potential and water content throughout the experimental period for the Burnt Woods and River Sand soil types are presented in Figure 25 and 26 by three soil depths. The soil water potential of both soil types at all three depths (10 cm, 15 cm, 20 cm) remained high, as did water content for

SOIL WATER RELEASE CURVES

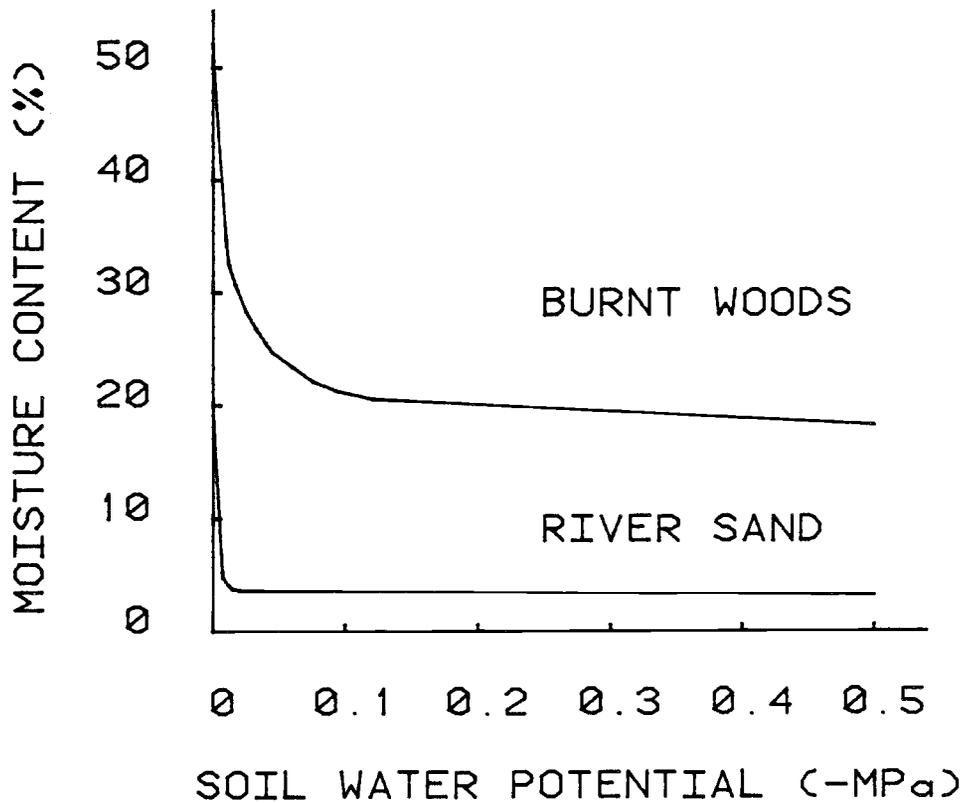


Figure 24. Soil water release curves for Burnt Woods soil (sandy clay loam) and River Sand soil (loamy sand) used in the nursery drought experiment.

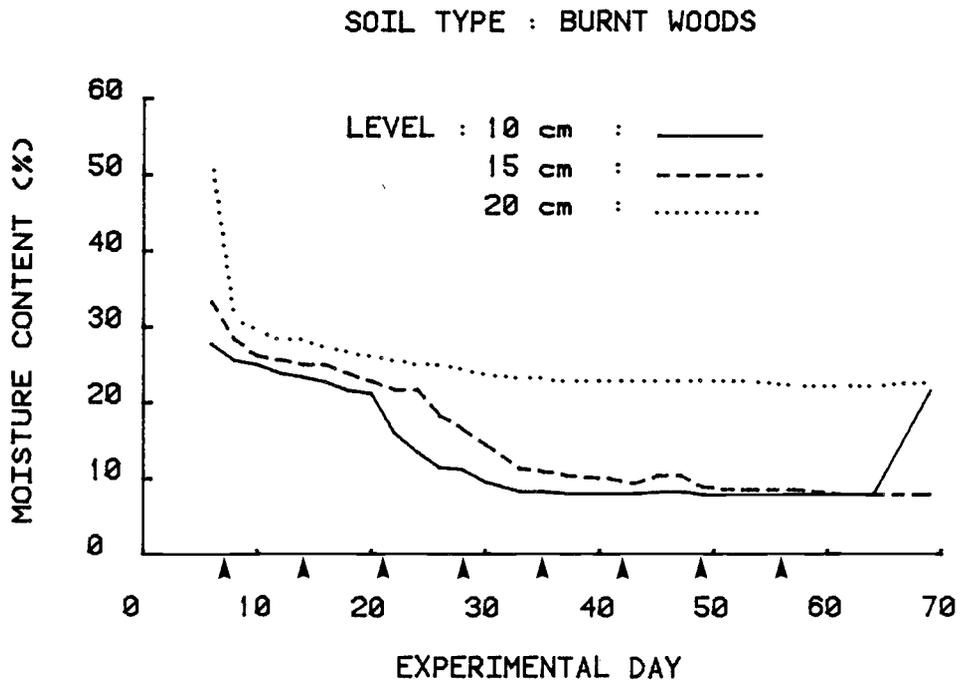
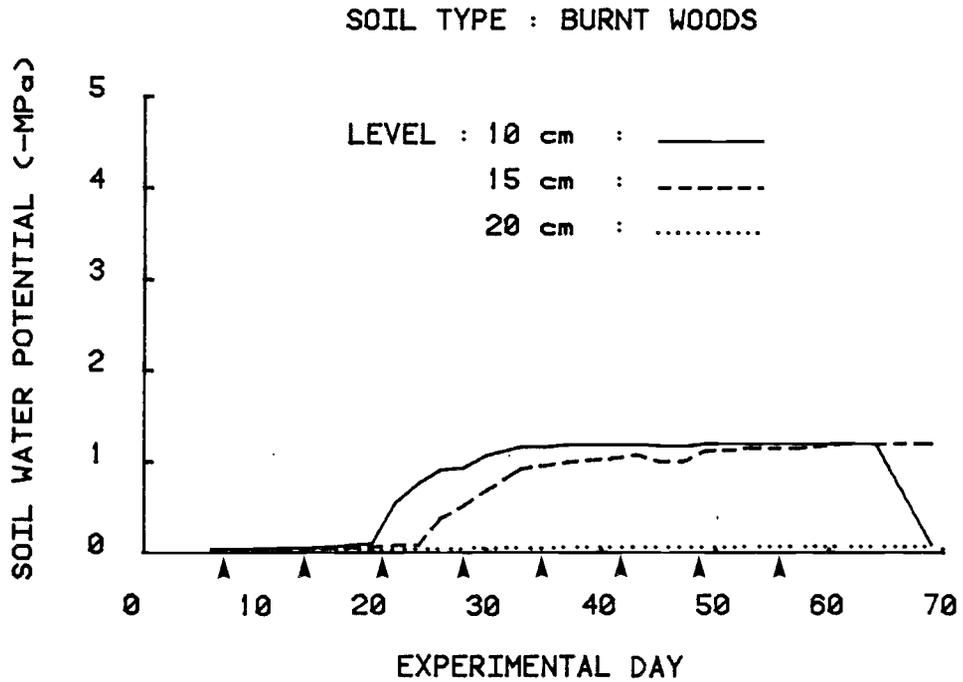


Figure 25. Progression in soil water potential (upper graph) and moisture content (lower graph) of Burnt Woods soil and at three profile depths during the nursery drought period ($n = 8$). Arrows denote assessment times.

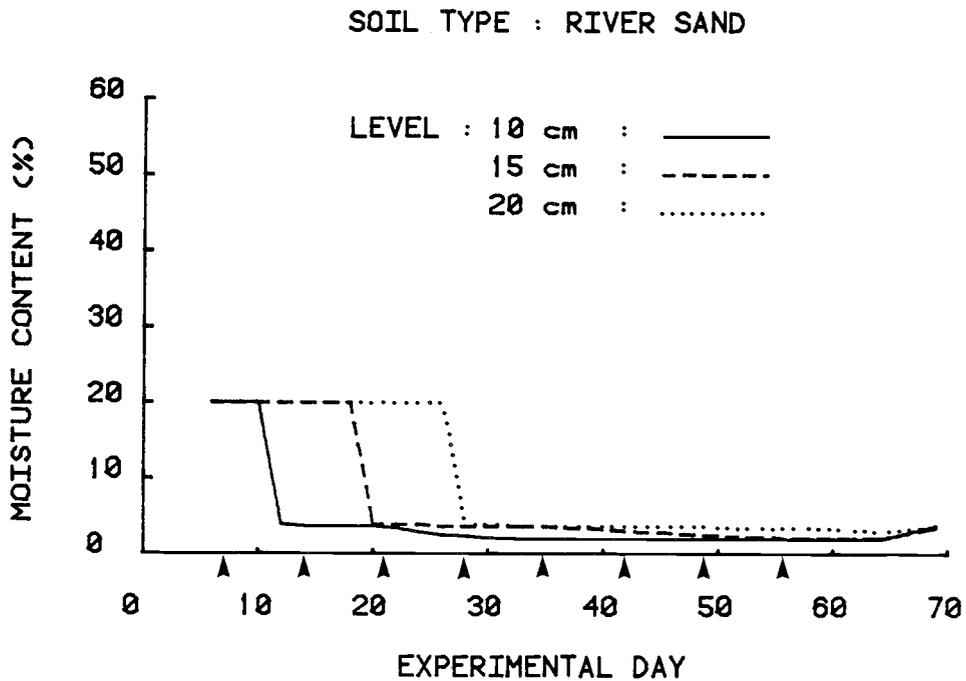
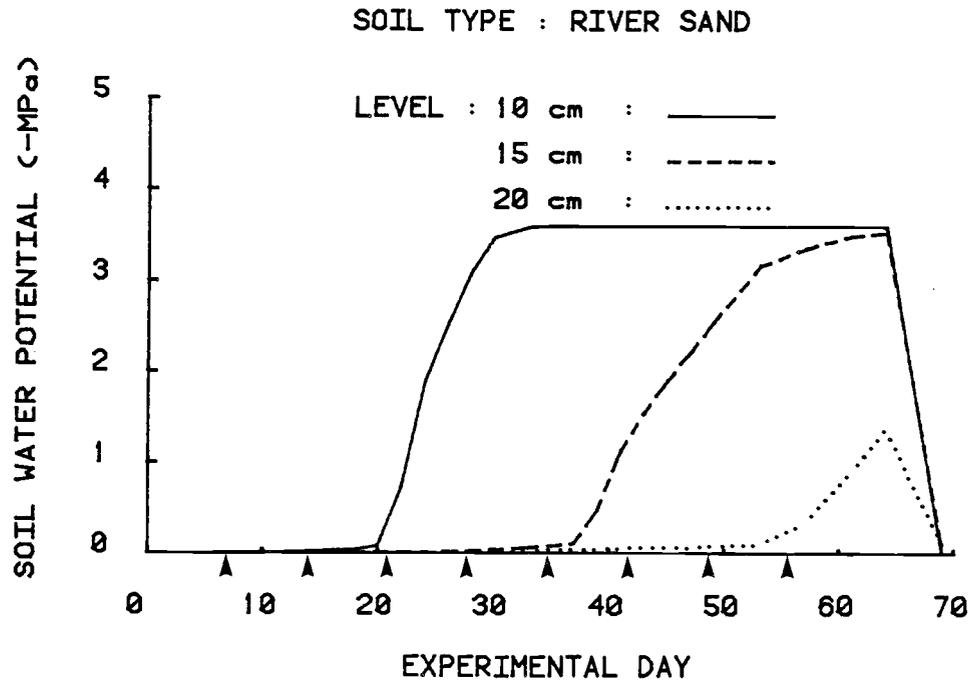


Figure 26. Progression of soil water potential (upper graph) and moisture content (lower graph) of River Sand soil at three profile depths during the nursery drought period ($n = 8$). Arrows denote assessment times.

the first 20 days of the experimental period. With time the soil water potential of the upper layers began to decrease. The water potential at the 10 cm depth in Burnt Woods soil decreased to a low of -1.2 MPa by Day 32 and remained relatively constant for the duration of the experimental period. Water potentials at the 15 cm level declined slowly for the first 24 days of the experimental period, then declined rapidly during the next 8 days to approximately -0.9 MPa (11% MC) after which further declines were minimal. At the 20 cm depth high soil water potentials were maintained throughout the drought period with moisture contents not decreasing to values below 25%.

The declines in soil water potential and water content observed in the River Sand soil throughout the experimental period are illustrated in Figure 26. For the first 10 days water contents were maintained within the soil profile below 10 cm at near field capacity i.e. about 20% MC. After 10 days, soil water potential at the 10 cm level decreased slowly, but soil water content decreased rapidly to approximately 3% MC. During this phase the largest of the soil pores were evacuated. Further decrements in soil water potential were accompanied by only small variations in water content. At the 15 cm level soil water content decreased to a low moisture content (3%) by day 20 and in terms of soil water potential it had not changed appreciably. By day 28 moisture content at the 20 cm depth had decreased to a similar low value of 3%. Considering the intent of the field experiment, i.e. to subject seedlings to a simulated field drought condition it can be concluded that this was achieved.

4.2.3 Seedling response to drought stress. Due to the number of factors involved in the field evaluation of responses to drought stress the presentation of data is approached in two ways. First, response data will be presented by species i.e. species will not represent a main order effect in the analysis of variance, instead soil type will be included. Thus, soil type differences can be evaluated. Secondly, consideration will be given to species within soil type.

4.2.3.1 Seedling morphology.

4.2.3.1.1 Epicotyl length. The progressions of epicotyl length in Douglas-fir and jack pine in relation to irrigation conditioning level and soil type are illustrated in Figure 27. Analysis of variance of epicotyl length by species revealed that irrigation level was significant in Douglas-fir, but not in jack pine. Moreover, soil type, KCl level and time did not significantly affect epicotyl length throughout the duration of the stress period (Table B-35).

When species are considered within soil types, species differences in the Burnt Woods soil type are significantly different (Tables B-36 and B-37). Similarly, analysis for River Sand soil irrigation and species effects on epicotyl length were significant (Tables B-36 and B-37).

4.2.3.1.2 Root collar diameter. The progressions of root collar diameter for species irrigation frequency by soil type are illustrated in Figure 28. Analysis of variance of root collar diameter by species indicated no significant treatment differences for either species (Table B-35). However, when analysis of variance was conducted by soil type species difference was significant, but only for the River Sand soil type (Tables B-36 and B-38).

4.2.3.2 Water relations: DOUGLAS-FIR. The progressions of total water potential, osmotic potential and turgor potential throughout the experimental period are presented by treatment level for Burnt Woods soil and River Sand soil types in Figure 29 and 30 respectively and are attended by mean summaries in Tables B-41, B-42 and B-43.

4.2.3.2.1 Total water potential: ψ_T . During the experimental period total water potential of Douglas-fir declined gradually in the Burnt Woods soil at all treatment levels (Figure 29). However, the decline in water potential was more rapid for daily irrigated seedlings than for weekly irrigated seedlings. From similar potential values of -0.29 MPa terminal potentials for daily and weekly irrigated seedlings were -0.81 MPa and 0.72 MPa (Table B-41). Analysis of variance revealed that differences due to

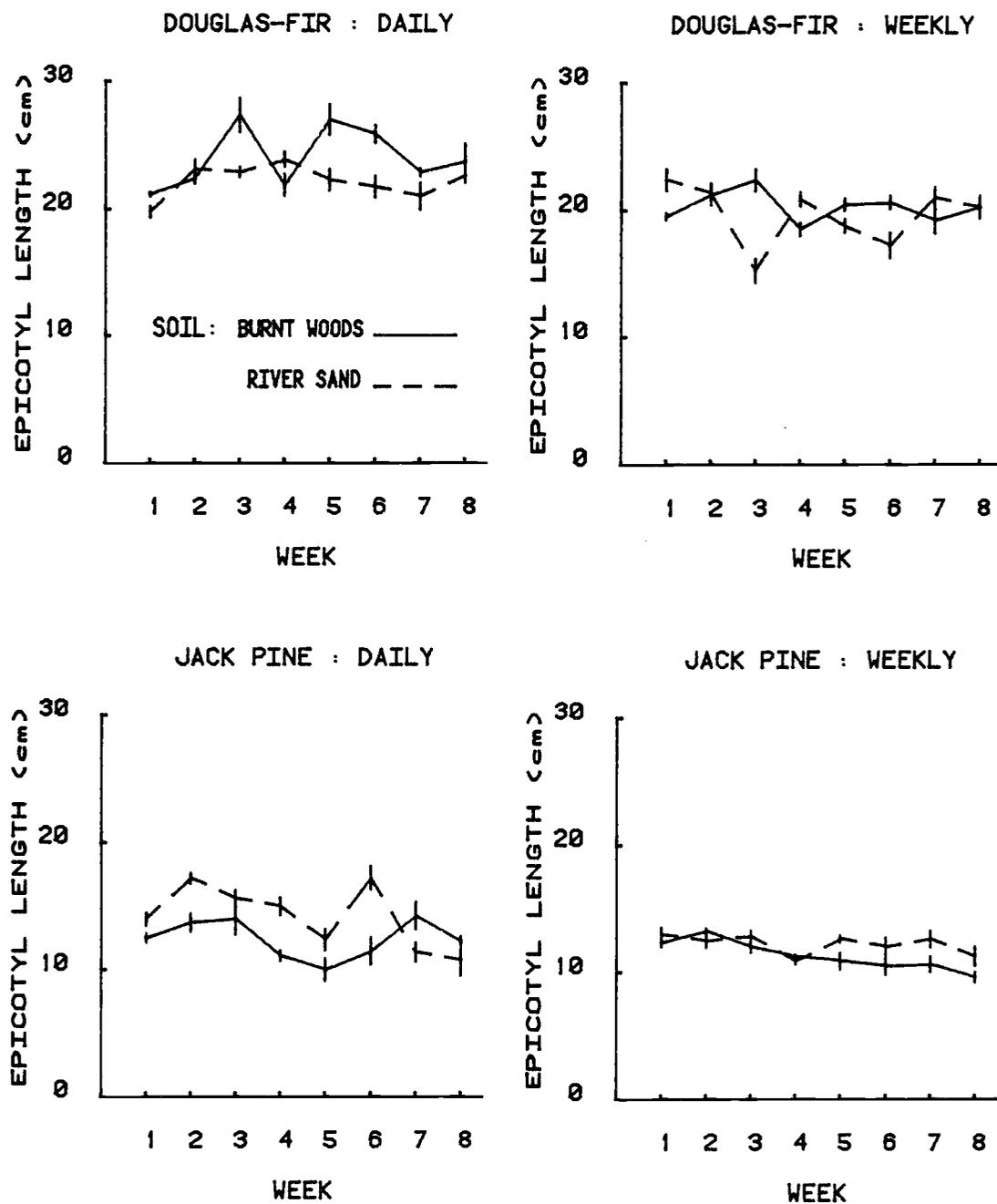


Figure 27. Progression of epicotyl lengths of conditioned DOUGLAS-FIR (upper graphs) and JACK PINE (lower graphs) seedlings during the nursery drought period in two soil types. Data presented by irrigation frequency averaged over KCl levels; vertical lines represent standard errors ($n = 4$).

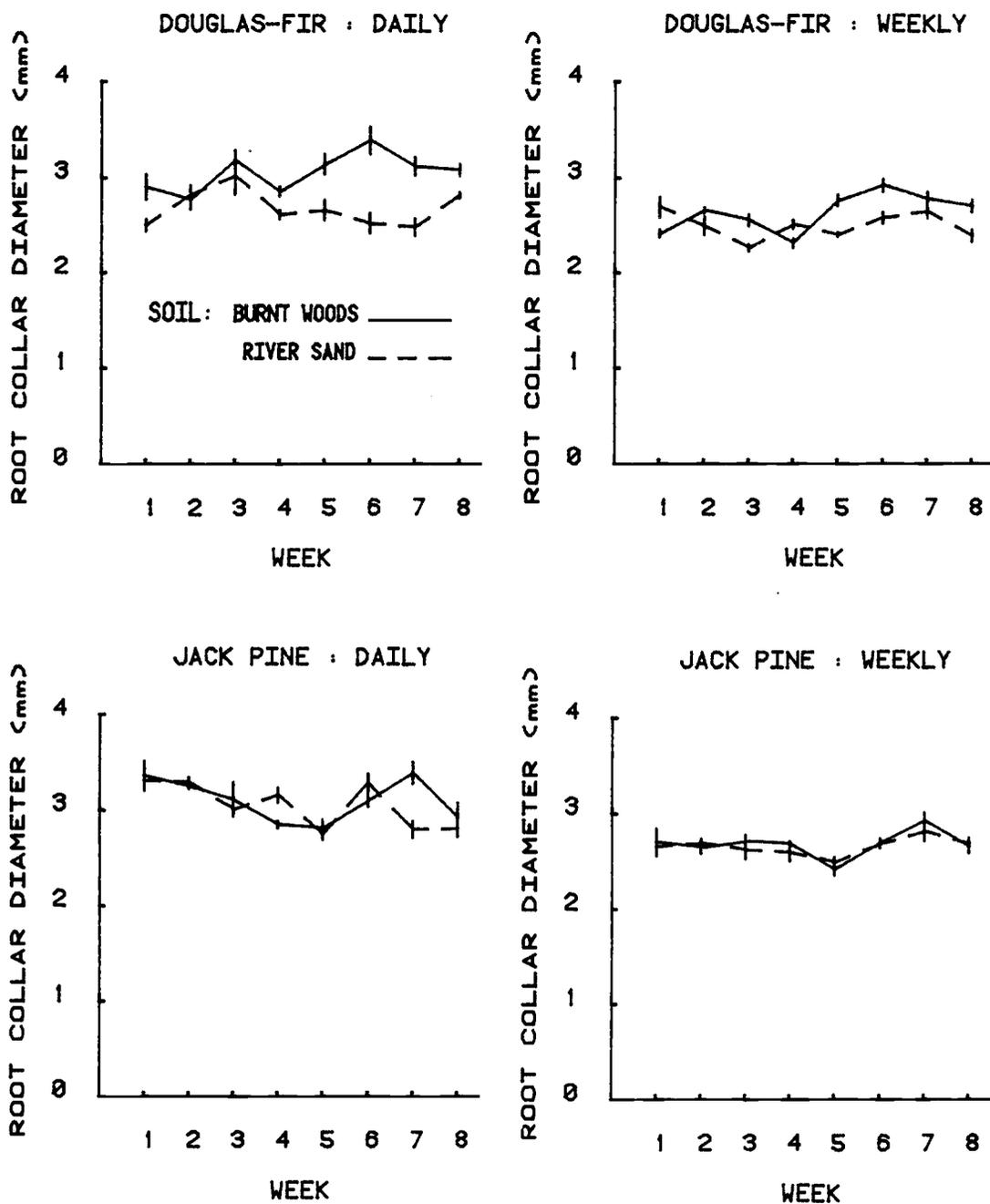


Figure 28. Progression of root collar diameters of DOUGLAS-FIR (upper graphs) and JACK PINE (lower graphs) seedlings during the nursery drought period in two soil types. Data presented by irrigation frequency averaged over KCl levels; vertical bars represent standard errors ($n = 4$).

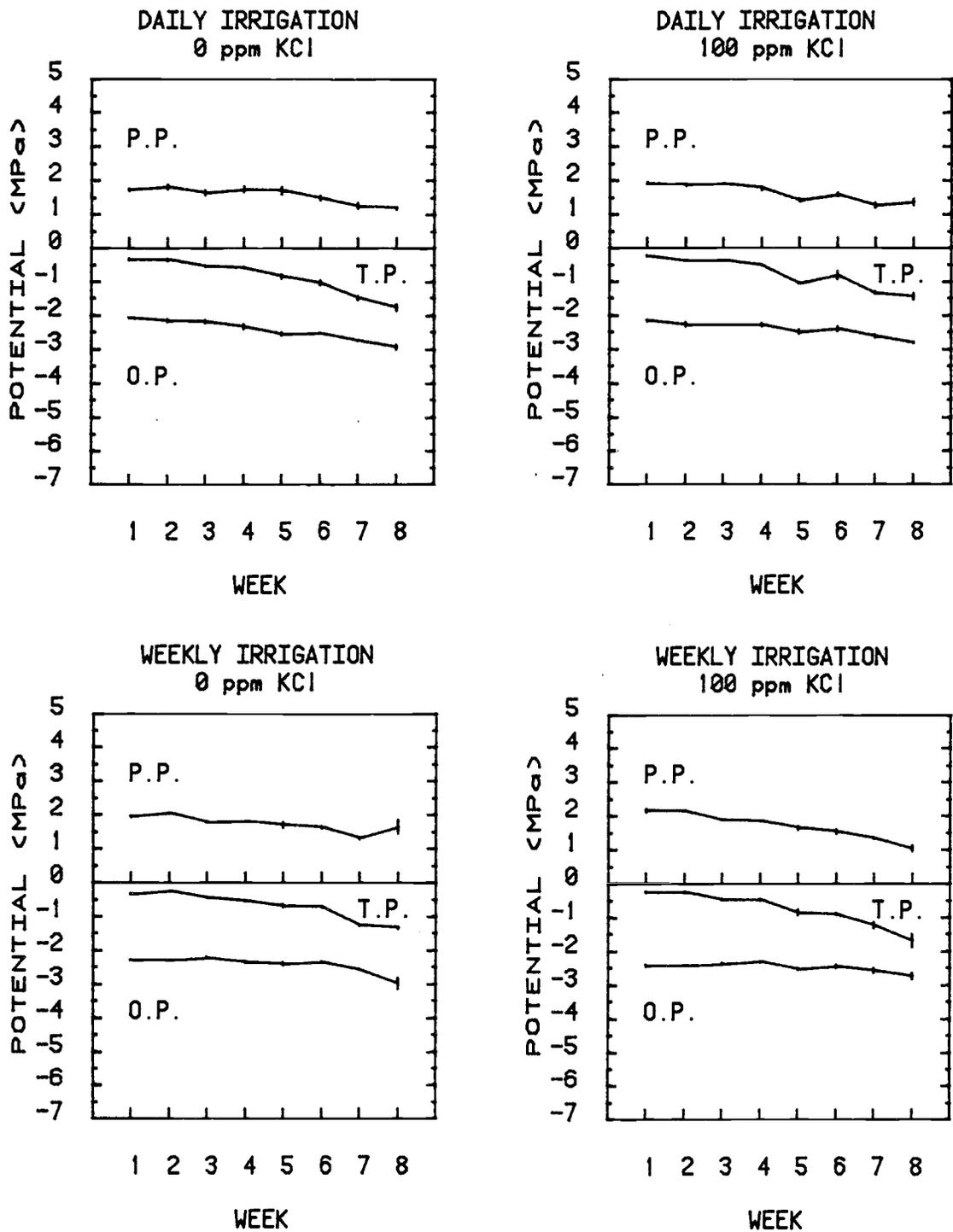


Figure 29. Progression of total water potential (T.P.), osmotic potential (O.P.), and pressure potential (P.P.) or turgor pressure of conditioned DOUGLAS-FIR during the nursery drought period on BURNT WOODS soil. Each graph is designated by conditioning treatment; vertical bars represent standard errors ($n = 2$).

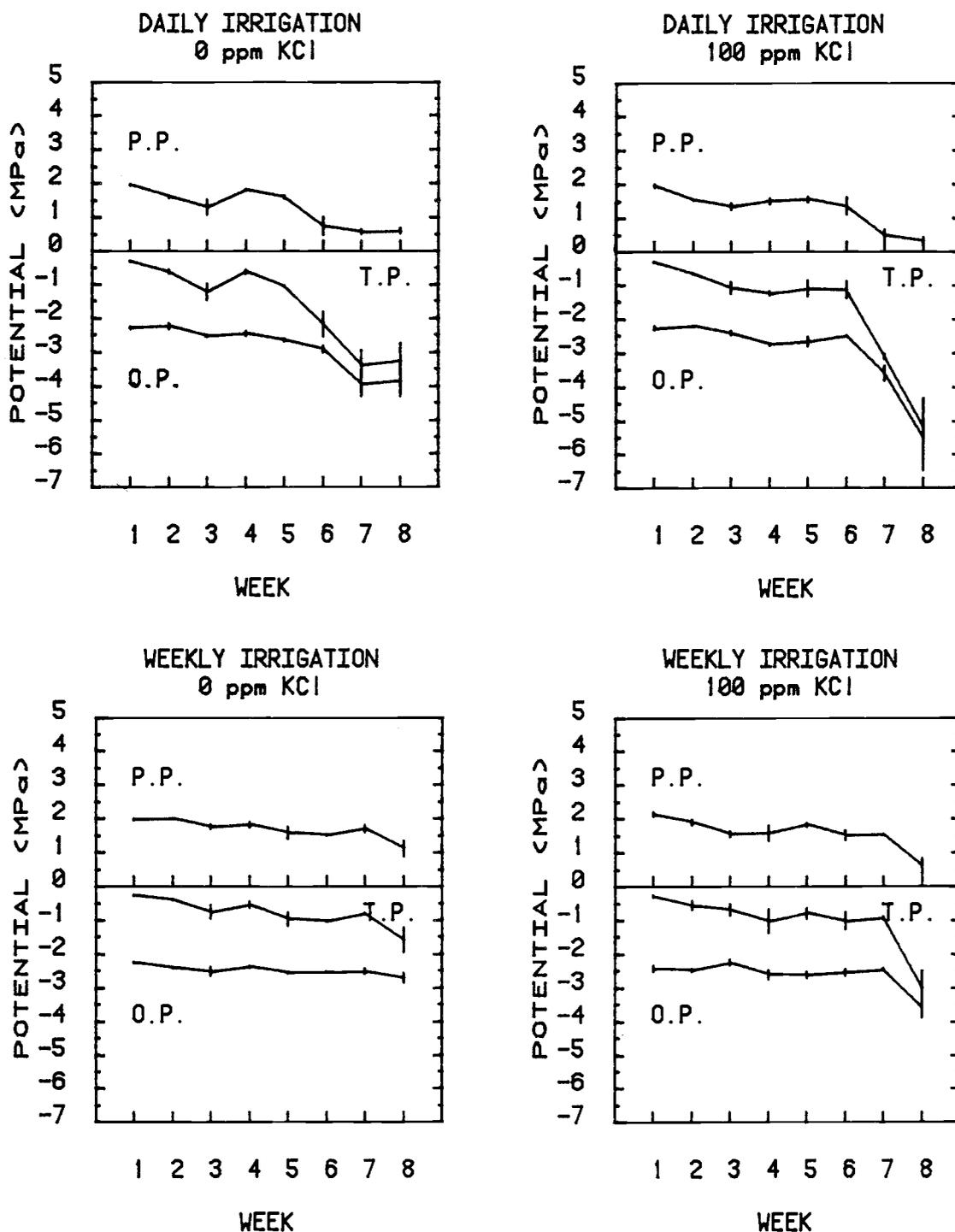


Figure 30. Progression of total water potential (T.P.), osmotic potential (O.P.), and pressure potential (P.P.) or turgor pressure of conditioned DOUGLAS-FIR during the nursery drought period on RIVER SAND soil. Each graph is designated by conditioning treatment; vertical bars represent standard errors (n = 2).

irrigation were significant and that these differences were dependent upon time (significant irrigation X time interaction) (Table B-39).

The declines in water potential of seedlings in the River Sand soil type were also gradual in the early stages of the drought period, but depending upon treatment, potentials began to decrease rapidly at various points during the drought period (Figure 30). Daily irrigated seedlings exhibited early rapid declines whereas potentials did not decrease until the last week of the drought period for weekly irrigated seedlings. On an irrigation basis (KCl levels not significant) plant water potentials of daily and weekly irrigated seedlings declined from similarly high potentials of -0.31 MPa and -0.27 MPa, respectively to -1.68 MPa and -0.91 MPa. Statistically, these differences were significant (Table B-39).

In summary, analysis of variance of plant water potential for Douglas-fir indicate highly significant differences between soil types and irrigation. Treatment effects were, however, dependent upon time during the drought period (Table B-39).

4.2.3.2.2 Osmotic potential: ψ_{π} . Osmotic potentials of Douglas-fir in Burnt Woods soil declined at a minimal rate throughout the entire drought stress period at all treatment levels (Figure 30). Initial values of osmotic potential of daily and weekly irrigated seedlings were -2.12 MPa and -2.35 MPa, respectively and declined to -2.42 MPa and -2.45 MPa (Table B-42). The minimal decline in osmotic potential reflects the low degree of stress seedlings were under throughout the stress period.

The osmotic potentials of seedlings in the River Sand soil paralleled the declines of plant water potentials during the drought stress period (Figure 30). Thus, the smallest declines in osmotic potential were associated with weekly irrigated seedlings. From initial values of -2.27 MPa and -2.34 MPa the osmotic potential of daily and weekly seedlings declined to -2.92 and -2.55 MPa respectively. Analysis of variance indicated that soil type and irrigation effects were statistically significant (Table B-39), but

these effects were dependent upon time.

4.2.3.2.3 Turgor pressure: ψ_p . Douglas-fir seedlings on Burnt Woods soil maintained turgor pressures throughout the drought stress period in excess of 1.0 MPa (Figure 29 and Table B-43). The gradual decline in turgor potential reflected the differential declines in both plant water potential and osmotic potential described under 4.2.3.2.1 and 4.2.3.2.2, respectively. Overall, weekly irrigated seedlings maintained higher turgor potentials (1.72 MPa) than daily irrigated seedlings (1.61 MPa).

Turgor pressures of Douglas-fir in the River Sand soil type fluctuated throughout the drought stress period, but consistently, turgor pressures were less than those recorded for Douglas-fir in the Burnt Woods soil type. With one exception, which may be due to anomalous data (e.g. daily irrigation: 0 ppm KCl), no significant increases in turgor pressure occurred. By analysis of variance, significant treatment effects were associated with irrigation frequency and differences over time (Table B-39).

4.2.3.2.4 Relative water content: RWC. The relative water content of Douglas-fir seedlings on Burnt Woods soil declined slowly over the duration of the drought period (Figure 31). Initially, relative water contents of daily and weekly irrigated seedlings were 94.6% and 91.7%, respectively and declined to 91.5% and 91.6%, respectively (Table B-34). Seedlings planted in River Sand soil also exhibited minimal declines in relative water contents throughout the drought stress period, except as noted in Figure 31. By the fifth and sixth week relative water content of daily irrigated seedlings declined abruptly to average terminal values of 73.5% and 65.2%. In one instance, there was also an abrupt decline in relative water content in weekly irrigated seedlings (e.g. weekly irrigation: 100 ppm KCl).

Analysis of variance indicates that significant treatment effects were associated with soil type and irrigation and that they were dependent upon time because of significant soil type X time and irrigation X time interactions (Table B-39).

4.2.3.3 Water relations: JACK PINE. The progressions of

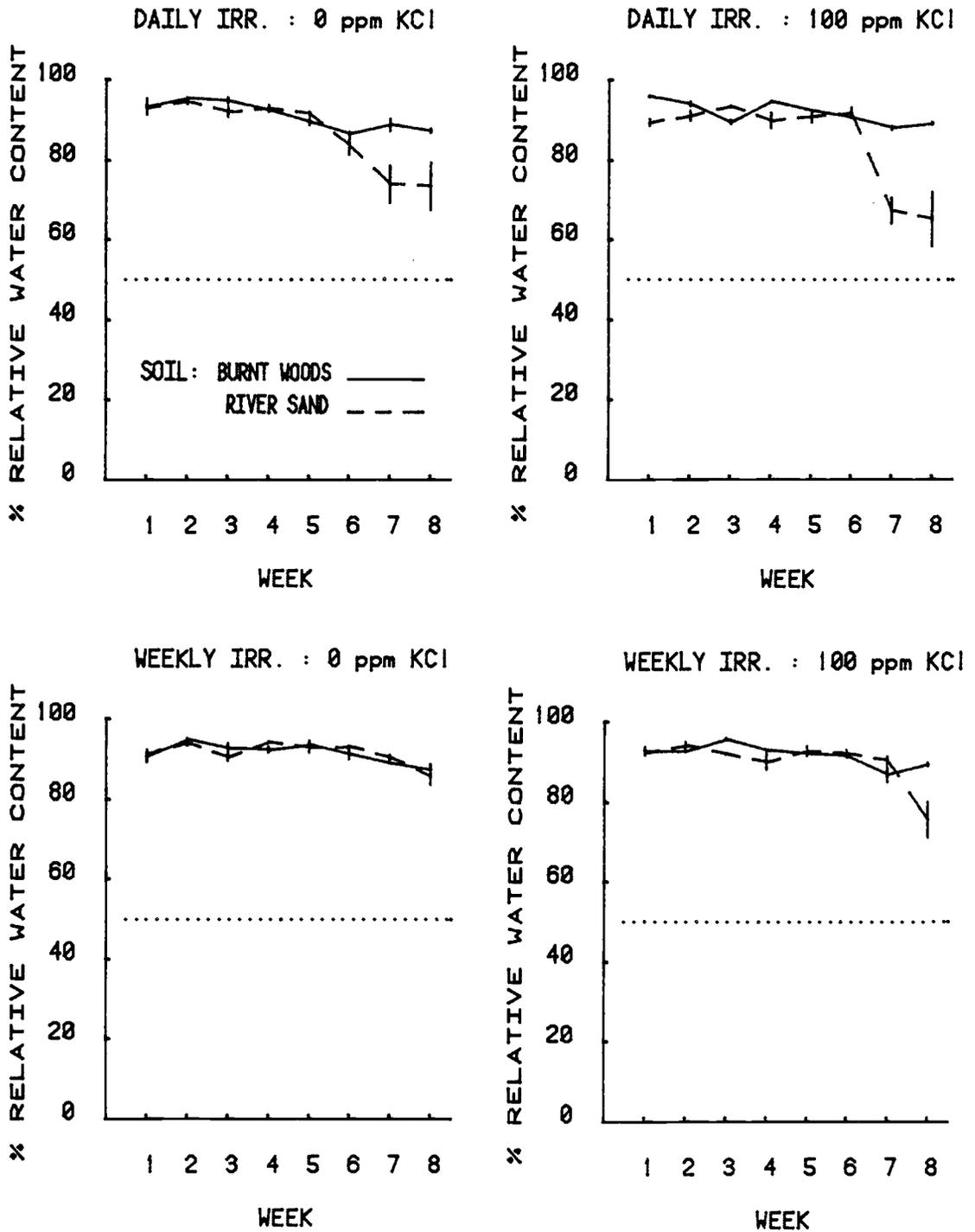


Figure 31. Progression of relative water content of conditioned DOUGLAS-FIR during the nursery drought period on Burnt Woods and River Sand soil types. Each graph is designated by conditioning treatments; vertical bars represent standard errors (n = 2).

plant water potential, osmotic potential and turgor pressure are presented in Figures 32 and 33 for Burnt Woods and River Sand soil types respectively. Analysis of variance of these parameters in relation to soil type, conditioning treatment and time is summarized in Table B-39.

4.2.3.3.1 Total water potential: ψ_T . The plant water potential of conditioned jack pine seedlings on Burnt Woods soil declined slowly and consistently throughout the drought stress period. Averaged over time and KCl levels, mean plant water potentials for daily and weekly irrigation treatments were -0.90 MPa and -0.83 MPa, respectively. Analysis of variance indicated that significant differences were due to time only (Table B-39).

Water potential of jack pine in the River Sand soil type declined more rapidly throughout the drought period than in seedlings in Burnt Woods soil (Fig. 33). Decreases in water potential, with few exceptions, began from the start of the drought period and when considered over KCl levels mean drought values for daily and weekly irrigation levels were -1.46 MPa and -1.27 MPa, respectively. Analysis of variance indicated however, that significant treatment differences were due to time only (Table B-39).

4.2.3.3.2 Osmotic potential: ψ_π . Osmotic potentials of jack pine in Burnt Woods soil declined slowly and consistently (Figure 32) and exhibited little treatment difference. Mean treatment values over time for daily and weekly irrigation were -2.13 MPa and -2.20 MPa, respectively. Osmotic potentials of jack pine in River Sand soil declined slowly during much of the course of the drought stress period. The decline became more rapid in concert with decline in total water potential. At two treatment levels, namely, Daily: 100 ppm KCl and Weekly: 100 ppm KCl, osmotic potentials decreased more rapidly than the decline in plant water potential and resulted in increased turgor pressure. Analysis of variance verified that significant differences over time occurred (Table B-39).

4.2.3.3.3 Turgor pressure: ψ_p . Only moderate

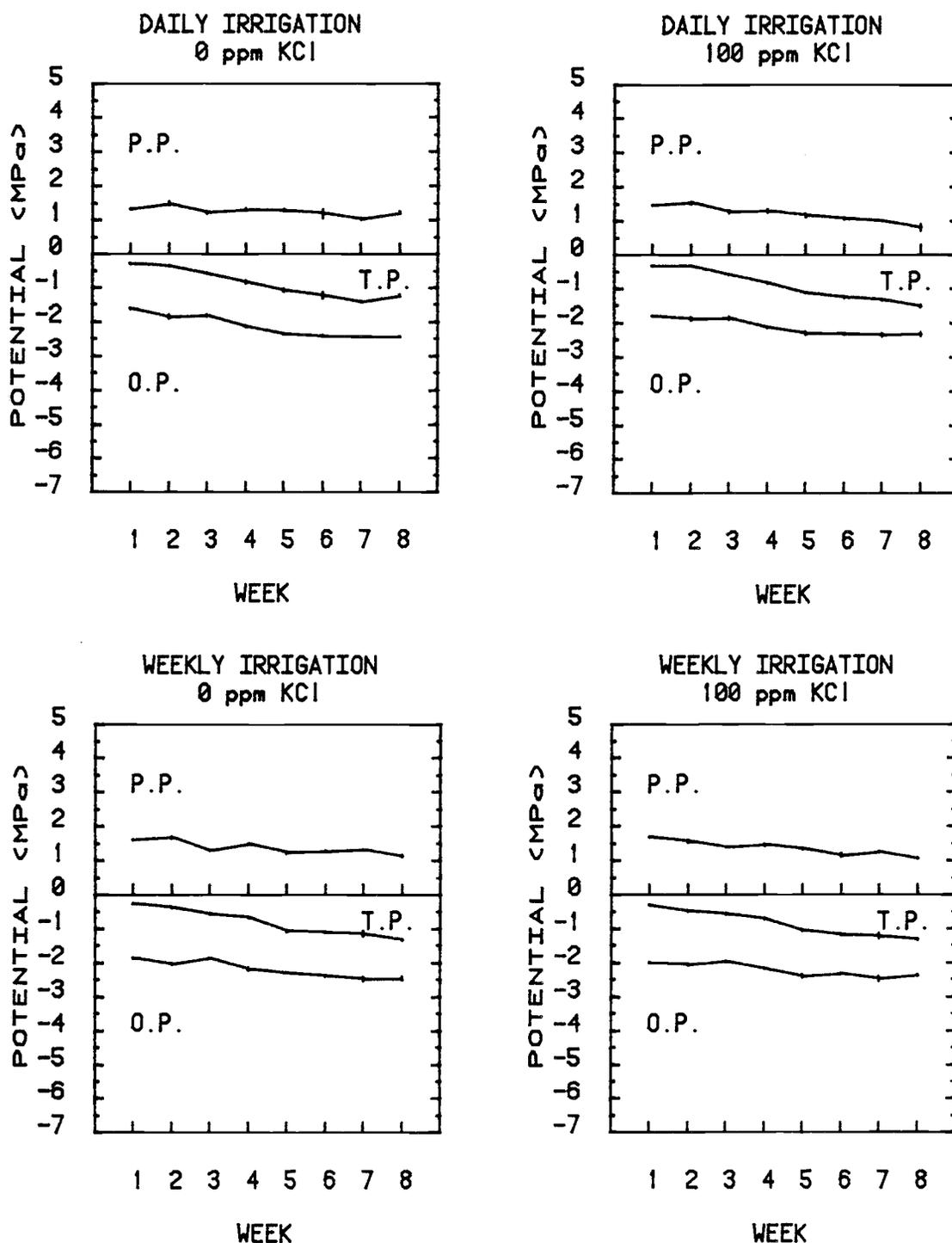


Figure 32. Progression of total water potential (T.P.), osmotic potential (O.P.), and pressure potential (P.P.) or turgor pressure of conditioned JACK PINE during the nursery drought period on BURNT WOODS soil. Each graph is designated by conditioning treatment; vertical bars represent standard errors ($n = 2$).

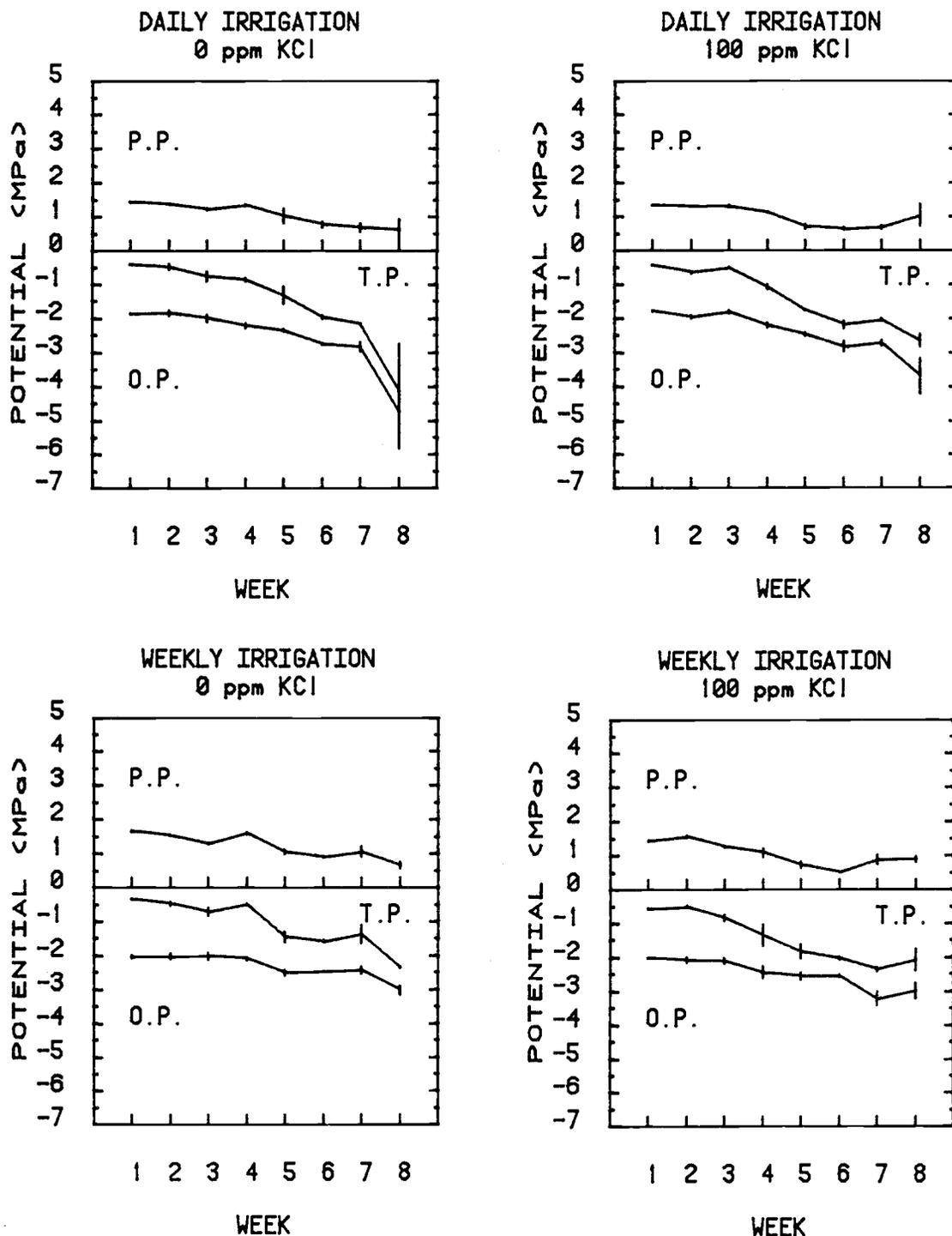


Figure 33. Progression of total water potential (T.P.), osmotic potential (O.P.), and pressure potential (P.P.) or turgor pressure (T.P.) of conditioned JACK PINE during the nursery drought period on RIVER SAND soil. Each graph is designated by conditioning treatment; vertical bars represent standard errors ($n = 2$).

declines in turgor pressure were noted for jack pine seedlings growing in Burnt Woods soil, but greater declines in turgor pressure occurred in seedlings in River Sand soil (Figures 32 and 33). Differences due to soil type were significant (Table B-39), but were dependent upon time (significant soil type X time interaction).

In only two instances in the later stages of drought stress in River Sand soil was there some indication that turgor pressure was maintained despite decreases in plant water potential. The increases in turgor were small and due entirely to decreases in osmotic potential relative to plant water potential (Table B-43). At this point, however, we have no information to discern whether the decrease in potential emanated from concentration of symplasmic water, accumulation of solutes or sampling variation.

4.2.3.3.4 Relative water content: RWC. The relative water contents of jack pine throughout the drought stress period varied dramatically with respect to soil type (Figure 34 and Table B-44). For daily and weekly irrigated jack pine in Burnt Woods soil overall drought means were similar: 81.6% and 82.0% respectively. Analysis of variance confirmed that treatment effects were not significant except those differences due to the progression of time (Table B-39).

Relative water contents of seedlings in River Sand soil remained high, initially, but as soil water deficits developed and plant water potential declined, so did relative water contents (Figure 34). Except for weekly irrigated seedlings at 0 ppm KCl marked declines in relative water contents occurred by the third or fourth week of the drought period with values of approximately 50% being recorded by week 8, the end of the experimental drought period. Mean drought values for daily and weekly irrigation treatments were 71.2% and 74.2%, respectively.

In summary, analysis of variance for jack pine indicates that none of the conditioning treatments of irrigation and KCl level significantly affected relative water contents nor were relative water contents affected by soil type.

4.2.3.4 Influence of soil type on water relations. The

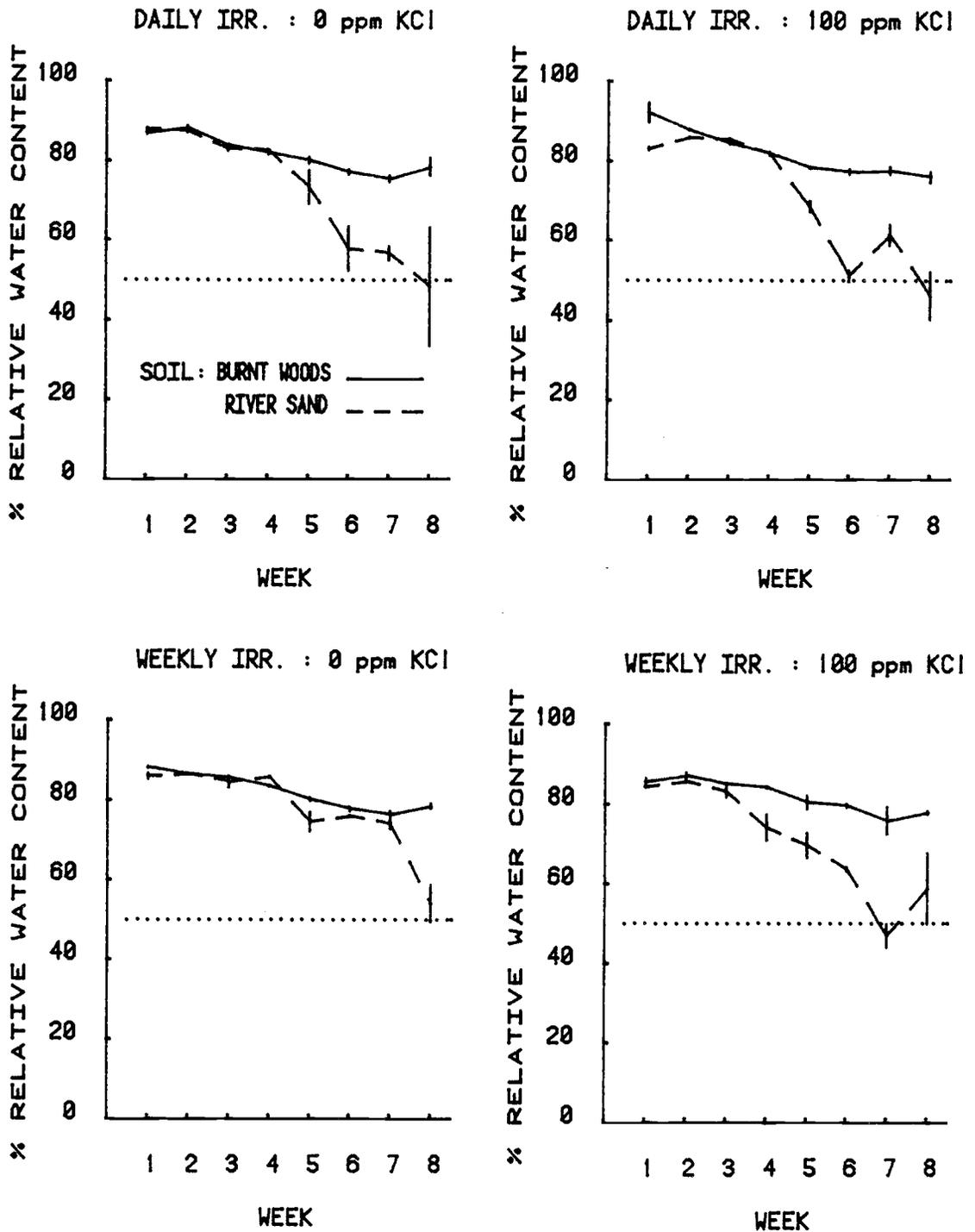


Figure 34. Progression of relative water content of conditioned JACK PINE seedlings during the nursery drought period on Burnt Woods and River Sand soil types. Each graph is designated by conditioning treatments; vertical bars represent standard errors (n = 2).

above sections, 4.2.3.2 and 4.2.3.3 presented results of soil type within species. To consider species response within soil types the reader's attention is directed to Figures 28 through 34 and Tables B-41 through B-44. Table 19 summarizes mean values of each water relations parameter over treatments and time.

Within the Burnt Woods soil type Douglas-fir maintained higher water potentials than jack pine. Moreover, turgor pressures and relative water contents were higher. Lower osmotic potentials of Douglas-fir may have facilitated higher turgor potentials and relative water contents. Analysis of variance of the water relation parameters indicated that the main order effects of species and time were the only significant factors, but were not independent of one another because of their significant interaction (Table B-40).

On River Sand soil, Douglas-fir and jack pine maintained relative differences in all parameters as previously noted for Burnt Woods soil (Table 17). Total water potential, turgor pressure and relative water contents of Douglas-fir were greater than in jack pine. Osmotic potentials were, however, lower. Analysis of variance conducted for River Sand soil suggested that for total water potential species differences were not significant. In most instances, except relative water content, factors were independent of one another in their effects on water relation parameters. The impact of soil differences on water relation parameters of Douglas-fir and jack pine are exemplified by relative water contents of the species in respective soil types: Burnt Woods: 91.5% vs 81.8% and River Sand: 88.3% vs 72.7%.

4.2.3.5 Relationships amongst water relation parameters.

4.2.3.5.1 Relative water content/Plant water potential. As might be expected from the soil water release curves (Figure 23) and water regime curves of Burnt Woods and River Sand soil types (Figures 25 and 26) the relationships between relative water content and plant water potential differ within species depending upon soil type (Figure 35 and 36). On both Burnt Woods and River Sand soil types relative water contents of Douglas-fir and jack pine declined as plant water potentials fell. However, the

TABLE 19. Means of water relation parameters averaged over treatment and sample time for DOUGLAS-FIR and JACK PINE by soil type.

Soil type	Species	Water Relation Parameter			
		Total Water Potential	Osmotic Potential	Turgor pressure	Relative water content
		----- MPa -----			%
Burnt Woods	Df	-0.768	-2.434	1.666	91.5
	Jp	-0.862	-2.164	1.302	81.8
River Sand	Df	-1.280	-2.731	1.451	88.3
	Jp	-1.361	-2.450	1.058	72.7

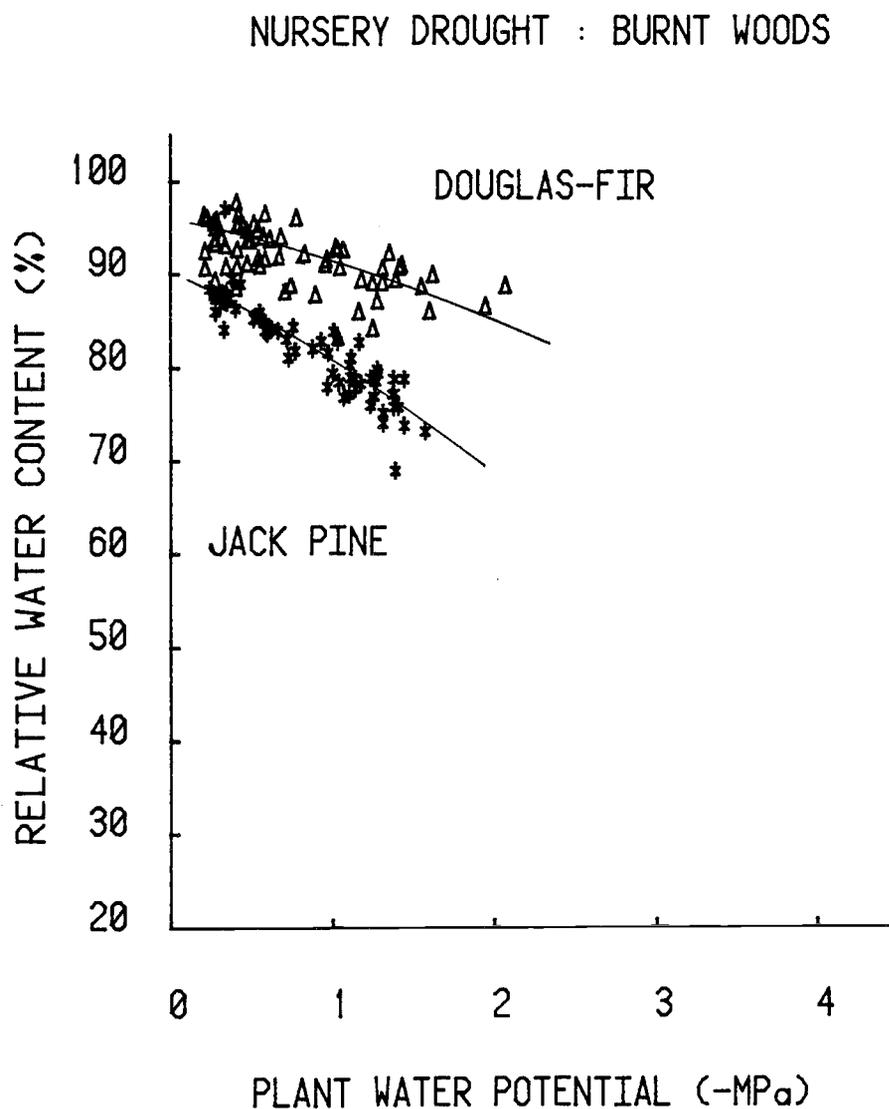


Figure 35. Relationship between relative water content and plant water potential of conditioned DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined from the nursery drought period on Burnt Woods soil and are fitted with free hand curves.

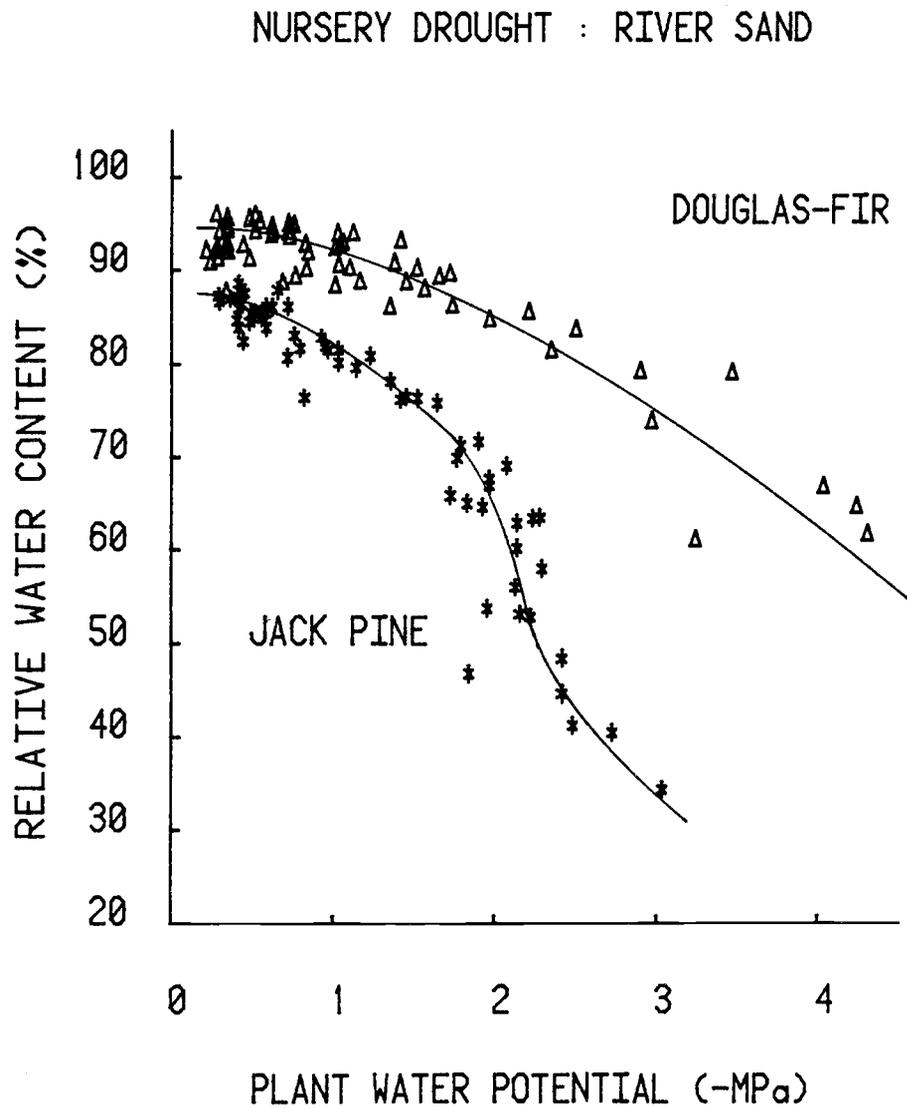


Figure 36. Relationship between relative water content and plant water potential of conditioned DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined from the nursery drought period on River Sand soil and are fitted with free hand curves.

rate and nature of the decline was dependent upon the rapidity that soil water stress developed (Figs. 35 and 36).

On both soil types Douglas-fir maintained higher relative water contents than jack pine at all plant water potentials. As soil water stress became extreme i.e. River Sand soil, plant water potentials in Douglas-fir continued to decline gradually, whereas in jack pine water potentials declined rapidly at values lower than ca 1.7 MPa.

4.2.3.5.2 Relative water content/Osmotic potential.

The relationships between relative water content and osmotic potential on Burnt Woods and River Sand soils clearly shows that at any osmotic potential the relative water content of Douglas-fir is at least 10% higher than for jack pine (Figs. 37 and 38). As osmotic potentials fall the difference becomes greater.

For River Sand soil the relationships are initially similar at osmotic potentials above -2.5 MPa, but below this potential the relationships extended to lower relative water contents and osmotic potentials. Clearly, Douglas-fir rather than jack pine, exhibited a greater capacity to maintain lower osmotic potentials, and higher relative water contents as soil water deficits increased. The critical point for jack pine appears to be approximately -2.0 MPa osmotic potential because at values lower than this relative water contents decline more rapidly.

4.2.3.5.3 Plant water potential/Osmotic potential.

In Burnt Woods soil osmotic potentials of Douglas-fir at any plant water potential are lower than jack pine and thereby exhibit higher turgor pressures (reflected by the vertical distance above the 1:1 line (Fig. 39). However, turgor pressure in Douglas-fir declines more rapidly than in jack pine.

In the more rapidly developing drought conditions of the River Sand soil the relationships are curvilinear (Fig. 40). Douglas-fir maintains higher initial turgor pressures than jack pine, but a plant water potentials of about -1.7 MPa are reached a differential decline in osmotic potential results in an increase in turgor pressure. Douglas-fir seedlings exhibited no similar decline

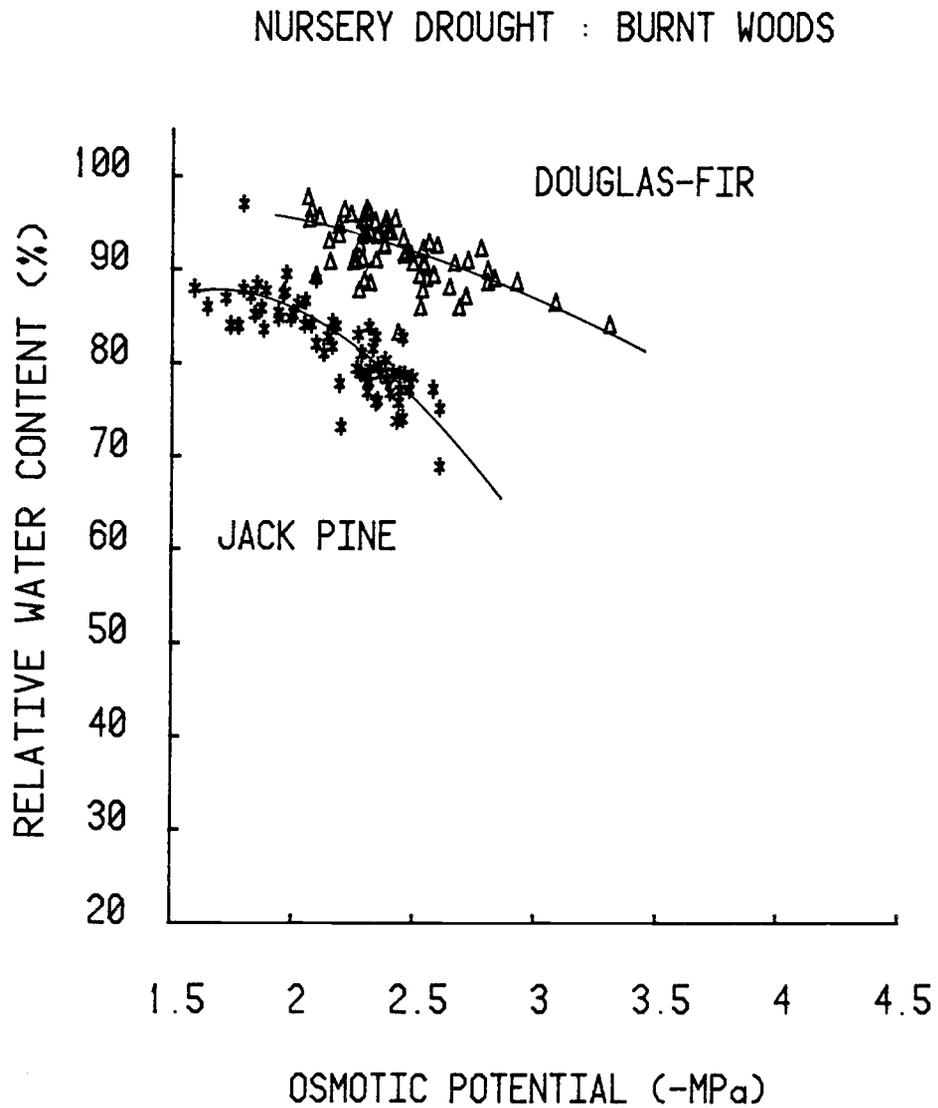


Figure 37. Relationship between relative water content and osmotic potential of conditioned DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined from the nursery drought period on Burnt Woods soil and are fitted with free hand curves.

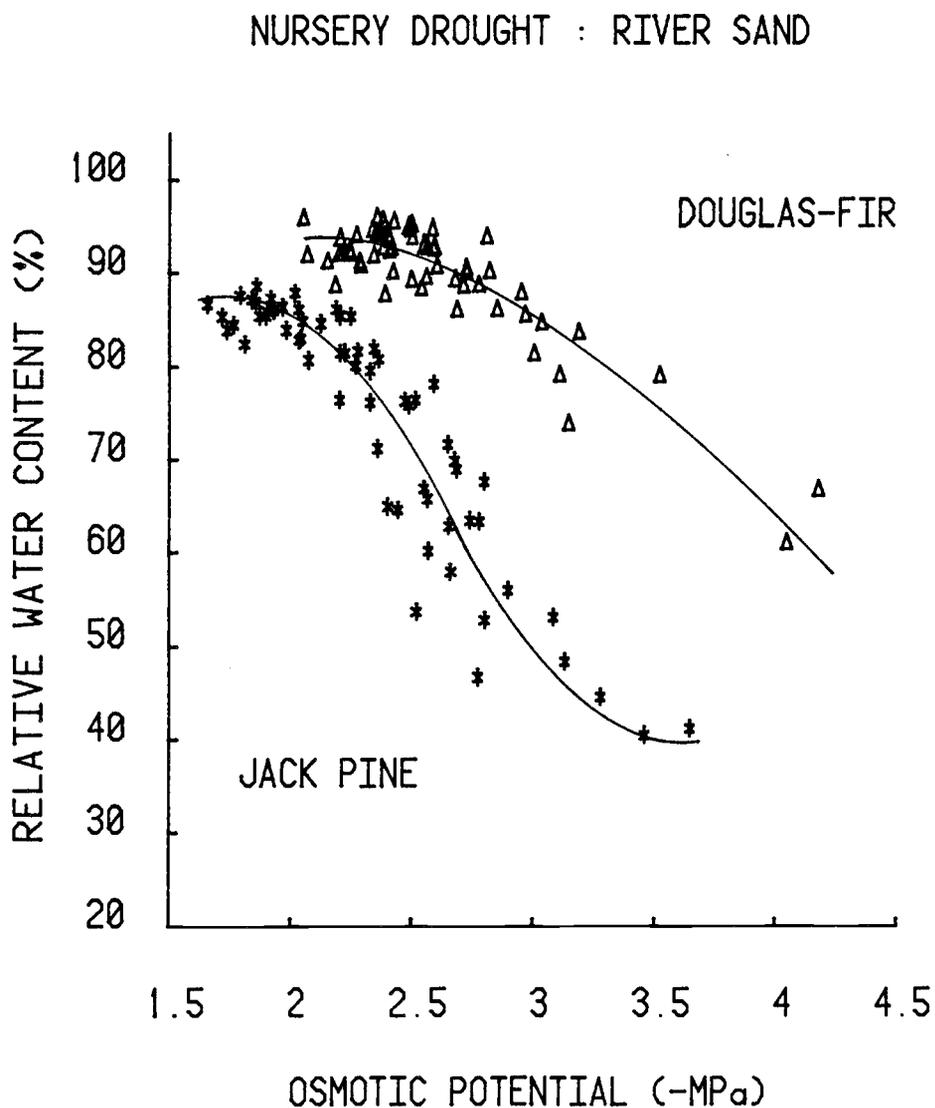


Figure 38. Relationship between relative water content and osmotic potential of conditioned DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined from the nursery drought period on River Sand soil and are fitted with free hand curves.

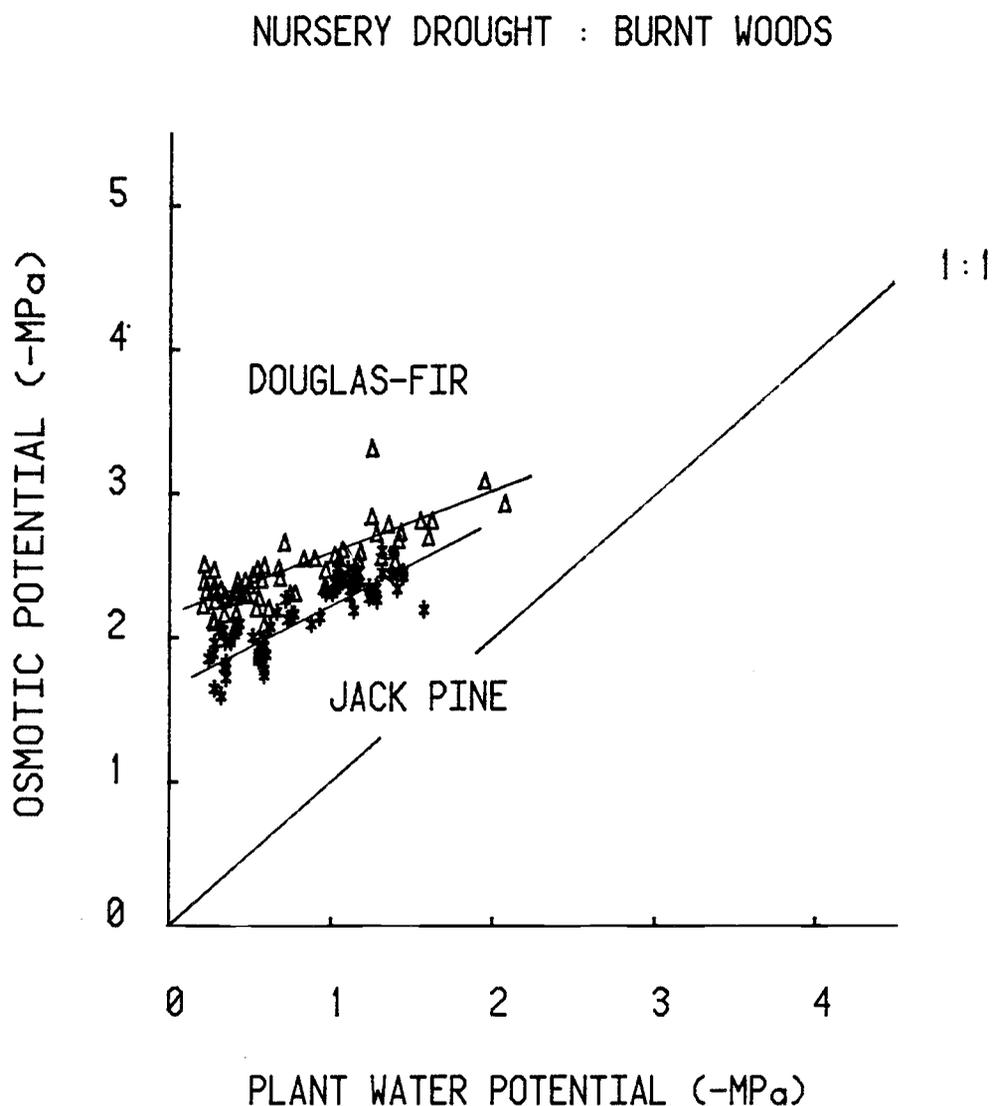


Figure 39. Relationship between osmotic potential and plant water potential of conditioned DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined from the nursery drought period on Burnt Woods soil and are fitted with free hand curves. The 1:1 line represents the potential state of zero turgor pressure.

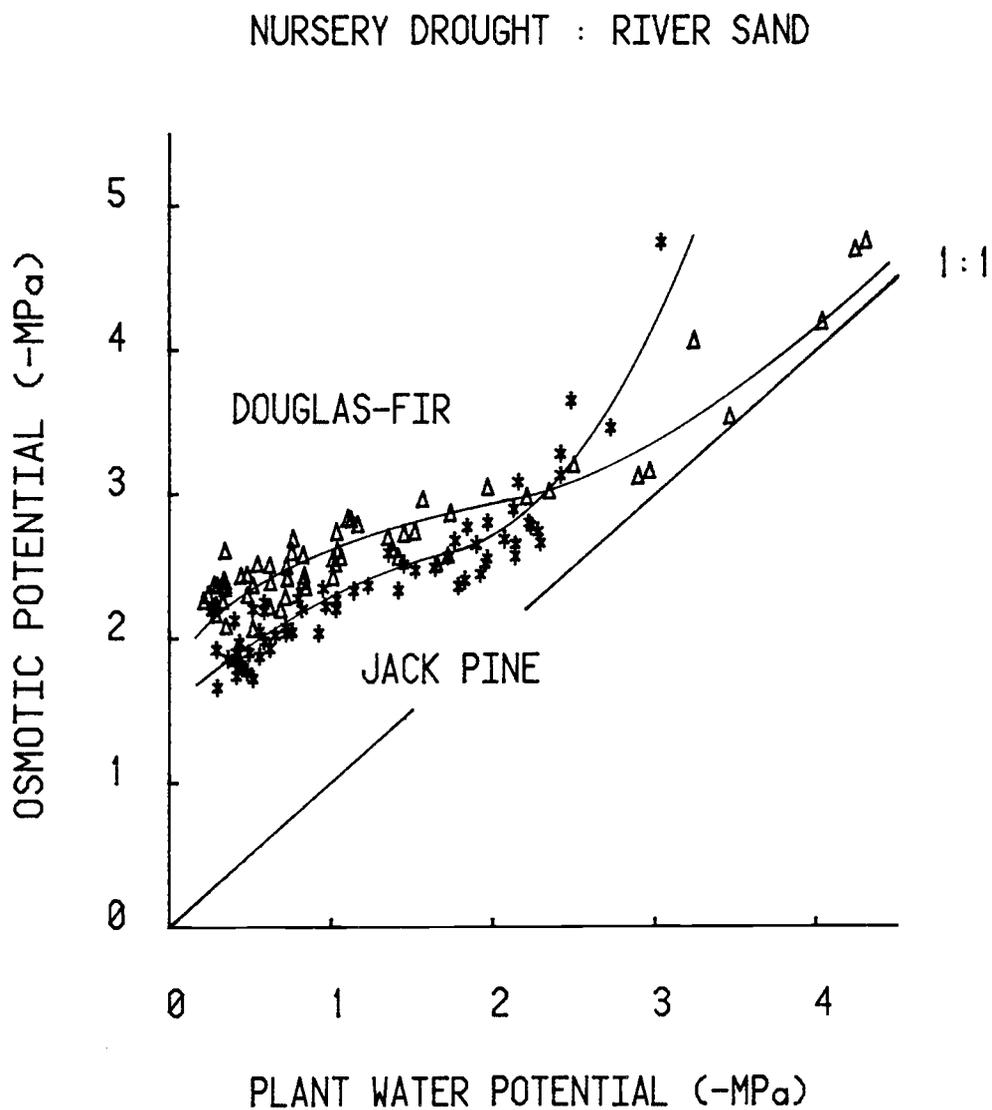


Figure 40. Relationship between osmotic potential and plant water potential of conditioned DOUGLAS-FIR (triangles) and JACK PINE (stars) seedlings. All data are combined from the nursery drought period on River Sand soil and are fitted with free hand curves. The 1:1 line represents the potential state of zero turgor pressure.

in osmotic potential, therefore, equilibration likely occurred at about -3.0 MPa.

4.2.3.6 Pressure-volume parameters. Pressure-volume relationships were determined on four occasions during the field drought stress period between July 2, 1984 and August 20, 1984. Specifically, 32 seedlings were randomly selected from treatments within replications on each sample date and analysed during the weeks of July 2, July 23, August 6, and August 20, 1984. The first sampling date, prior to planting, required that only 16 seedlings be selected. In total, 112 pressure-volume curves were determined during the field drought experiment.

Analysis of variance of each estimated parameter was conducted, but since the first sample involved 16 seedlings it was excluded from analysis. Therefore the summaries of analyses for Douglas-fir and jack pine incorporate assessments of the three latter runs only (Tables B-45 and B-46, respectively). Mean values by species, soil type and time of assessment are presented in Table 20. In both Douglas-fir and jack pine, significant treatment effects at the main order level were rarely detected, except for differences of most parameters when time was included in the analysis (Tables B-45 and B-46).

4.2.3.6.1 Osmotic potential at full turgor, OPFT (-MPa). Regardless of soil type OPFT in Douglas-fir and jack pine did not change significantly throughout the drought period (Tables 20, B-45 and B-46). Differences between species were, however, markedly different on both soil types.

4.2.3.6.2 Osmotic potential at zero turgor, OPZT (-MPa). As soil water deficits increased in Burnt Woods OPZT significantly decreased from -2.42 MPa to -2.74 MPa (Table B-45). Although there was an apparent decline in OPZT in jack pine (-2.30 MPa to -2.45 MPa) it was not statistically significant. In River Sand soil, neither Douglas-fir nor jack pine exhibited significant declines in OPZT.

4.2.3.6.3 Relative water content at turgor loss point, RWC @ TLP. Statistically, RWC @ TLP in Douglas-fir and jack

TABLE 20. Summary of mean water relation parameters determined by the pressure volume technique on four sampling dates for DOUGLAS-FIR and JACK PINE seedlings during a nursery drought period on two soil types.

Soil type	PV Sp.	Run	RWC @				Ra	ME @	Dry Wt.	WSFT
			OPFT	OPZT	TLP	RSWC @		.995 RWC	Turgid Wt.	
			--- MPa ---				MPa			
Burnt Woods	Df	1	1.97	2.55	0.84	0.77	0.29	13.25	0.30	1.67
		2	1.96	2.42	0.86	0.81	0.27	13.74	0.29	1.74
		3	2.07	2.59	0.86	0.80	0.29	16.59	0.38	1.39
		4	2.08	2.74	0.84	0.76	0.34	8.66	0.32	1.31
	Jp	1	1.49	2.09	0.80	0.59	0.49	1.50	0.28	1.35
		2	1.54	2.30	0.76	0.67	0.28	1.78	0.30	1.76
		3	1.56	2.35	0.77	0.67	0.30	1.50	0.31	1.57
		4	1.61	2.45	0.76	0.66	0.30	1.08	0.31	1.53
River Sand	Df	1	1.91	2.55	0.84	0.77	0.29	13.25	0.30	1.67
		2	2.00	2.42	0.86	0.82	0.18	16.88	0.27	2.17
		3	2.18	2.67	0.86	0.82	0.22	16.57	0.31	1.67
		4	1.80	2.63	0.83	0.68	0.46	6.70	0.30	1.18
	Jp	1	1.49	2.09	0.80	0.59	0.49	1.50	0.28	1.35
		2	1.54	2.29	0.76	0.67	0.27	2.31	0.29	1.81
		3	1.51	2.31	0.78	0.65	0.36	1.01	0.29	1.56
		4	1.43	2.35	0.75	0.61	0.36	1.08	0.30	1.52

pine was not significantly affected by any treatment nor did it vary significantly over time regardless of soil type (Tables 20, B-45 and B-46). Douglas-fir and jack pine in both soil types exhibited similar values for RWC @ TLP on both soil types e.g. 0.85 and 0.77, respectively.

4.2.3.6.4 Relative symplasmic water content at turgor loss point, RSWC @ TLP. Mean values of RSWC @ TLP for Douglas-fir and jack pine were similar on both soil types (Table 20). Analysis of variance indicated that irrigation was significant only in jack pine, but in both species differences in RSWC @ TLP changed significantly over time (Tables B-45 and B-46).

4.2.3.6.5 Relative apoplasmic water content, Ra. In both Douglas-fir and jack pine Ra varied significantly over the drought period (Tables B-45 and B-46). In Douglas-fir on both Burnt Woods and River Sand soil types, Ra increased from 0.27 to 0.34 and from 0.18 to 0.46, respectively. There was, however, no significant difference between soil types.

In jack pine, the increases in Ra over time were less than that previously reported for Douglas-fir e.g. 0.28 to 0.30 on Burnt Woods soil and 0.27 to 0.36 on River Sand soil.

4.2.3.6.6 Modulus of elasticity at near full turgor, ME @ .995 RWC (MPa). Statistically, ME @ .995 RWC in jack pine was not affected by any treatment effect or time; but varied significantly with time in Douglas-fir (Tables 20, B-45 and B-46). The most notable aspects of the data are the large values of ME @ .995 RWC for Douglas-fir on both soil types relative to those of jack pine; differences are in the order of 9 fold. Attention is directed to the dramatic decrease in ME @ .995 RWC in Douglas-fir detected for the last pressure-volume assessment.

4.2.3.6.7 Ratio of sample dry weight to fresh weight. In Douglas-fir sample dry weight relative to its fresh weight was not significantly affected by any treatment over time (Table B-45). Soil type differences significantly affected this ratio in jack pine, but values did not vary significantly over time (Table 20).

4.2.3.6.8 Ratio of weight of symplasmic water at full turgor to sample dry weight. The weight of symplasmic water at full turgor relative to sample dry weight in Douglas-fir was significantly affected by soil type and time (Tables 20 and B-45), and in jack pine values of this ratio varied significantly only over time (Table B-46). It is clear from the data presented in Table 20 that the ratio of WSFT/Dwt, first increased, then decreased from initially high values in both Douglas-fir and jack pine. Declines over time probably reflect the progression of lignification of sample tissue and differential partitioning of cellular water as the drought stress period progressed.

4.2.4 Progression of seedling physiology during drought stress. All seedlings within each replication and treatment were evaluated weekly and subjectively categorized as to their state of health. Seedling mortality was also recorded on the survival plots (32 seedlings per treatment). Assessments began during the fifth week of the drought period before there was any visible decline in seedling health status.

4.2.4.1 Seedling health condition. The progressive decline in the health status of survival plot seedlings of Douglas-fir and jack pine during the drought stress period are indicated in Tables 21 and 22, for Burnt Woods and River Sand soil types, respectively, by treatment level. The decline in health condition began to emerge by the seventh week of the drought stress period. Initially, seedlings responded by exhibiting discoloration of foliage (green to pale yellow). Advanced stages of decline in seedling health status were evidenced by incipient wilting, then severe wilting and browning of foliage at which point seedlings were considered to be dead.

Distinct differences in health condition occurred between seedlings on the contrasting soil types. Douglas-fir seedlings on Burnt Woods soil were in good overall condition, exhibiting only isolated occurrences of foliage discoloration. However, the health condition of seedlings on River Sand soil declined rapidly. The health condition of daily irrigated Douglas-fir exhibited a tendency

TABLE 21. Weekly progression of the average physiological state of conditioned DOUGLAS-FIR and JACK PINE seedlings growing in Burnt Woods soil during a period of increasing soil water deficits.

		1 Date / Physiological Code																													
		5/8					12/8					19/8					26/8					2/9					9/9				
Sp.	Treat- ment	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
	2																														
Df	DO	*					*					*					*					*					*				
	D100	*					*					*					*					*					*				
	WO	*					*					*					*					*					*				
	W100	*					*					*					*					*					*				
Jp	DO	*					*					*					*					*					*				
	D100	*					*					*					*					*					*				
	WO	*					*					*					*					*					*				
	W100	*					*					*					*					*					*				

1

Physiological Code:

1 excellent condition

2 good condition with some discoloration

3 incipient wilting with discoloration

4 wilted appearance, leaves wrinkled

5 mortality, foliage wilted, light brown

2

Treatment description:

DO : Daily irrigation and 0 ppm KCl

D100 : Daily irrigation and 100 ppm KCl

WO : Weekly irrigation and 0 ppm KCl

W100 : weekly irrigation and 100 ppm KCl

TABLE 22. Weekly progression of the average physiological state of conditioned DOUGLAS-FIR and JACK PINE seedlings growing in River Sand soil during a period of increasing soil water deficits.

		1 Date / Physiological Code																													
		5/8					12/8					19/8					26/8					2/9					9/9				
Sp.	Treat- ment	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
	2																														
Df	D0	*				*					*					*					*					*					*
	D100	*				*					*					*					*					*					*
	W0	*				*					*					*					*					*					*
	W100	*				*					*					*					*					*					*
Jp	D0	*				*					*					*					*					*					*
	D100	*				*					*					*					*					*					*
	W0	*				*					*					*					*					*					*
	W100	*				*					*					*					*					*					*

1

Physiological Code:

1 excellent condition

2 good condition with some discoloration

3 incipient wilting with discoloration

4 wilted appearance, leaves wrinkled

5 mortality, foliage wilted, light brown

2

Treatment description:

D0 : Daily irrigation and 0 ppm KCl

D100 : Daily irrigation and 100 ppm KCl

W0 : Weekly irrigation and 0 ppm KCl

W100 : Weekly irrigation and 100 ppm KCl

to decline more rapidly than weekly irrigated seedlings; no similar distinction could be made for level of KCl. For jack pine, there was early indication of a more rapid decline in the health condition of daily irrigated seedlings, but by the last assessment date (9/9) all treatment levels had shown evidence of seedling mortality.

4.2.4.2 Seedling mortality. The occurrence of mortality varied depending upon species and soil type (Table 23). Mortality in Douglas-fir on Burnt Woods soil occurred in daily irrigated seedlings at 0 ppm KCl and weekly irrigated seedlings at 100 ppm KCl. Jack pine exhibited no mortality regardless of conditioning treatment on Burnt Woods soil.

On River Sand soil seedling mortality was much greater than observed on Burnt Woods soil. Highest mortality by September 9, 1984 in Douglas-fir was confined to seedlings conditioned by daily irrigation and, in jack pine, mortality counts were nearly identical for irrigation conditioning treatments.

The dependence of seedling mortality on conditioning treatment was assessed by evaluating the hypothesis that seedling mortality was independent of irrigation and KCl by Chi-square analysis. Analyses were conducted by species for each soil type and are summarized in Table 24. With respect to the hypothesis that mortality was independent of irrigation in Douglas-fir it would be accepted for Burnt Woods soil but rejected for River Sand soil at $P = 0.05$.

The hypothesis was accepted for jack pine in River Sand. Examination of the data (Table 23) reveals that mortality in jack pine on River Sand soil was uniformly high by the last sample date (i.e. September 9, 1984). An extreme point in seedling physiology had been exceeded and precluded any benefit due to conditioning treatments from being portrayed. The above hypothesis was, therefore, reevaluated using data from the September 2, 1984 (9/2) assessment. Indeed, the analysis strongly indicated (Table 24) that there is sufficient evidence to reject the hypothesis and accept the alternative, that jack pine seedling mortality on Burnt Woods soil was dependent upon irrigation conditioning. In only one instance

TABLE 23. Mortality counts (replications combined) of DOUGLAS-FIR and JACK PINE seedlings located in treatment survival plots (32 seedlings per treatment) by soil type and date of assessment.

Treatment		Soil type / Sample Date											
		Burnt Woods						River Sand					
Sp. Irrig. KCl.		5/8	12/8	19/8	26/8	2/9	9/9	5/8	12/8	19/8	26/8	2/9	9/9
Df	Daily	0	1	1	1	2	6	1	1	1	1	4	14
	100	0	0	0	0	0	0	0	0	1	7	12	21
	Weekly	0	0	0	0	0	0	0	0	1	1	3	10
	100	1	1	2	2	5	11	0	0	1	1	3	7
Jp	Daily	0	0	0	0	0	0	0	0	0	2	9	20
	100	0	0	0	0	0	0	0	1	3	6	15	25
	Weekly	0	0	0	0	0	0	0	0	0	0	0	21
	100	0	0	0	0	0	0	0	0	0	2	5	26

TABLE 24. Summary of Chi-Square analysis (probabilities) conducted to test hypotheses associated with the independence of mortality in irrigation and level of applied KCl.

Hypothesis	Species	Soil type	
		Burnt Woods	River Stand
Irrigation	Df	0.1661	0.0017
	Jp	No mortality	0.6960 (>.001 2/9)
KCl	Df	0.1949	0.4796
	Jp	No mortality	0.0495

did potassium chloride increase seedling mortality e.g. jack pine in River Sand soil (Table 24).

5. DISCUSSION

A seedling plant is not a simple organism. Their complexity is underlined when we consider the intricate nature of response mechanisms that plants exercise during periods of stress. The physiology of drought stress is not well understood, but research clearly shows that modifications to drought stress mechanisms can occur to enhance drought resistance (Turner, 1979). In agronomic situations this may translate into increased yield and in forestry, it may increase the probability of seedling survival on droughty sites.

At no time in the life of a seedling is the ability to maintain favorable water relations more important than after planting. It is crucial that sufficient water be absorbed to maintain physiological processes necessary for growth since these processes are diminutively affected by small increases in water stress at relatively high water potentials e.g. -0.2 MPa (Hsiao, 1973). This underlines the importance of available water during the period of early seedling establishment. It is inevitable however, that once seedlings are placed in the ground their water potential will decline in the face of soil moisture deficits. Without recovery at night, further declines in water potential may lead to irreversible physiological damage and eventual seedling death. During drought stress, seedlings must develop resistance to declines in water potential while maintaining physiological integrity. Alternatively, they must initiate root growth at low water potentials to increase absorptive capacity and mitigate drought stress. There is clear evidence to suggest that many conifer seedlings can tolerate drought (e.g. Ferrell and Woodard, 1966; Kaufmann, 1979), but there is also much speculation as to whether conifer seedlings possess the ability to effect drought resistance mechanisms e.g. osmotic adjustment to maintain growth during periods of soil water deficits. Furthermore, there have been only few studies that have dealt specifically with this question in relation to conditioning practices.

The present research was conducted under the hypothesis that

Douglas-fir and jack pine seedlings can be conditioned by irrigation and nutrition to enhance their response to drought stress, and the results clearly support this hypothesis from a number of standpoints. The discussion of the results, presented by experiment, will focus upon supporting evidence, anomalies and implications to the establishment process.

5.1 Growth Room Experiment

5.1.1 Conditioning responses. Conditioning seedlings to enhance their adaptive ability to drought can be manifested by morphological and physiological changes (Bradford and Hsiao, 1982). In the present study, seedlings subjected to irrigation and nutritional conditioning demonstrated distinct morphological and nutritional differences (Table 4). Daily irrigated Douglas-fir and jack pine seedlings were larger than weekly irrigated seedlings. Top:root ratios of daily irrigated seedlings were 44 and 22 percent larger than weekly irrigated Douglas-fir and jack pine seedlings, respectively. Since root weights did not differ significantly within species it might be assumed that differences in top:root ratios were due entirely to changes in shoot dry weight. Indeed, it was observed that daily irrigated seedlings exhibited luxuriant growth with long needles and presumably, much greater evaporative surface area than weekly irrigated seedlings. Hermann (1964) confirmed that under water stress conditions in the field, seedlings with large tops exhibit greater mortality than seedlings with small tops. However, he conceded that the quality of the root system i.e. its degree of root fibrosity is perhaps the real determinant in seedling survival (also see Clarke, 1975). Conditioning seedlings did not induce marked differences in root areas. This suggests that weekly irrigating did not induce sufficient stress (-0.54 vs -1.24 MPa) to prompt increased root growth as suggested by Acevedo and Hsiao (1974) for annual crops. Alternatively, root mortality was not sensitive to recurrent stress during conditioning. Marshall and Waring (1985) provided some preliminary evidence to support the contention that fine root mortality may not be a direct and immediate result of drought, but from a depletion of carbohydrates.

The application of 100 ppm KCl did not alter any aspect of seedling morphology that might have some benefit during drought stress (B-12). K concentrations were higher in foliage and roots of daily irrigated seedlings than in weekly irrigated seedlings and regardless of plant part was not dependent upon level of applied KCl. Potassium was adequately supplied during the common production period through fertilization, therefore, seedlings exhibited little differential absorption to levels of applied KCl. Chlorine concentrations, on the other hand, were significantly affected by the level of applied KCl, and higher concentrations of Cl^- were consistently observed in roots than in the foliage. The nutrient data (Table 5) suggest that Douglas-fir and jack pine exhibit differential absorption of Cl^- . For example, in unamended soil Cl^- concentrations in tops and roots in jack pine are higher than in Douglas-fir, but in amended soils the reverse was true.

Although K has been unequivocally implicated in stomatal function (Raschke, 1975; Humble and Raschke, 1971), so has Cl^- , but to a lesser degree. The requirement of most plants for Cl^- during photosynthesis and cell enlargement is very low, but accumulation of Cl^- obviously occurs in roots when concentrations are relatively high in the soil. In such instances, Cl^- may be employed as an important component of the osmotica for the maintenance of turgor during periods of drought stress (Cutler and Rains, 1978; Mengel and Kirkby, 1982) or for normal functioning in some plants (von Uexkull, 1984).

5.1.2 Responses to drought stress. One day before seedlings were placed in the drought environment all were well irrigated to bring the rooting medium to a state of maximum water holding capacity. Evaluation of water potentials of both species at the start of the drought period revealed no significant differences due to conditioning treatments, however, species differed significantly: -0.81 MPa vs -0.40 MPa for Douglas-fir and jack pine, respectively. Whether or not significant differences due to conditioning treatments should be detected at the outset of the drought stress period is unclear. It may be argued that if conditioning treatments

alter seedling water relations the effects would not be apparent until the seedlings begin to experience water stress. Any species difference prior to stress, therefore, may reflect inherent physiological differences with respect to internal water balance at high soil water levels. It is frequently observed that conditioning by drought stressing causes reductions in osmotic potentials at full turgor relative to well watered controls (Kandiko et al., 1980; Cutler et al., 1977) and that low osmotic potential ought to confer a large measure of drought resistance (Tyree, 1976). It was revealed by analysis of variance that only irrigation conditioning significantly affected osmotic potential in both species (Table B-15). Consistently, weekly irrigated Douglas-fir and jack pine seedlings exhibited lower osmotic potentials than daily irrigated seedlings providing differentials of 0.20 MPa and 0.32 MPa, respectively. Apparently, however, osmotic potentials of stressed and non-stressed seedlings need not differ at full turgor. Observations on cotton plants in a growth chamber revealed that at full turgor osmotic potentials were similar, but during the development of stress water potentials at zero turgor were lower in stressed plants at zero turgor than in non-stressed plants (Ackerson and Hebert, 1981). Similar observations were recorded by Joly (1984) in irrigated and stressed Douglas-fir seedlings. At the start of an experimental drought period Joly (1984) noted that osmotic potentials were similar between the two groups of Douglas-fir seedlings, but as soil water deficits increased osmotic potentials of non-irrigated seedlings declined to lower levels than those of irrigated Douglas-fir.

In contrast, the present results show that in both species, osmotic potentials at near full turgor were lower in weekly irrigated seedlings than daily irrigated seedlings e.g. Douglas-fir weekly vs daily: -1.38 vs -1.12 MPa; jack pine weekly vs. daily: -1.21 vs -0.83 MPa (Table B-16). Moreover, higher relative water contents were distinctly associated with Douglas-fir and weekly irrigated seedlings within species (Table B-17). The significance in achieving lower osmotic potentials in conditioned plants during

drought stress is that the plant can incur lower water potentials before turgor pressures are reduced to zero. If root growth is maintained at lowered osmotic potentials the plant will achieve increased absorptive capacity to possibly mitigate the stress.

Soil water contents were generally above 50 percent at the start of the first drought period in the growth room, but rapidly declined to low levels (7 percent) after five days. Plant water potentials declined accordingly, but differences between species were not significant. This was somewhat unexpected because of apparent differences in root structure (Fig. 7) and leaf surface area between species. By visual inspection, jack pine seedlings possessed greater surface area than Douglas-fir, and therefore was expected to transpire more water than Douglas-fir and develop lower water potentials.

Lopushinsky (1969) evaluated stomatal function in terms of transpiration and found that pine species were relatively sensitive to increasing leaf water stress. Sensitivity of Douglas-fir was intermediate. Moreover, the relative leaf turgidities at which stomata closed in lodgepole pine (like jack pine) were approximately 82 percent and for Douglas-fir 85 percent, values which corresponded to leaf water potentials of -1.5 MPa and -1.9 MPa, and soil water contents of 7.5 percent and 7.0 percent, respectively. Given this information and in consideration of the present results of the first drought period, Douglas-fir at 100 ppm KCl, within each irrigation treatment, did not reach leaf water potentials of -1.9 MPa until later in the drought period compared to 0 ppm seedlings (Fig. 9). Jack pine presumably closed stomata earlier than Douglas-fir as leaf water potentials fell to -1.5 MPa prior to the fifth experimental day, with one exception (Fig. 10). The present results support the rating in species sensitivity to stress given by Lopushinsky (1969) and Jarvis and Jarvis (1963). Moreover, within each species, stress conditioning may have delayed attainment of the threshold leaf water potential for stomata closure. Values of relative turgidities reported by Lopushinsky (1969) for stomatal closure are supported by

the present data except by daily irrigated jack pine which exhibited relative water contents of approximately 70 percent at a leaf water potential of -1.5 MPa.

Weekly irrigated seedlings exhibited altered water relations compared to well watered controls. Further difference was variously attributable to the application of KCl. To explore the broad relationships amongst water relation parameters, data were grouped by species. The evidence presented in Figure 9, 10 and 11 together with existing research data suggest that jack pine has perhaps greater tolerance to soil water deficits than Douglas-fir. However, consideration of Figures 12, 13 and 14 provides clear evidence to question this notion, if not reject it altogether. Douglas-fir demonstrated a distinct advantage over jack pine in the conservation of water during drought stress; osmotic potentials of Douglas-fir were always less than those of jack pine at similar relative water contents. Based on these data, Douglas-fir would be expected to reach zero turgor at a lower water potential than jack pine. This is essentially confirmed by parameters determined from pressure-volume curves (Table 8) in which the water potential at zero turgor (equivalent to osmotic potential at zero turgor, OPZT) of Douglas-fir and jack pine were determined, on the average, to be -2.44 MPa and -1.61 MPa, respectively.

These values of water potential at zero turgor are difficult to reconcile with data presented in Figure 13 in which the relationship between osmotic and water potential for Douglas-fir and jack pine is presented. In the zone of positive turgor (i.e. above the 1:1 line) jack pine rapidly approached zero turgor. At a water potential of approximately -1.7 MPa there was an abrupt decline in osmotic potential relative to water potential resulting in an apparent increase in turgor pressure. This aspect is exemplified in daily irrigated jack pine seedlings (Figure 10).

A rapid decline in osmotic potential suggests an increase in solute concentration during drought, a phenomenon which has been observed in many species (Turner and Jones, 1980). According to Turner (1979) and Radin (1983) solute concentration may increase in

plant tissue during drought principally by 1) net solute accumulation which would be considered indicative of osmotic adjustment, 2) dehydration and attendant decrease in cell volume, and 3) simple dehydration without a decrease in cell volume.

Values of modulus of elasticity (Table 8) in Douglas-fir decreased during the drought period from a high of 14.70 MPa to a low of 4.39 MPa. This suggests that as water loss occurred cell walls and tissues became more elastic and shrank to enclose a smaller volume of water of increasing solute concentration. Apparently, this did not occur until after the fifth day of drought stress as solute potentials of Douglas-fir seedlings, regardless of conditioning treatment, remained stable during this period (Fig. 9). Declines in osmotic potential during the latter part of the drought period occurred in concert with declines in modulus of elasticity.

In jack pine, elastic properties of cells and tissues increased during early drought stress from 1.96 MPa to 3.14 MPa, then decreased to 1.01 MPa. These values are considerably lower than values recorded for Douglas-fir and other species (Joly, 1984; Tyree et al., 1978). From the outset of drought stress, osmotic potentials decreased rapidly as relative water content declined (Fig. 11). These data suggest that the principal response of jack pine to declines in water potential and relative water content is for cells to shrink to enclose a decreasing symplasmic water volume. The resultant decrease in osmotic potential relative to declines in total water potential lead to apparent increases in turgor pressures (Fig. 10).

In a strict sense (Turner and Jones, 1980), neither species can be said to have undergone osmotic adjustment. Joly (1984) found no evidence to suggest that osmotic adjustment operates in Douglas-fir seedlings subjected to drought stress. Both irrigated and stressed seedlings exhibited reduction in osmotic potentials at full and zero turgor. These declines, however, could not be unequivocally attributed to active accumulation of solutes because of simultaneous declines in the modulus of elasticity (cell walls became more elastic).

Buxton et al. (1985) followed the response of three boreal conifer seedling species during a 12 day drought period. Although variability was present, osmotic adjustment was considered to have occurred within 24 to 48 hours of the initiation of the drought. They noted, however, that relative turgidities of all three species fell while pressure potentials remained at or above control levels. No explanation was offered in this respect. Maintenance of turgor pressures can be achieved in the short run with declines in relative turgidity as long as the elasticity properties of the cell walls permit an attendant decrease in cell volume. Since estimates of tissue elasticity were not recorded by Buxton et al. (1985) the occurrence of true osmotic adjustment is questionable.

Whether or not the decline in osmotic potential is due to osmotic adjustment or simply to dehydration is perhaps less important as long as turgor pressures are maintained above a lethal threshold level. Throughout the drought period turgor pressure of Douglas-fir steadily declined to a low point then levelled off. None of the conditioning effects was found to be significant (Table B-13). Jack pine declined in a similar fashion to Douglas-fir, but after 5 to 8 days of drought exposure turgor pressures increased. This was due almost entirely to rapid declines in osmotic potential, presumably by dehydration.

Assuming that turgor pressures were above threshold levels for cell extension at the outset of the stress period epicotyl growth might be expected to occur. No evidence was obtained to support this (Fig. 6). However, increases in root area and root dry weight were noted. We may not assume that turgor pressures in leaf and root tissue are similar. It is possible that declines in root turgor were minimized if decreases in osmotic potential occurred because of increasing concentrations of K and Cl^- during drought stress (Table 9). K and Cl^- are considered to be important components of osmotica (Morgan, 1984) and turgor maintenance in roots has been observed in various species (Gracean and Oh, 1972; Osonubi and Davies, 1978; Malik et al., 1979). Kandiko et al. (1980) studied the water relations of roots and suggested that the

water potential in roots has a distinctly different relationship to water loss than observed in shoots. Apparently roots are able to remain turgid with minor loss of water, whereas, shoots lose turgor pressure exponentially (in the absence of osmotic adjustment).

Clearly, seedlings responded differentially to drought stress depending upon their prestress history and this has been borne out in many research studies. Few studies, however, have considered the response of seedlings to recurrent water stress after a period of relief. If studies are conducted over a full growing season, the water relation responses can be confounded by ontogenic effects (Joly, 1984). In studies conducted over shorter time periods, as in the present study, confounding effects are negligible.

After stress relief, living seedlings were again subjected to a second drought stress. As in the first stress cycle water loss from the soil, primarily by seedling transpiration, was rapid (Fig. 15). Initially, transpiration by jack pine was greater than Douglas-fir, but was not consistent throughout the drought period. Water losses were initially greater in jack pine and may suggest that stomatal opening in Douglas-fir was delayed.

Several theories have been forwarded to explain this phenomena with residual abscisic acid being the most tenable one e.g. Mansfield and Davies (1984). Apparently, at the onset of stress abscisic acid accumulates in leaf tissue, perhaps initiated by a decrease in turgor pressure and affects the K transport system into guard cells. The return of favorable water relations does not necessarily cause rapid increase in ABA catabolism. In fact, elevated levels of ABA may remain in guard cells for several days, thereby diminishing the rate of stomata opening. Although this is only speculative, the water potential isotherms of Douglas-fir (Fig. 17) and jack pine (Fig. 18) clearly indicate that initially, a slower rate of decline in water potential occurred in the former than in the latter as exposure to drought continued. Slow rates of decline in water potential were also more persistent in weekly irrigated (or stressed) seedlings than in daily irrigated seedlings.

Jack pine exhibited a consistent decline in water potential, but during the later stages of stress development water potentials remained higher than those of Douglas-fir. Reasons for higher water potentials in jack pine during the latter part of the drought period are not clear. It is probable that stomatal control had all but ceased, and also that absorption from the soil medium during night time was insufficient for Douglas-fir to recover from low water potential. Figure 7 illustrates that jack pine possessed greater root fibrosity and, therefore, may have possessed a greater capacity to absorb water at low soil water contents.

With increasing drought stress osmotic potentials declined, gradually causing a concomitant decline in turgor pressure. In two instances, osmotic potentials equilibrated with total water potential, and turgor pressures fell to zero. Continued declines in osmotic potential (e.g. weekly watered Douglas-fir at 100 ppm KCl) were due to dehydration and the rapid increase in turgor pressure was probably an artifact of the method. Modulus of elasticity increased slightly in Douglas-fir, but then declined at the termination of the drought period. Whether the changes in the modulus of elasticity in Douglas-fir significantly affected the tissue water relations is difficult to ascertain. Statistical analysis did not reveal any change in the elastic modulus due to treatment over time (Table 12). The decrease in osmotic potential of Douglas-fir at full turgor observed during the drought stress (.29 MPa) may be due to an accumulation of solutes and would suggest the occurrence of osmotic adjustment.

The modulus of elasticity of jack pine, which was in the order of 5 fold lower than in Douglas-fir, did not appear to be significantly affected by either of the conditioning treatments during the second drought stress period (Table B-30). Furthermore, osmotic potentials at full turgor pressure were not significantly affected by conditioning treatment, but changed significantly during the progression of the drought period. The specific response to drought stress exhibited by jack pine, in contrast to Douglas-fir, is suggested to involve loss of osmotic water and attendant

decreases in cell size. The highly elastic cell walls of jack pine, relative to the inelastic cell walls of Douglas-fir would, in theory, allow for passive accumulation of solutes as the volume of osmotic water decreased (Radin, 1983). In some species, dehydration and accumulation of solutes can lead to the maintenance of turgor pressure. This response is tentatively proposed to have occurred in jack pine.

In our attempt to isolate mechanisms which govern the water relations of conditioned plants during drought stress consideration must be given to not only the effects of the conditioning treatments, but also to the immediate effect of the 10 day drought stress and recovery period. When compared at similar exposure times i.e. 10 days, seedlings of the second drought exposure maintained markedly higher relative water contents than those seedlings of the first drought (Table 25). Higher total water potentials were also associated with higher relative water contents. Since seedlings were subjected to similar stress conditions during both stress periods seedlings may have experienced metabolic and/or physical alterations which permitted slow rates of decline in relative water content and plant water potential.

It was alluded to earlier that ABA may persist in previously stressed leaf tissue, thereby limiting gaseous exchange despite the restoration of favorable water relations. The 10 day stress relief period between the first and second drought exposures may have provided insufficient time for ABA levels to fully dissipate. Elevated ABA levels during the second drought exposure period might, therefore, be expected to result in increased resistance to transpirational losses.

Exposure to drought stress is also known to promote lignification and cell wall thickening, processes which may provide the basis for increase apoplasmic water content. No significant increases in apoplasmic water content were observed in either species at any treatment level in the growth room experiment. The relative apoplasmic water content was greater in jack pine (0.45) than in Douglas-fir (0.31). It was put forward by Gaff and Carr (1961) that

TABLE 25. Comparative relative water contents and total water potentials of DOUGLAS-FIR and JACK PINE seedlings in first and second drought periods after 10 days of stress development.

Species	Treat ¹ ment	Parameter / Drought stress			
		Relative Water Content		Plant Water Potential	
		1	2	1	2
		----- % -----		----- -MPA -----	
Douglas-fir	D0	78.1	87.8	2.08	1.58
	D100	77.6	90.8	2.14	1.60
	W0	89.1	90.8	1.64	1.56
	W100	88.3	93.8	1.65	1.14
Jack pine	D0	62.4	70.0	1.51	1.20
	D100	62.5	71.0	2.34	1.32
	W0	73.1	80.5	1.53	1.10
	W100	70.9	78.1	1.51	1.22

1

Treatment designation

D0: Daily irrigation/0 ppm KCl

D100: Daily irrigation/100 ppm KCl

W0: Weekly irrigation/0 ppm KCl

W100: Weekly irrigation/100 ppm KCl

cell walls may contain a high proportion of cell water e.g. 40 percent in Eucalytus globosus, and that this water may act as a buffer against water loss from the protoplasts. Structural alterations of cell walls have been recognized to occur in plants growing in arid environments (Maximov, 1929; Stocker, 1960) or subjected to water stress (Cutler et al., 1977). In the present study anatomical examination of tangential and radial cell wall thickness in stems and morphology of leaf cross-sections failed to reveal any alterations that might be attributed to conditioning treatments.

Estimates of osmotic water (relative to dry weight) did not appear to change significantly over time within treatments and species (Table 12). Heiner and Lavender (1972) also failed to detect any differences in needle structure amongst Douglas-fir seedlings of several seed sources that had been exposed to drought stress. Additional evidence to support that drought stress conditions of the growth room did not cause response in water relations due to cellular alterations is provided by the lack of significant changes in the volume of osmotic water (relative to dry weight) and dry weight per unit fresh weight (Table 12). Had the drought stress conditions caused changes in cellular dimensions it would be reflected by changes in these parameters.

A comparison of the relationship between relative water content and plant water potential (Fig. 20) will reveals that the decline in plant water potential per unit decline in relative water content was larger in Douglas-fir than in jack pine. These relationships differ markedly with the same relationships determined in the first drought period (Fig. 12). It is often suggested that larger declines in water potential per unit decline in relative water content reflects drought tolerance (Jones et al., 1981). A greater decline in plant water potential would maintain a larger gradient between the leaf and soil allowing for greater absorption of water for transpiration as soil water content declines. Osmotic potentials were also lower at all relative water contents in Douglas-fir than in jack pine as stress increased (Fig. 21). In jack pine, osmotic potentials at near full turgor were similar in both stress periods, but as

relative water content declined osmotic potentials exhibited a slow rate of decline per unit decrease in relative water content.

The differential declines in osmotic potential of Douglas-fir and jack pine with respect to relative water content provide further evidence to suggest that Douglas-fir actively accumulated solutes during drought stress. This response is consistent with species that exhibit osmotic adjustment.

It is worthwhile to point out an apparent anomaly between estimates of osmotic potential at zero turgor (OPZT). Based upon pressure-volume curve analysis (Table 12) OPZT for Douglas-fir and jack pine are -2.64 MPa and -2.01 MPa, respectively. From Figure 22 OPZT is not well defined for either species. Determination of osmotic potential by the cell sap method and the applied correction factor possibly underestimated (made more negative) the true osmotic potential. The rapid decrease in osmotic potential in jack pine relative to plant water potential is particularly curious. This phenomenon would, according to equation [2.1.4], result in an increase in turgor pressure. However, observations of foliage during the drought stress period gave no indication that turgor increased. Tyree and Dixon (1983) noted minor rehydrations of green tissues after reaching an initial minimum water potential of about -2.0 MPa. They hypothesized that the source of water was from cavitated tracheids. Further experimentation by Dixon *et al.* (1984) confirmed this hypothesis. The increase in turgor inferred from Figures 14 and 22 may have been due to the influx of water from the stem as cavitation of tracheids occurred. If this occurred, the relative water content of the foliage would be expected to increase. At some treatment levels, decreases in the rate of decline in relative water content of species' foliage occurred (Figs. 11 and 19), but provided no definitive support for the occurrence of an increase in symplasmic water during the apparent increase in turgor pressure portrayed in Figures 14 and 22. Should, however, the seedling foliage rehydrate by means of water derived from cavitated tracheids it is expected that any benefits would be transient because cavitation causes a large attendant increase in resistance

to water flow in the xylem. Cavitation would also have the effect of retarding, if not preventing, the further movement of water to the foliage.

Growth of various plant components have been reported to increase in size or dry weight during development of drought stress e.g. in leaves (Fereris et al., 1978; Cutler et al., 1977) and in roots (Gracean and Oh, 1972; Sharp and Davies, 1979). Usually, this phenomenon is explained by turgor maintenance or by decreases in solute potential. Root area indices provided the only indication of growth during the development of drought stress (Fig. 16). Marked differences were apparent between Douglas-fir and jack pine. Within species, root area indices of weekly irrigated seedlings exhibited growth at lower soil water contents and plant water potentials than daily irrigated seedlings. Whether or not these increases can be also explained by turgor maintenance remains speculative without direct evaluation. Cutler et al. (1977) noted the importance of K as a component of osmotica, but found that in leaf tissue its concentration did not vary diurnally, but basic sugars, citrate and malate were concluded as being of primary importance. If root growth in the present study was a result of turgor maintenance because of solute accumulation, the differential concentrations of Cl^- in both species at the two irrigation levels would lend support to this hypothesis. It is also possible, however, that Cl^- simply accumulated in the roots during drought and did not provide a major source of osmoticum for decreases in the osmotic potential of root cells for turgor maintenance and growth.

The effect of stress history on plant response to drought is obviously complex. It has been clearly shown that RWC/water potential curves shifted in the right direction to explain differences in water relations recorded during the first and second drought stress periods. The basis for this shift in the isotherm is has not been unequivocally ascertained, but findings from other research suggest that the response may be a composite effect of many factors. Structural alterations have been discounted as a significant factor in the present research. Although foliage was

not analyzed, the root nutrient data indicate that mean concentrations of seedlings undergoing the second drought were, in the main, lower than the first drought seedlings (Table 14). If nutrient concentrations respond in a typical fashion in the foliage one might conclude that enhanced water relations of seedlings exhibited during the second drought stress are due primarily to factors other than nutrition. Other researchers e.g. Wilson and Ludlow (1983) and Buxton et al. (1985) also found no evidence of enhancement of water relations by the application of specific nutrients. However, Jensen (1981a) showed that osmotic adjustment induced by uptake of inorganic ions at the outset of water stress helped to maintain turgor and reduce dehydration and wilting in bean plants. The lack of consistent results suggests that further research in this area should be undertaken.

5.1.3 Recovery from drought stress. It is important that conditioning treatments do not impair the ability of a droughted plant to respond when soil water is restored to higher levels. The recovery process is obviously complicated as it involves all physiological processes. Most research reveals that recovery is not immediate, but is a process that continues for varying lengths of time depending upon rate of stress development (Jones and Rawson, 1979) and extent of the stress (Begg and Turner, 1976).

In the first drought period the rate of decline of total water potential was greater in jack pine than in Douglas-fir (Table B-14) and within species, it was greater for daily irrigated seedlings than weekly irrigated seedlings. It might be expected that less complete recovery would be exhibited by jack pine versus Douglas-fir and for daily vs weekly irrigated seedlings. Indeed, the mortality of jack pine exceeded that of Douglas-fir at Day 2 of the recovery period (Table 10). Mortality in both species was confined to daily irrigated seedlings. No mortality was recorded for weekly irrigated seedlings regardless of species and KCl level. These data clearly demonstrate an apparent early advantage of Douglas-fir over jack pine in resisting the effects of drought stress, and that stress conditioning enhances the ability of seedlings to survive drought.

Little change was noted by the fourth sample day and for all weekly irrigated seedlings complete recovery occurred; all seedlings were observed to be turgid. Sanchez-Diaz and Kramer (1973) observed that when corn and sorghum recovered from drought, leaf water potentials did not return to prestress levels, but were 35 to 25 percent lower in corn and sorghum, respectively. After seven days Douglas-fir failed to achieve prestress levels of water potential i.e. -0.81 vs -0.65 MPa, but jack pine exceeded the prestress levels by 0.03 MPa (i.e. -0.40 vs -0.43 MPa).

The effects of the second drought stress on mortality were dramatic. Daily irrigated conditioned seedlings exhibited dramatic increases in mortality and for weekly irrigated seedlings mortality ranged from 13 to 26 percent. The second drought period was four days longer than the first; hence, on a time basis the results are not directly comparable. Henson's data (1982) indicate that for previously conditioned pearl millet, enhanced adjustment to a second stress period was dissipated by an intermediate recovery period. Accumulated osmotica during stress conditioning may have dissipated during drought recovery, and were not immediately available during a subsequent stress period to lower osmotic potential to maintain turgor.

In the present study, mortality in both species was declared dependent upon irrigation conditioning but not KCl level. These results suggest that the benefits seedlings derived from the applied conditioning treatments were maintained through the first stress recovery period. Despite the possibility that the first drought stress may have altered, or otherwise modified the initial conditioned state of the seedling, the benefit of irrigation conditioning did not appear transitory. Table 15 shows that although mortality was experienced by weekly irrigated seedlings it was greater in daily irrigated seedlings (at Day 10) by factors of 3.5 and 2.8 for Douglas-fir and jack pine, respectively. Since jack pine exhibited 30 percent less mortality than Douglas-fir in daily irrigated seedlings it is tempting to speculate that jack pine possesses a degree of drought tolerance which allows it to endure

dehydration to lower levels than Douglas-fir. Earlier, relative water content/plant water potential isotherms suggested that Douglas-fir was more drought resistant of the two species, but under extreme water stress, jack pine seems to prevail.

5.1.4 Long term performance after successive drought and recovery periods. It has been occasionally observed that after stress relief growth occurs more rapidly than before stress (Brix, 1962). The basis for this observation is difficult to explain, especially in view of the possibility of membrane disruption that may occur during drought stress (Leopold *et al.*, 1981; Pearce, 1985). Moreover, the photosynthetic apparatus and certain enzyme systems may be impaired during moderate to severe stress (Hsiao, 1973). As dehydration occurs membrane structure undergoes modification (Hsiao, 1973). On rapid rehydration membrane expansion may not be rapid enough to accommodate the inflow of water, thereby, causing membrane rupture.

Although seedling mortality was substantially higher as a result of the second drought stress, growth of surviving seedlings was not precluded during a 12 week favorable growth period. The majority of the jack pine seedlings exhibited lammas shoot growth and buds on lateral branches were formed in Douglas-fir. Previously, it was suggested that jack pine possessed a greater degree of drought tolerance than Douglas-fir. The results presented in Table 16 further substantiate this claim. It is also suggested that the potential to recover from drought stress is greater in jack pine than in Douglas-fir as exemplified by species differences in mortality, health condition, and relative root activity (Table 16).

During the period of stress relief it is important for the seedling to regain photosynthetic efficiency and to initiate active root growth. At the end of 12 weeks, jack pine exhibited more root activity than Douglas-fir. Increases in root dry weight in jack pine and Douglas-fir over the response period were 749 and 438 percent, respectively. It may be inferred from these data that the photosynthetic system was intact and that the seedling root systems, despite fine root mortality during drought, were able to renew

growth supported by currently produced photosynthates. This represents an important factor in seedling survival, particularly on droughty sites.

5.2 Nursery experiment

It is often noted that greenhouse or growth room experimentation provide plant response data that are atypical of plant responses had the experiment been conducted under field conditions (Jordan and Ritchie, 1971). Consequently, confirmation of biological relationships and processes is sought by conducting experimentation under field conditions. Thus, the relationships determined for Douglas-fir and jack pine in the growth room experiment were sought under tightly controlled field nursery conditions. These conditions specifically provided for protection against animal damage, solarization of young seedling foliage and unwanted natural precipitation. The impact of soil characteristics on water stress development in Douglas-fir and jack pine was evaluated by planting seedlings on two distinctly different soil types.

5.2.1 Conditioning responses. Cultural plans for seedling production were essentially similar to those employed in the growth room experiment with two notable exceptions. First, failure of greenhouse environment controls necessitated a five week extension of the common production period and second, conditioning treatments were carried out under the cover of a large outdoor growing area. Because seedlings were to be outplanted, conditioning against solarization was required. By week 14, both species had attained epicotyl lengths (Fig. 23) similar to seedlings first raised for the growth room experiment (Fig. 6). Apart from significant species differences, epicotyl length was at no time significantly affected by frequency of irrigation or level of applied KCl (Table B-31). The development of water stress on a daily and weekly basis differed by about 0.4 MPa which obviously was insufficient to cause early differences in seedling development. Evaluation of seedling morphology prior to planting, however, indicated that the response of daily and weekly irrigated seedlings was significantly different

and for root area index, only KCl level was significant (Table B-32). Anatomical differences in stems and needles due to conditioning treatment were not detected by analysis of variance so the means by which conditioning affected survival remains unresolved.

Nutritionally, marked differences in some nutrients occurred e.g. P, K, and Cl^- showed marked increases in the roots (Table 18). No explanation could be found for these differences. In any case, species differences were maintained.

5.2.2 Response to field drought stress. The two soil types differed substantially in their textural classification and in terms of their soil water release curves (Fig. 24). At any given soil water potential, the Burnt Woods soil (a sandy clay loam) had a higher water content than the River Sand soil (a loamy sand). Early in the drought period, the Burnt Wood soil exhibited variation in water content with profile depth (Fig. 25). On the other hand, water content was similar throughout the profile in the River Sand soil (Fig. 26). The depletion of water from the upper 15 cm of the profile of the Burnt Woods soil was gradual, but after the tenth day, further declines in water content at the 20 cm level were minimal. In the River Sand soil water was successively depleted to lower profile levels and by the 28th experimental day the water content throughout the soil profile was uniformly low (i.e. 3 to 5 percent) (Fig. 26). Therefore, the soil types employed in this field test provided marked differences in rate of soil water depletion and magnitude of stress.

These differences were reflected in the rates of decline of the water relation parameters of both Douglas-fir and jack pine. Declines in plant water potential in seedlings on Burnt Woods soil were moderate and at no time did turgor pressure in any treatment appear to have been maintained by a differential decrease in osmotic potential relative to plant water potential. On the other hand, it appeared that both Douglas-fir and jack pine derived some benefit from weekly irrigation (Figs. 30 and 33). Mean water potentials calculated over the duration of the experimental period were always

higher (less negative) in weekly irrigated seedlings than in daily irrigated seedlings (Table B-41). Except in two instances, turgor pressures gradually declined and were consistently higher for weekly irrigated seedlings than daily irrigated seedlings on both soil types (Table B-43). Turgor pressures of Douglas-fir were higher than jack pine and hence, relative water contents of the foliage were also higher (Table B-44). Relative water contents of species were higher in Burnt Woods soil than on River Sand soil. Indeed, marked declines in the relative water content of jack pine were noted when soil water potentials reached approximately -3.0 MPa.

Evaluation of water relation parameters by pressure-volume methods revealed several interesting facts which should help to elucidate the cellular water response to drought stress. First, none of the bulk tissue parameters in either species was significantly and consistently affected by conditioning treatment or soil type (Tables B-45 and B-46). However, some parameters in each species varied significantly during the drought period. It is noteworthy that in Douglas-fir, on both soil types, modulus of elasticity values did not vary significantly until the last sample date (Table 20), at which time values declined by at least 50 percent. This point of decline corresponded with rapid declines in relative water content. Joly (1984) reported the tendency of modulus of elasticity of irrigated Douglas-fir to increase throughout the growing season. The elastic modulus values reported here also tended toward higher values as the drought stress continued, but then decreased substantially with decline in relative water content. A similar trend was noted for Douglas-fir subjected to drought stress in the growth room experiment (Table 12). The elastic modulus in jack pine showed no significant change throughout the drought stress period, but values tended to increase before declining (Table 20) and was similar to the drought stress responses previously reported (Table 12).

For previously stressed (non-irrigated) Douglas-fir seedlings, Joly (1984) reported increases in relative apoplasmic water content (R_a) and decreases in modulus of elasticity relative to well

irrigated control seedlings. It may appear, therefore, that the elasticity of the cell wall may be influenced by the number of stress cycles and severity of water deficits. Small cells are more elastic (Steudle *et al.*, 1977) and this property may be encouraged by stress conditioning. Turner (1979) illustrated that an increase in cell wall elasticity in the absence of solute accumulation provides for increases in solute concentration because of cell volume shrinkage, a process that maintains positive turgor to lower values of water potential.

The relationships amongst the water relation parameters of Douglas-fir and jack pine reveal that the responses to increasing water deficits on the two soil types were essentially the same. Although soil characteristics, such as structure, texture, pore size distribution etc. influence the soil water release curve, the relationships amongst the water relation parameters suggest that major control of water relations rests with the plant itself. For example, over the extent of similar water potentials provided by the soil types the relationships of relative water content to plant water potential on Burnt Woods soil (Fig. 33) and River Sand (Fig. 36) are similar. The declines in relative water content with the fall in water potential occurred at nearly similar rates, within species, to a plant water potential of approximately -2.0 MPa. The relationship on River Sand soil was extended because of the large soil water deficits that developed. Similar observations can be made for the other relationships involving osmotic potential. Furthermore, these relationships are not dissimilar to those determined for Douglas-fir and jack pine under growth room conditions. Basic species differences persisted in both environments, and therefore were not an artifact of experimental conditions.

It was previously noted in the growth room experiment that for a given change in relative water content there was a greater change in plant water potential in Douglas-fir than in jack pine. In soils that lose soil water quickly, as demonstrated by the River Sand soil, it is important that large gradients in plant water potential

be maintained to allow for continued absorption of water. Douglas-fir exhibited this characteristic. In contrast, jack pine under conditions of the nursery experiment does not demonstrate this capability and at plant water potentials lower than -1.0 the loss of water appears to accelerate (Fig. 38). This response is not consistent with drought resistance.

Osmotic potentials declined more rapidly in Douglas-fir than in jack pine with the result that turgor pressures were initially higher on both soil types. The mean difference between species on both soil types was 0.36 MPa. Osmotic potentials at zero turgor were not easily discerned from Figures 37 and 38. Extrapolated determinations gave values that coincided with values determined by the pressure-volume technique (Table 20). By species, however, osmotic potentials at zero turgor were higher (less negative) in River Sand soil than Burnt Woods soil. Less rapid development of water stress appears to favor maintenance of turgor to lower water potentials.

At the start of the sixth week of the experimental period all seedlings on both soil types exhibited excellent health (Tables 21 and 22). With progression of the stress development the physiological condition of Burnt Woods seedlings diminished only slightly and interestingly, weekly irrigated seedlings at 100 ppm KCl were first to exhibit effects from drought stress. Both Douglas-fir and jack pine on River Sand soil progressed continuously to a state of low vigor and high incidence of mortality. With few exceptions early mortality was confined to seedlings conditioned by weekly irrigation and 100 ppm KCl (Table 23). At the termination of the experiment, Douglas-fir had the only mortality in Burnt Woods soil. Douglas-fir mortality in the River Sand soil was about half of that recorded for jack pine. Highest mortality occurred at the highest KCl levels except in one instance. Analysis of these nursery data (Table 24) indicate that mortality was dependent on irrigation conditioning, a fact borne out in the growth room experiment. However, this dependence held only for seedlings under stress in the River Sand soil. This would suggest that the extent of the benefits

from conditioning are dependent upon the rate of development and duration of stress.

The results of this study clearly show that during rapid development of water stress (growth room) jack pine exhibited dehydration tolerance for a short period of time. During extended water stress species that can undergo osmotic adjustment may prevail at lower water potentials relative to non-adjusting or drought tolerant plants. Douglas-fir exhibited a tendency to adjust osmotically to maintain higher turgor pressures and relative water contents than jack pine as soil water deficits increased (Table 19). The consequence of this adjustment was lower incidence of mortality in Douglas-fir.

Analyses of data to test the dependence of mortality on KCl level in the growth room experiment provided enough evidence to reject the hypothesis of dependence. However, hypothesis testing for jack pine in the nursery experiment showed that mortality was dependent upon KCl level. Mortality was on the average 25 percent higher at 100 ppm KCl. Reasons for this effect remain unclear. Nutrient analysis of foliage and roots prior to planting did not reveal any indication of nutrient concentration that might be considered abnormally high and therefore toxic. However, Cl^- concentrations were, in some cases, substantially higher in the nursery experiment. Possibly in jack pine, the increase in nutrient concentration (notably Cl^-) as seedling tissues dehydrated created solute levels intolerable to seedling metabolism resulting in seedling death. Whether this explanation is tenable remains to be verified.

6. SUMMARY, CONCLUSIONS, AND IMPLICATIONS OF RESULTS

Douglas-fir and jack pine seedlings were raised in a greenhouse environment for periods of 10 and 15 weeks before undergoing water stress and nutrient conditioning for a minimum of six weeks. It was hypothesized that these treatments would provide the basis for enhanced water relations during periods of drought stress. The research was undertaken by conducting two distinctly different, but related experiments. In the first, a growth room study, attempts were made to measure and evaluate water relations, morphological and nutritional responses of the experimental seedlings during two successive drought stress periods under controlled conditions of photoperiod and temperature. In the second, a nursery study, conditioned seedlings were planted in two contrasting soil types, and permitted to endure a eight week precipitation free period during which water relations, morphological parameters, and survival were monitored. Conditions of the nursery trial were designed to simulate a protected field environment that might be encountered during an actual reforestation project.

Within species, the effects of KCl levels on all morphological parameters were similar, whereas the effects of daily and weekly irrigation significantly affected all morphological parameters except root dry weight and root area index. Conditioning treatments had no effect on anatomical characteristics of cell wall thickness and leaf cross-sections, but significant differences occurred in K and Cl^- concentrations of foliage and roots of both species.

The effects of conditioning treatments on response to drought stress were unique for each species. Declines in plant water potential occurred more rapidly in daily irrigated seedlings than in weekly irrigated seedlings, suggesting the presence of some operative mechanisms to control water stress in weekly irrigated seedlings. The decline in water potential was variously paralleled by osmotic potential resulting in a delayed decline or increase in turgor pressure. Weekly irrigated seedlings had higher relative water contents throughout each drought stress period.

Determination of water relation parameters by pressure-volume analysis provided no evidence to explain response differences between daily and weekly irrigated seedlings. Low precision in determining parameter values and natural variation may have precluded detection of significant differences in certain variables. Relative apoplasmic water content and modulus of elasticity are two important parameters which, in other studies, have explained differences in water relations of stressed versus well watered control plants during periods of soil water deficits. In stressed plants, it is known that relative apoplasmic water content increases and modulus of elasticity decreases. These changes would explain present observations in the absence of well defined osmotic adjustment. It is also possible that both conditioning treatments may have had a significant effect on metabolic processes which were then manifested in response variations to drought stress. At the species level, Douglas-fir exhibited characteristic behavior of a drought resistant species compared to jack pine; e.g. for a given change in relative water content there was a greater decline in plant water potential. In addition, osmotic potentials at full and zero turgor were consistently lower in Douglas-fir than in jack pine. However, the difference within species was greater in jack pine than in Douglas-fir. Exceptionally high cell wall elasticity in jack pine may have accounted for this difference as tissues dehydrated.

During exposure to a second drought stress which followed a 10 day recovery period, Douglas-fir exhibited a restrained decline in water potential compared to jack pine. These declines were less rapid than observed in the first drought period. Each species had lower osmotic potentials at high relative water contents and displayed lower rates of decline in relative water content with declines in water potential. Only jack pine, however, demonstrated a significant increase in turgor pressure as water and osmotic potentials differentially declined. Higher relative water contents were again associated with stress conditioned seedlings and no differences were attributed to KCl levels. The apparent maintenance

of turgor in jack pine is supported by non-significant change in the elastic modulus over the duration of the stress period. However, values reported for the modulus of elasticity were very low, suggesting that decreases in osmotic potential could also have occurred because of dehydration and reduction in cell size.

Recovery from drought stress was affected by irrigation conditioning. The incidence of mortality as a result of the first drought period was dependent upon irrigation level; highest mortality was observed in daily irrigated seedlings of both Douglas-fir and jack pine. Level of KCl had no effect on mortality. The relationships amongst relative water content, plant water potential, and osmotic potential suggest that Douglas-fir exhibits enhanced ability to resist drought more successfully than jack pine. Lower Douglas-fir mortality compared to jack pine (Table 10) substantiates this categorization.

Recovery from the second drought stress indicates that while mortality was still dependent only upon irrigation treatment Douglas-fir was less capable of withstanding drought than jack pine. The increased severity of second drought stress clearly exceeded the adaptive ability of Douglas-fir to resist drought. On the other hand, jack pine demonstrated its ability to tolerate drought stress to lower levels of relative water content, e.g. RWC @ TLP for Douglas-fir vs jack pine: .86 vs .79, respectively.

Confirmation of results obtained in the growth room study were attempted by conducting similar experimentation under protected nursery conditions. Conditioned Douglas-fir and jack pine seedlings were planted in raised seedbeds of two distinctly different soil types which possessed unique soil moisture characteristic curves. In the Burnt Woods soil (a sandy clay loam), both Douglas-fir and jack pine exhibited minimal stress development and slow rates of decline in turgor pressure. In the River Sand soil (a loamy sand soil), water potentials declined rapidly. Douglas-fir demonstrated a continuing capacity to maintain higher turgor pressures than jack pine against declines in total water potential. Excluding data from the last sampling date in the nursery experiment, modulus of

elasticity values for Douglas-fir tended toward higher values on both soil types, whereas they tended to vary or decline in jack pine. This may be taken to suggest that turgor maintenance in Douglas-fir was, at least in part, the result of solute accumulation.

Mortality of seedlings growing on Burnt Woods soil was limited to Douglas-fir and unrelated to conditioning treatment. On the other hand, the occurrence of mortality on the River Sand soil was variously dependent on conditioning treatment. Significantly higher mortality occurred in daily irrigated Douglas-fir seedlings than in weekly irrigated seedlings. At the eighth week of drought stress, mortality in jack pine seedlings was equally high across irrigation conditioning treatments. At extreme plant water stress KCl conditioning at 100 ppm had a marginally negative and significant effect on jack pine mortality (Table 24).

After eight weeks of mounting drought stress Douglas-fir exhibited 41 percent mortality compared to 72 percent mortality in jack pine. This is in sharp contrast to the occurrence of species mortality in the growth room experiment in which mortality in jack pine was less than in Douglas-fir (Table 15). This difference is believed to reflect the effect of rate of stress development and the inherent ability of each species to respond to drought. Drought stress in the growth room developed rapidly and probably precluded response mechanisms, such as osmotic adjustment from mitigating the effects of drought. Species mortality was, therefore, a measure of dehydration tolerance.

Without the ability to adjust osmotically the benefit of irrigation conditioning appears to be effective only within a range of plant water stress. Once this range is exceeded, differently conditioned seedlings can experience equally high mortality. The advantage during slow stress development in the River Sand soil was clearly with Douglas-fir because osmotic adjustment provided for physiological functions to occur to lower plant water potentials than in non-adjusting plants.

Conditioning seedlings to enhance their physiology during

drought stress must not, however, preclude their potential for growth once favorable conditions prevail. This aspect was evaluated with seedlings from the growth room study. Seedlings that had been twice exposed to severe drought and survived were placed in a favorable growth room environment for 12 weeks and growth response recorded. Dramatic increases in root collar diameter and root dry weight were recorded for both species. Increases in growth by jack pine far exceeded those of Douglas-fir. Weekly irrigated seedlings displayed better growth than daily irrigated seedlings. Mortality was confined entirely to Douglas-fir. Conclusions drawn were that conditioning treatments do not markedly impair future performance of surviving drought stress seedlings.

Finally, it may be recalled that in both southwest Oregon and some northern regions of Ontario typical planting times are often followed by periods of low precipitation which can induce drought stress in young conifer seedlings. If these periods of drought are severe enough and act over a long enough period of time, seedling mortality can be high. Also, without growth, survival cannot be assured. The results presented here have shown clearly that both Douglas-fir and jack pine seedlings can be conditioned, principally by irrigation control, to accentuate their respective drought resistant mechanisms under certain conditions. During the early phase of seedling establishment the importance of drought resistance through turgor maintenance is heightened because of the need for root extension and crown development. The use of conditioned seedlings by the forest manager may provide the advantage required to successfully reforest drought prone sites.

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APPENDIX A

Explanation of Symbols

ψ_T	total water potential
ψ_π	osmotic potential
ψ_p	pressure potential/turgor pressure
ψ_τ	matric potential
RWC	relative water content
OPFT	osmotic potential at full turgor
OPZT	osmotic potential at zero turgor
RWC @ TLP	relative water content at turgor loss point
RSWC @ TLP	relative symplasmic water content at turgor loss point
ME @ .995 RWC	modulus of elasticity evaluated at 0.995 RWC
Ra	relative apoplasmic water content

TABLE B-1. Summary of analysis of variance (F values) and significance levels of epicotyl length of Douglas-fir and jack pine seedlings for each week (equivalent to seedling age in weeks) during the conditioning period.

Source of variation	df	WEEK						
		11	12	13	14	15	16	17
Block	3				..			
					**	*	***	***
Irrig. (I)	1	5.08	2.11	2.07	50.06	33.61	140.97	124.84
Error (a)	3							
KCl (K)	1	0.29	0.04	3.81	1.56	0.0004	3.02	6.15
I X K	1	0.01	0.49	4.64	0.04	0.42	0.30	0.59
Error (b)	6							
		***	***	***	***	***	***	***
Species (S)	1	66.36	83.90	218.14	299.01	840.42	831.92	375.32
					***	***	***	*
I X S	1	0.41	0.57	3.17	20.54	26.07	24.92	8.25
K X S	1	0.95	0.008	2.77	1.74	0.20	0.71	0.75
						*		
I X K X S	1	0.95	3.95	1.67	1.77	5.96	0.80	0.07
Error (c)	12							

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-2. Summary of analysis of variance (F values) and significance levels of morphological parameters of 17 week-old Douglas-fir and jack pine seedlings.

Source of variation	df	Morphological Parameter						
		Root Collar Dia.	Shoot Length	Shoot Dry Wt.	Root Area Index	Root Dry Wt.	Sdlg. Dry Wt.	Top Root Ratio
Block	3							
		***	***	***			***	*
Irrig. (I)	1	133.62	155.94	201.99	8.22	0.29	95.42	23.94
Error (a)	3							
KCL (K)	1	0.16	5.75	1.46	1.34	0.49	1.00	1.44
K X I	1	0.25	0.00	2.25	2.61	3.71	2.79	0.40
Error (b)	6							
		***	***	***	***		***	***
Species (S)	1	47.59	412.53	73.96	48.34	0.71	43.75	60.15
S X I	1	3.77	9.22	1.16	1.13	1.71	1.44	1.71
S X K	1	0.27	0.11	0.65	0.70	0.35	0.35	0.05
		**						
S X I X K	1	7.93	0.02	0.76	0.02	0.049	0.56	0.84
Error (c)	12							

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-3. Summary of analysis of variance (F values) and significance levels of foliar nutrient concentrations of 17 week-old conditioned Douglas-fir and jack pine seedlings.

Source of variation	df	Nutrient					
		N	P	K	Ca	Mg	Cl ⁻
Block	3						
Irrig. (I)	1	0.04	55.60	33.37	2.77	0.08	2.82
Error (a)	3						
KCl (K)	1	0.11	3.71	2.59	0.47	1.99	75.56
I X K	1	0.01	16.21	0.16	0.84	21.66	5.87
Error (b)	6						
Species (S)	1	9.14	1001.40	324.06	34.18	19.41	5.45
I X S	1	1.66	30.08	44.94	0.17	0.02	2.35
K X S	1	4.18	0.00	4.24	0.04	1.13	1.96
I X K X S	1	2.81	1.35	0.56	0.06	0.49	0.07
Error (c)	12						

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-4. Summary of analysis of variance (F values) and significance level of root nutrient concentrations of 17 week-old conditioned Douglas-fir and jack pine seedlings.

Source of variation	df	Nutrient					
		N	P	K	Ca	Mg	Cl ⁻
Block	3						
Irrig. (I)	1	8.32	***	***	9.99	***	6.99
Error (a)	3						
KCl (K)	1	0.79	0.03	0.72	1.26	0.09	***
I X K	1	1.53	0.00	0.36	0.14	0.30	0.04
Error (b)	6						
Species (S)	1	***	***		***	**	*
I X S	1	13.54	18.56	1.56	31.28	10.48	7.32
K X S	1	0.19	3.22	1.84	0.11	7.50	4.41
I X K X S	1	1.22	*	4.83	1.61	0.36	0.01
I X K X S	1	0.01	0.28	0.06	0.59	0.90	0.82
Error (c)	12						

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-5. Summary of analysis of variance (F values) and significance levels of morphological parameters of seedlings on four occasions (experimental day) during the first growth room drought period.

Variable:	Epicotyl length				Root collar diameter				
	df	Day				Day			
		1	5	8	10	1	5	8	10
Block	2								
Irrig. (I)	1	*	*	**	*		*		
Error (a)	2	27.24	35.32	445.47	26.58	5.01	31.72	17.58	5.83
KCl	1	0.26	2.60	0.02	1.08	0.01	4.30	0.02	0.00
I X K	1	2.49	0.22	0.73	0.33	2.85	1.22	2.13	0.27
Error (b)	4								
Species	1	**	**	**	**	0.47	**	0.33	**
I X S	1	37.96	190.13	40.76	59.71	0.07	**	0.11	*
K X S	1	0.22	0.35	1.43	2.11	0.53	48.53	0.03	7.79
I X K X S	1	0.05	4.92	1.02	0.04	0.15	2.98	0.33	0.06
Error (c)	8	0.08	0.07	0.47	2.95	6.86	*	0.06	

(continued ...)

1

Significance levels

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.005$

TABLE B-5 (continued)

Variable:		Root area index				Root dry weight			
		Day				Day			
Source of variation	df	1	5	8	10	1	5	8	10
Block	2								
Irrig. (I)	1	7.37	0.05	5.68	2.08	1.03	6.31	78.83	0.98
Error (a)	2							*	
KCl	1	0.78	1.56	0.14	2.51	0.05	3.16	0.05	2.05
I X K	1	1.90	1.30	21.65	0.00	2.02	3.30	4.14	0.62
Error (b)	4			**					
Species	1	***	23.92	5.30	4.14	18.46	0.63	1.30	0.01
I X S	1	0.72	4.24	0.63	0.00	0.78	10.96	0.69	3.02
K X S	1	0.15	0.60	0.05	0.00	0.26	0.15	0.00	0.35
I X K X S	1	0.00	3.16	1.89	0.01	0.26	4.15	0.35	0.01
Error (c)	8						*		

TABLE B-6. Summary of analysis of variance (F values) and significance level of morphological parameters of seedlings over time during the first growth room drought period.

Source of variation	df	Morphological Parameter			
		Height	Root Collar Dia.	Root Area Index	Root Dry Wt.
Blocks	2				
		***	**		**
Irrig. (I)	1	9483.91	99.38	15.12	1281.95
Error (a)	2				
KC1 (K)	1	2.52	0.43	4.04	2.73
I X K	1	0.94	1.78	0.19	0.13
Error (b)	4				
		***	***	***	
Species (S)	1	386.16	37.41	30.84	0.38
		*	***		**
I X S	1	5.90	17.60	1.90	11.92
K X S	1	0.00	1.67	0.22	0.00
I X K X S	1	0.55	3.45	0.08	0.77
Error (c)	8				
				***	***
Time (T)	3	0.83	2.64	9.05	14.86
					*
I X T	3	0.88	0.60	2.42	3.83
K X T	3	1.12	0.36	1.41	0.79
				*	
I X K X T	3	0.52	1.04	3.28	2.52
S X T	3	0.28	2.22	0.84	0.45
I X S X T	3	0.33	2.62	1.67	1.89
K X S X T	3	1.08	0.24	0.25	0.18
I X K X S X T	3	0.98	0.18	2.23	1.52
Error (d)	48				

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-7. Formulae employed to estimate standard errors involving time as a treatment (after Little and Hills, 1978).

Means compared	Standard Errors \bar{S}_y	t-values ¹
1. irrigation means (A)	$\sqrt{E_a / r b c d}$	t_a
2. sample time means (D) for same irrigation (A) and species	$\sqrt{E_d / r b}$	t_d
3. sample time means (D) for same species (C)	$\sqrt{E_d / r a b}$	t_d
4. Species means (C) for same sampling time (D)	$\sqrt{E_c / r a b}$	t_c
5. Species means (C) for same irrigation (A) and same or different sample time (D)	$\sqrt{(d-1)E_d + E_c / r a b}$	$t_{cd} = (d-1)$

¹

1. t_a, t_c, t_d indicate tabular t-values for degrees of freedom for $E_a, E_c,$ and E_d respectively.
2. A (not included in analysis), B, C, and D are treatments applied to main plots, subplot, sub-subplot and sub-sub-subplots respectively.
3. Least significant difference is LSD calculated as:

$$LSD = t \sqrt{2} \bar{S}_y$$

TABLE B-8. Effects summary of irrigation, species and sample time for epicotyl length during the first growth room drought period and least significant differences for determination of mean differences.

Irrigation	Species	Sample time (Day)				Irrig. means
		1	5	8	10	
----- cm -----						
Daily	Douglas-fir	32.73	33.58	36.50	32.92	
	Jack pine	21.75	22.50	22.75	21.33	28.01
Weekly	Douglas-fir	27.13	27.50	26.67	26.33	
	Jack Pine	17.06	17.33	17.25	18.41	22.21

Species	Species X Sample time (Day)			
	1	5	8	10
Douglas-fir	29.93	30.54	31.59	29.63
Jack pine	19.41	19.92	20.00	19.87

LEAST SIGNIFICANT DIFFERENCES (P = .05)

$$LSD = t \sqrt{2} S_{\bar{y}} \quad (\text{see Table B-7})$$

1. Irrigation means : 0.25
2. Sample time means (D) for same irrigation (A) and species (C) : 4.03
3. Sample time means (D) for same species (C): 2.85
4. Species means (C) for sample time (D): : 2.50
5. Species means (C) for same irrigation level (A) and same or different sample time (D) : 5.52

TABLE B-9. Effects summary of irrigation, species and sample time for root collar diameter during the first growth room drought period and least significant differences for determination of mean differences.

Irrigation	Species	Sample time (Day)				Irrig. means
		1	5	8	10	
		----- mm -----				
Daily	Douglas-fir	2.60	2.60	2.83	2.38	
	Jack pine	2.92	3.67	2.98	3.31	2.90
Weekly	Douglas-fir	2.49	2.62	2.43	2.43	
	Jack Pine	2.51	2.60	2.47	2.62	2.52

Species	Species X Sample time (Day)			
	1	5	8	10
Douglas-fir	2.54	2.63	2.63	2.41
Jack pine	2.72	3.14	2.73	2.97

LEAST SIGNIFICANT DIFFERENCES (P = .05)

$$LSD = t \sqrt{2} \bar{S}_y \quad (\text{see Table B-7})$$

1. Irrigation means : 0.17
2. Sample time means (D) for same irrigation (A) and species (C) : 0.47
3. Sample time means (D) for same species (C): 0.33
4. Species means (C) for sample time (D): : 0.25
5. Species means (C) for same irrigation level (A) and same or different sample time (D) : 0.62

TABLE B-10. Effects summary of irrigation, species and sample time for root area index during the first growth room drought period and least significant differences to determine mean differences.

Irrigation	Species	Sample time (Day)				Irrig. means
		1	5	8	10	
		2				
		----- cm -----				
Daily	Douglas-fir	25.78	28.25	27.13	18.61	
	Jack pine	31.41	42.60	35.40	29.94	29.79
Weekly	Douglas-fir	21.42	34.60	24.48	22.90	
	Jack Pine	29.08	35.39	28.11	34.55	28.55

Species	Species X Sample time (Day)			
	1	5	8	10
Douglas-fir	23.60	31.43	25.81	20.76
Jack pine	30.25	39.00	31.78	32.25

LEAST SIGNIFICANT DIFFERENCES (P = .05)

$$LSD = t \sqrt{2} S_{\bar{y}} \quad (\text{see Table B-7})$$

1. Irrigation means : 1.34
2. Sample time means (D) for same irrigation (A) and species (C) : 7.75
3. Sample time means (D) for same species (C): 5.48
4. Species means (C) for sample time (D): : 6.54
5. Species means (C) for same irrigation level (A) and same or different sample time (D) : 11.51

TABLE B-11. Effects summary of irrigation, species and sample time for root dry weight during the first growth room drought period and least significant differences to determine mean differences.

Irrigation	Species	Sample time (Day)				Irrig. means
		1	5	8	10	
		----- g -----				
Daily	Douglas-fir	0.278	0.438	0.503	0.352	
	Jack pine	0.283	0.695	0.553	0.465	0.446
Weekly	Douglas-fir	0.276	0.498	0.403	0.520	
	Jack Pine	0.249	0.373	0.338	0.447	0.388

Species	Species X Sample time (Day)			
	1	5	8	10
Douglas-fir	0.277	0.468	0.453	0.436
Jack pine	0.266	0.534	0.446	0.456

LEAST SIGNIFICANT DIFFERENCES (P = .05)

$$LSD = t \sqrt{2} S_{\bar{y}} \quad (\text{see Table B-7})$$

1. Irrigation means : 0.007
2. Sample time means (D) for same irrigation (A) and species (C) : 0.155
3. Sample time means (D) for same species (C): 0.110
4. Species means (C) for sample time (D): : 0.119
5. Species means (C) for same irrigation level (A) and same or different sample time (D) : 0.204

TABLE B-12. Summary of analysis of variance (F values) and significance levels of water relation parameters for 17 week old Douglas-fir and jack pine seedlings during the first growth room drought period.

Variable:	Total water potential				Osmotic potential				
	Sample time (Day)				Sample time (Day)				
	1	5	8	10	1	5	8	10	
Source of variation	df								
Block	2								
Irrig. (I)	1	2.19	3.31	6.16	5.77	158.68	1.06	52.37	30.46
Error (a)	2								
KCl (K)	1	0.01	0.12	0.04	12.85	5.81	0.31	0.09	9.71
I X K	1	1.46	0.50	0.00	11.95	0.41	0.01	0.29	10.59
Error (b)	4								
Species	1	197.24	0.00	13.70	0.94	252.06	8.89	0.28	40.88
I X S	1	0.61	0.03	2.85	0.06	4.71	1.95	1.04	4.77
K X S	1	4.28	1.03	3.11	1.86	0.86	0.19	1.41	0.28
I X K X S	1	0.34	12.84	3.53	5.65	13.00	4.14	1.10	2.70
Error (c)	8								

(continued ...)

1

Significance levels

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.005$

TABLE B-13. Summary of analysis of variance (F values) and significance levels of water relation parameters of conditioned Douglas-Fir and jack pine seedlings over time during the first growth room drought period.

Source of variation	df	Water Relation Parameter			
		Water Potential	Osmotic Pressure	Turgor Pressure	Relative Water Content
Blocks	2				
		*	***		**
Irrig. (I)	1	36.98	224.71	0.64	108.43
Error (a)	2				
		**	*		
KC1 (K)	1	31.25	11.48	1.99	3.06

I X K	1	32.46	5.26	4.55	2.36
Error (b)	4				
			*	*	***
Species (S)	1	2.41	6.22	8.44	453.46
			*		
I X S	1	0.18	10.86	5.24	0.59
K X S	1	4.75	14.21	1.04	0.22
		*			
I X K X S	1	5.49	1.70	2.18	0.48
Error (c)	8				
		***	***	***	***
Time (T)	3	88.56	139.39	15.80	196.77
			***	***	***
I X T	3	5.05	22.87	10.62	12.93
		***			*
K X T	3	4.14	1.55	3.94	3.30
I X K X T	3	3.74	2.12	2.19	0.04
		*	***	***	***
S X T	3	3.22	22.40	20.28	24.05
				*	
I X S X T	3	0.38	1.62	3.51	2.25
K X S X T	3	1.19	0.66	2.61	0.17
I X K X S X T	3	5.14	2.22	5.44	0.21
Error (d)	48				

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-14. Means of total water potential of Douglas-fir and jack pine evaluated on four occasions (experimental day) during the first growth room drought period.

Species	Treatment	Sample time (Day)				Means
		1	5	8	10	
----- - MPa -----						
Douglas-fir	D0	0.82	1.46	3.19	3.29	2.08
	D100	0.84	1.83	2.66	3.70	2.14
	W0	0.77	1.67	2.24	2.17	1.64
	W100	0.82	1.23	2.24	2.59	1.65
						Species Mean: 1.88
Jack pine	D0	0.45	1.70	1.92	2.32	1.51
	D100	0.38	1.63	2.41	5.60	2.34
	W0	0.40	1.28	1.98	2.84	1.53
	W100	0.37	1.61	1.94	2.48	1.51
						Species Mean: 1.72

TABLE B-15. Means of osmotic potential of Douglas-fir and jack pine evaluated on four occasions (experimental day) during the first growth room drought period.

Species	Treatment	Sample time (Day)				Means
		1	5	8	10	
----- - MPa -----						
Douglas-fir	D0	1.83	2.01	3.67	3.69	2.73
	D100	2.13	2.18	2.97	4.19	2.81
	W0	2.17	2.39	2.55	2.78	2.45
	W100	2.19	2.25	2.55	2.98	2.47
						Species Mean: 2.61
Jack pine	D0	1.27	2.01	3.50	5.00	2.82
	D100	1.29	1.92	3.92	6.37	3.21
	W0	1.51	1.84	2.39	3.86	2.33
	W100	1.68	2.10	2.46	3.61	2.40
						Species Mean: 2.69

TABLE B-16. Means of turgor pressure for Douglas-fir and jack pine evaluated on four occasions (experimental day) during the first growth room drought period.

Species	Treatment	Sample time (Day)				Means
		1	5	8	10	
		----- MPa -----				
Douglas-fir	D0	1.01	0.55	0.49	0.41	0.64
	D100	1.30	0.35	0.31	0.48	0.66
	W0	1.40	0.72	0.31	0.61	0.81
	W100	1.36	1.01	0.32	0.39	0.82
						Species Mean: 0.85
Jack pine	D0	0.82	0.31	1.58	2.68	1.31
	D100	0.90	0.29	1.50	0.76	0.90
	W0	1.11	0.56	0.41	1.02	0.81
	W100	1.31	0.48	0.53	1.13	0.89
						Species Mean: 0.96

TABLE B-17. Relative water contents of Douglas-fir and jack pine needles on four occasions (experimental day) by treatment during the first growth room drought period.

Species	Treatment	Sample time (Day)				Mean
		1	5	8	10	
		----- % -----				
Douglas-fir	D0	92.7	87.5	61.9	65.4	78.1
	D100	91.7	87.9	66.3	59.7	77.6
	W0	93.9	90.8	83.8	86.1	89.1
	W100	93.6	92.2	87.6	78.2	88.3
						Species Mean: 83.3
Jack pine	D0	88.2	68.3	46.6	38.4	62.4
	D100	89.7	68.7	50.8	31.8	62.5
	W0	89.9	81.8	62.1	52.9	73.1
	W100	89.8	77.5	62.5	47.7	70.9
						Species Mean: 67.2
Species	Irrigation	Irrigation X treatment				Mean
		1	5	8	10	
		----- % -----				
Douglas-fir	D	92.2	87.7	64.1	62.6	76.7
	W	93.75	91.5	85.7	82.2	88.3
Jack pine	D	89.0	68.5	48.7	35.10	60.3
	W	89.9	79.7	62.2	50.3	70.5

TABLE B-18. Summary of analysis of variance (F values) and significance levels of morphological parameters of conditioned Douglas-fir and jack pine seedlings on seven occasions (experimental day) during the second growth room drought period.

Variable:		Epicotyl Length						
		Sample time (Day)						
Source of variation	df	1	4	6	8	10	12	14
Block	2							
		*		*	*	*		
Irrig.(I)	1	20.01	0.83	26.56	19.69	51.45	8.81	3.42
Error (a)	2							
KCl (K)	1	0.00	2.89	0.05	0.00	1.84	0.23	0.01
I X K	1	0.73	1.20	1.91	0.59	0.09	0.03	1.56
Error (b)	4							
		***	***	***	***	***	***	**
Species (S)	1	80.25	86.23	61.18	240.62	230.41	66.33	215.64
					**	*		
I X S	1	3.34	2.82	1.96	13.92	9.10	0.04	2.63
K X S	1	0.47	1.70	0.77	4.67	0.04	0.13	0.62
I X K X S	1	0.04	0.00	3.71	0.96	0.72	1.83	3.97
Error (c)	8							

(continued ...)

1

Significance level

* $P \leq .05$

** $P \leq .01$

*** $P \leq .005$

TABLE B-18 (continued)

Variable:		Root Collar Diameter						
		Sample time (Day)						
Source of variation	df	1	4	6	8	10	12	14
Block	2						*	
Irrig.(I)	1	16.90	0.33	3.86	3.37	13.43	20.21	1.58
Error (a)	2							
KCl (K)	1	1.79	0.15	2.73	0.11	1.98	0.04	0.12
		*				***		
I X K	1	7.88	1.16	4.34	0.14	15.75	0.12	1.84
Error (b)	4							
				***			*	
Species (S)	1	1.60	4.93	15.66	0.07	1.53	11.20	0.17
I X S	1	0.20	2.47	0.02	0.33	0.75	1.71	0.86
K X S	1	1.93	0.85	1.01	0.56	0.14	0.24	0.08
I X K X S	1	2.11	1.26	0.68	0.78	0.02	2.20	4.31
Error (c)	8							

(continued ...)

TABLE B-18 (continued)

Variable:		Root Area Index						
		Sample time (Day)						
Source of variation	df	1	4	6	8	10	12	14
Block	2							
Irrig.(I)	1	11.44	0.76	8.91	5.03	2.29	3.78	5.08
Error (a)	2							
KCl (K)	1	0.00	24.27**	0.19	1.77	0.01	2.16	1.89
I X K	1	0.67	14.83*	3.01	2.90	2.77	1.80	2.95
Error (b)	4							
Species (S)	1	0.97	11.35**	8.23*	19.42***	3.97	9.08*	2.40
I X S	1	0.03	0.06	0.28	0.04	0.01	1.14	2.63
K X S	1	0.85	0.00	0.46	0.03	0.05	1.52	0.10
I X K X S	1	1.45	1.38	2.28	0.07	0.01	0.20	0.13
Error (c)	8							

(continued ...)

TABLE B-18 (continued)

Variable:		Root Dry Weight						
		Sample time (Day)						
Source of variation	df	1	4	6	8	10	12	14
Block	2							
Irrig.(I)	1	0.04	0.14	0.52	2.06	0.00	0.22	0.42
Error (a)	2							
KCl (K)	1	0.20	3.09	9.14*	1.65	0.27	1.07	0.68
I X K	1	1.46	0.58	4.38	1.37	8.28*	1.99	1.58
Error (b)	4							
Species (S)	1	5.18	0.60	0.01	0.00	0.16	1.55	1.73
I X S	1	0.15	0.02	0.02	0.53	0.00	7.96*	0.23
K X S	1	0.39	0.56	0.09	0.01	0.13	0.66	0.06
I X K X S	1	1.13	2.37	1.86	0.31	0.00	1.01	1.27
Error (c)	8							

1
 TABLE B-19. Summary of analysis of variance (F values) and significance levels of morphological parameters of conditioned Douglas-fir and jack pine seedlings over time during the second growth room drought period.

Source of variation	df	Morphological Parameter			
		Epicotyl Length	Root Collar Dia.	Root Area Index	Root Dry Wt.
Blocks	2				
Irrig. (I)	1	*	10.51	12.97	0.15
Error (a)	2	25.19			
KCl (K)	1	0.01	0.37	5.43	0.74
I X K	1	0.02	0.17	0.37	0.22
Error (b)	4				
Species (S)	1	***	***	***	0.79
I X S	1	***	1.04	0.06	0.92
K X S	1	*	0.39	0.01	0.28
I X K X S	1	0.30	0.30	0.00	0.04
Error (c)	8				
Sample (T)	6	1.03	***	***	1.82
I X T	6	*	1.77	0.16	0.53
K X T	6	0.51	0.14	0.88	0.84
I X K X T	6	1.14	1.31	1.63	1.24
S X T	6	0.92	1.59	1.27	1.02
I X S X T	6	0.90	1.06	0.64	1.35
K X S X T	6	0.82	0.66	0.60	0.20
I X K X S X T	6	1.91	1.84	0.73	1.21
Error (d)	96				

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-20. Effects summary of irrigation, species and sample time on epicotyl length during the second growth room drought period and least significant difference for determination of mean differences.

Irrig.	Spe- cies	Sample time (Day)							Irrig. means
		1	4	6	8	10	12	14	
----- cm -----									
Daily	Df	33.58	31.92	34.67	34.92	35.08	33.50	33.00	26.71
	Jp	18.58	19.67	21.50	18.58	19.00	21.50	18.33	
Weekly	Df	27.50	29.08	27.08	29.67	26.83	29.50	29.00	23.19
	Jp	17.58	20.58	17.92	19.67	16.08	16.92	17.25	

Spe- cies	Species X Sample time (Day)						
	1	4	6	8	10	12	14
Df	30.54	30.50	30.88	32.30	30.96	31.50	31.00
Jp	18.08	20.13	19.71	19.13	17.54	19.21	17.79

LEAST SIGNIFICANT DIFFERENCES (P = .05)

$$LSD = t \sqrt{2} S_{\bar{y}} \quad (\text{see Table B-7})$$

1. Irrigation means : 3.01
2. Sample time means (D) for same irrigation (A) and species (C) : 3.34
3. Sample time means (D) for same species (C): 2.36
4. Species means (C) for sample time (D): : 1.47
5. Species means (C) for same irrigation level (A) and same or different sample time (D) : 5.91

TABLE B-21. Effects summary of irrigation, species and sample time on root collar diameter during the second growth room drought period and least significant differences for determination of mean differences.

Irrig.	Spe- cies	Sample time (Day)							Irrig. means
		1	4	6	8	10	12	14	
----- mm -----									
Daily	Df	2.74	3.04	2.98	2.97	2.93	2.48	2.63	2.92
	Jp	2.97	3.15	3.36	2.91	2.98	3.15	2.46	
Weekly	Df	2.56	2.67	2.60	2.89	2.44	2.45	2.60	2.73
	Jp	2.67	3.30	2.86	3.05	2.73	2.74	2.67	

Spe- cies	Species X Sample time (Day)						
	1	4	6	8	10	12	14
Df	2.65	2.86	2.79	2.93	2.69	2.47	2.62
Jp	2.82	3.23	3.11	2.98	2.86	2.95	2.57

LEAST SIGNIFICANT DIFFERENCES (P = .05)

$$LSD = t \sqrt{2} S_{\bar{y}} \quad (\text{see Table B-7})$$

1. Irrigation means : 0.24
2. Sample time means (D) for same irrigation (A) and species (C) : 0.42
3. Sample time means (D) for same species (C): 0.29
4. Species means (C) for sample time (D): : 0.26
5. Species means (C) for same irrigation level (A) and same or different sample time (D) : 0.77

TABLE B-22. Effects summary of irrigation, species and sample time on root area index during second the growth room drought period and least significant differences for determination of mean differences.

Irrig.	Spe- cies	Sample time (Day)							Irrig. means
		1	4	6	8	10	12	14	
		2 ----- cm -----							
Daily	Df	32.21	33.09	31.59	27.77	26.95	24.43	23.93	33.08
	Jp	35.21	44.60	42.91	42.26	36.33	38.19	23.68	
Weekly	Df	36.48	37.05	39.03	36.67	33.82	34.67	24.01	39.45
	Jp	40.86	50.37	51.21	49.94	42.36	41.22	34.64	

Spe- cies	Species X Sample time (Day)						
	1	4	6	8	10	12	14
Df	34.35	35.07	35.31	37.22	30.39	29.55	23.97
Jp	38.04	47.49	47.06	46.10	39.35	39.71	29.16

LEAST SIGNIFICANT DIFFERENCES (P = .05)

$$\text{LSD} = t \sqrt{2} \bar{S}_y \quad (\text{see Table B-7})$$

1. Irrigation means : 7.61
2. Sample time means (D) for same irrigation (A) and species (C) : 9.43
3. Sample time means (D) for same species (C): 6.66
4. Species means (C) for sample time (D): : 9.87
5. Species means (C) for same irrigation level (A) and same or different sample time (D) : 11.17

TABLE B-23. Effects summary of irrigation, species and sample time on root dry weight during the second growth room drought period and least significant differences for determination of mean differences.

Irrig.	Species	Sample time (Day)							Irrig. means
		1	4	6	8	10	12	14	
		----- g -----							
Daily	Df	0.50	0.59	0.51	0.50	0.53	0.40	0.50	0.50
	Jp	0.41	0.56	0.50	0.55	0.50	0.68	0.35	
Weekly	Df	0.53	0.54	0.56	0.64	0.54	0.58	0.50	0.52
	Jp	0.40	0.49	0.56	0.58	0.50	0.47	0.43	

Species	Species X Sample time (Day)						
	1	4	6	8	10	12	14
Df	0.52	0.57	0.54	0.57	0.54	0.49	0.50
Jp	0.41	0.53	0.53	0.57	0.50	0.58	0.39

LEAST SIGNIFICANT DIFFERENCES (P = .05)

$$LSD = t \sqrt{2} S_{\bar{y}} \quad (\text{see Table B-7})$$

1. Irrigation means : 0.18
2. Sample time means (D) for same irrigation (A) and species (C) : 0.19
3. Sample time means (D) for same species (C): 0.13
4. Species means (C) for sample time (D): : 0.22
5. Species means (C) for same irrigation level (A) and same or different sample time (D) : 0.39

TABLE B-24. Summary of analysis of variance (F values) and significance levels of total plant water potential, osmotic potential, turgor pressure and relative water content of conditioned Douglas-fir and jack pine seedlings on seven occasions (experimental day) during the second drought period.

Variable:	Plant Water Potential							
	Source of variation	df	Sample time (Day)					
			1	4	6	8	10	12
Block	2			*				*
Irrig. (I)	1	0.01	1.50	22.34	3.84	0.77	1.93	51.07
Error (a)	2							
KCl (K)	1	0.26	0.04	0.01	3.86	2.30	13.69	1.97
I X K	1	0.30	3.07	0.14	1.46	1.11	6.84	4.42
Error (b)	4							
Species (S)	1	39.33	8.46	0.22	0.28	5.50	38.23	11.84
I X S	1	1.81	0.04	0.01	0.06	1.45	2.37	1.74
K X S	1	4.49	0.10	0.63	0.00	4.19	4.09	1.22
I X K X S	1	1.87	0.11	1.16	1.17	1.30	0.42	1.03
Error (c)	8							

(continued ...)

1

Significance levels

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.005$

TABLE B-24 (continued)

Variable:		Osmotic Potential						
		Sample time (Day)						
Source of variation	df	1	4	6	8	10	12	14
Block	2							*
Irrig. (I)	1	3.83	0.00	3.09	0.98	1.16	10.80	72.20
Error (a)	2							
KCl (K)	1	0.17	3.95	1.40	3.84	2.41	158.77	1.24
I X K	1	0.15	0.45	4.56	0.46	0.16	20.04	1.79
Error (b)	4							
Species (S)	1	269.80	114.58	22.58	2.26	3.40	11.46	6.36
I X S	1	1.35	0.01	0.93	0.08	0.29	0.08	0.94
K X S	1	1.41	0.23	1.57	3.78	1.31	1.41	0.00
I X K X S	1	0.00	1.22	0.00	0.24	0.68	0.45	0.03
Error (c)	8							

(continued ...)

TABLE B-24 (continued)

Variable:		Turgor Pressure						
		Sample time (Day)						
Source of variation	df	1	4	6	8	10	12	14
Block	.2							
Irrig. (I)	1	0.63	48.00 *	6.62	1.13	1.17	11.06	1.90
Error (a)	2							
KCl (K)	1	0.12	1.34	0.47	0.87	0.45 *	0.84	0.15
I X K	1	0.16	3.08	0.37	1.38	13.58	1.00	0.02
Error (b)	4							
Species (S)	1	28.85 ***	14.54 **	18.84 ***	3.32	3.31	16.71 ***	0.06 *
I X S	1	3.28	0.10	0.44	0.00	4.00 *	4.15	10.65
K X S	1	0.89	0.01	0.05	2.78	7.83	1.42	2.16
I X K X S	1	1.15	1.51	1.10	2.40	1.15	0.02	0.99
Error (c)	8							

(continued ...)

TABLE B-24 (continued)

Variable:		Relative Water Content						
		Sample time (Day)						
Source of variation	df	1	4	6	8	10	12	14
Block	2							
		***	***	***	*	*	*	***
Irrig. (I)	1	18.08	35.14	40.91	5.43	5.58	5.74	58.68
Error (a)	2							
		*				*	***	
KCl (K)	1	9.89	0.00	0.85	1.75	9.05	17.08	1.52
			*					
I X K	1	0.04	6.49	1.01	0.89	1.67	0.07	0.64
Error (b)	4							
		***	***	***	***	***	***	***
Species (S)	1	36.20	106.00	96.50	59.79	37.38	15.45	21.99

I X S	1	0.08	4.63	20.65	3.21	0.00	0.16	3.72
K X S	1	0.24	0.01	0.89	4.11	2.73	0.42	0.38
I X K X S	1	0.29	0.07	0.49	0.26	2.71	0.67	0.94
Error (c)	8							

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 TABLE B-25. Summary of analysis of variance (F values) and significance levels of water relations parameters of conditioned Douglas-fir and jack pine seedlings over time during the second growth room drought period.

Source of variation	df	Water Relations Parameter			
		Total Potential	Osmotic Potential	Turgor Pressure	Relative Water Content
Blocks	2				
		*	*		**
Irrig. (I)	1	20.37	79.71	1.81	126.56
Error (a)	2				
KCl (K)	1	4.55	3.33	0.25	1.15
		*			
I X K	1	12.64	1.52	1.28	0.00
Error (b)	4				
		***	***		***
Species (S)	1	32.99	48.39	0.15	911.71
I X S	1	0.15	1.17	2.20	9.04
K X S	1	0.71	0.25	1.40	7.92
I X K X S	1	0.20	0.41	0.06	0.04
Error (c)	8				
		***	***	***	***
Sample (T)	6	171.74	124.98	11.05	141.97
		***	***	*	
I X T	6	6.84	10.43	2.83	1.05
		***	***		***
K X T	6	4.05	3.90	0.50	5.47
I X K X T	6	1.89	1.52	1.93	1.21
		***	*	***	***
S X T	6	9.30	2.25	5.30	6.13
		*		***	**
I X S X T	6	1.98	0.52	6.75	3.02
		**		*	
K X S X T	6	3.33	0.91	2.55	1.82
I X K X S X T	6	1.21	0.31	1.05	1.28
Error (d)	96				

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-26. Means of total water potential of conditioned Douglas-fir and jack pine seedlings evaluated on seven occasions (experimental day) during the second growth room drought period.

Species	Treatment	Sample time (Day)							Mean
		1	4	6	8	10	12	14	
----- MPa -----									
Df	D0	0.71	1.02	1.23	1.23	3.69	3.81	5.86	2.51
	D100	0.77	0.87	1.09	2.14	3.14	5.99	6.20	2.89
	W0	0.77	0.77	0.92	1.50	3.84	3.50	4.87	2.31
	W100	0.80	0.88	0.98	1.52	1.53	4.14	4.60	2.07
									Species Mean: 2.44
JP	D0	0.66	0.70	1.16	1.51	1.95	2.35	4.25	1.82
	D100	0.45	0.68	1.28	2.09	2.11	3.00	6.20	2.26
	W0	0.51	0.48	0.97	1.39	2.16	2.56	3.03	1.58
	W100	0.48	0.59	0.98	1.72	2.33	2.41	2.83	1.62
									Species Mean: 1.82

TABLE B-27. Means of osmotic potential of conditioned Douglas-fir and jack pine seedlings evaluated on seven occasions (experimental day) during the second growth room drought period.

Species	Treatment	Sample time (Day)							Mean
		1	4	6	8	10	12	14	
----- MPa -----									
Df	D0	2.14	2.11	2.13	2.32	4.11	4.32	6.96	3.47
	D100	2.15	2.19	2.15	2.46	3.32	6.31	8.28	3.83
	W0	2.15	2.15	2.24	2.36	3.71	3.62	5.01	3.03
	W100	2.19	2.16	2.19	2.40	2.61	4.45	4.99	3.00
									Species Mean: 3.34
JP	D0	1.65	1.61	2.00	1.87	3.13	3.74	5.19	2.74
	D100	1.58	1.62	1.99	2.61	2.58	4.56	6.64	3.08
	W0	1.72	1.54	1.80	1.97	2.53	2.81	4.36	2.39
	W100	1.69	1.70	1.90	2.36	2.85	3.31	4.13	2.56
									Species Mean: 2.69

TABLE B-28. Means of turgor pressure of conditioned Douglas-fir and jack pine seedlings evaluated on seven occasions (experimental day) during the second growth room drought period.

Species	Treatment	Sample time (Day)							Mean
		1	4	6	8	10	12	14	
		----- MPa -----							
Df	D0	1.43	1.10	1.08	1.09	0.42	0.52	1.11	0.96
	D100	1.38	1.32	1.06	0.32	0.18	0.32	2.08	0.95
	W0	1.38	1.39	1.32	0.86	0.00	0.12	0.14	0.72
	W100	1.38	1.28	1.22	0.88	1.08	0.31	0.39	0.93
								Species Mean:	0.89
JP	D0	0.99	0.90	0.85	0.36	1.19	1.39	0.94	0.95
	D100	1.13	0.94	0.70	0.52	0.47	1.56	0.44	0.82
	W0	1.21	1.06	0.82	0.58	0.38	0.25	1.33	0.80
	W100	1.20	1.11	0.92	0.63	0.52	0.90	1.29	0.94
								Species Mean:	0.88

TABLE B-29. Means of relative water content of conditioned Douglas-fir and jack pine seedlings evaluated on seven occasions (experimental day) during the second growth room drought period.

Species	Treatment	Sample time (Day)							Mean
		1	4	6	8	10	12	14	
----- % -----									
Df	D0	88.8	93.2	93.0	93.6	70.3	66.7	50.3	79.4
	D100	89.9	95.4	94.1	91.6	83.2	57.8	48.8	80.1
	W0	91.3	96.9	92.9	92.1	77.2	74.8	67.3	84.6
	W100	93.3	95.0	92.3	95.3	93.1	61.4	64.8	85.1
									Species Mean: 82.3
JP	D0	81.7	81.1	66.5	70.3	50.3	52.6	46.6	64.2
	D100	85.0	82.6	73.1	51.4	63.1	42.5	35.0	61.8
	W0	84.8	88.6	83.8	77.3	68.0	57.8	45.2	72.2
	W100	86.7	87.0	84.0	70.5	62.4	54.4	45.0	70.0
									Species Mean: 67.1
Species	Irrigation	Irrigation X Time (Day)							Mean
		1	4	6	8	10	12	14	
----- % -----									
Df	Daily	89.4	94.3	93.6	92.6	76.7	62.3	49.5	79.8
	Weekly	92.3	96.0	92.6	93.7	85.2	68.1	66.1	84.8
Jp	Daily	83.4	81.8	69.9	60.9	56.7	47.6	40.8	63.0
	Weekly	85.8	87.8	83.9	73.9	65.2	56.1	45.1	71.0

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 TABLE B-30. Summary of analysis of variance (F values) and significance levels of water relation parameters determined by the pressure-volume technique of conditioned Douglas-fir and jack pine seedlings over time during the second growth room drought period. See Appendix A for definitions of abbreviations.

Source of variation	df	OPFT	OPZT	RWC @ TLP	TSWC @ TLP	Ra	ME @ .995	Dwt./ T.Wt.	WSFT/ Dwt.
Blocks	1								
Irrig. (I)	1	7.76	0.05	0.71	2.79	0.11	1.78	7.53	1.47
Error (a)	1								
KCl (K)	1	0.23	0.37	1.73	0.03	1.97	0.25	0.18	0.61
I X K	1	1.27	0.01	0.02	1.37	4.15	0.13	0.77	2.29
Error (b)	2								
		***	***	***	***	***	***	**	
Species (S)	1	228.55	162.39	153.93	131.06	68.65	27.82	28.49	5.31
I X S	1	0.16	1.79	8.23	3.84	0.31	0.89	0.42	0.13
K X S	1	0.45	3.05	4.65	0.21	1.14	0.58	0.63	0.69
I X K X S	1	0.36	3.30	3.16	0.88	1.43	0.00	0.32	0.24
Error (c)	4								
		***	***						
Sample (T)	2	8.26	12.23	2.96	3.01	1.97	0.08	1.21	1.21
I X T	2	0.05	0.60	0.42	0.86	0.10	0.84	1.16	0.15
								*	*
K X T	2	2.02	2.59	1.08	0.16	2.91	1.95	5.54	3.91
I X K X T	2	1.36	0.34	1.49	1.88	0.01	1.50	0.23	0.07
		*			*				
S X T	2	5.56	2.05	3.17	3.79	0.56	0.20	0.46	0.72
I X S X T	2	2.87	1.00	0.68	2.28	4.28	0.50	0.09	3.61
K X S X T	2	0.38	0.45	0.44	0.25	0.20	2.71	0.27	0.91
I X K X S X T	2	1.06	1.89	2.94	2.07	0.83	0.76	0.06	0.16
Error (d)	16								

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-31. Summary of analyses of variance (F values) and significance level of epicotyl length of Douglas-fir and Jack pine seedlings for each week during the conditioning period.

Source of variation	df	Sample Week					
		15	16	17	18	19	20
Block	4						
Irrig. (I)	1	0.25	0.02	0.03	2.78	1.98	6.18
Error (a)	4						
KCl (K)	1	0.56	0.00	0.09	0.45	0.12	0.16
I X K	1	0.02	0.10	0.11	0.05	0.71	1.26
Error (b)	8						
Species (S)	1	1.16	12.02	65.53	52.42	102.16	109.90
I X S	1	0.73	0.68	1.02	0.27	0.49	1.13
K X S	1	0.02	0.51	0.05	0.05	0.05	0.19
I X K X S	1	0.02	0.27	0.56	0.42	0.53	1.60
Error (c)	16						

1

Significance level

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-32. Summary of analysis of variance (F values) and significance levels of morphological parameter of 21 week-old conditioned Douglas-fir and jack pine container seedlings.

Source of variation	df	Root Collar Dia.	Shoot Length	Shoot Dry Wt.	Root Area Index	Root Dry wt.	Sdlg. Dry Wt.	Top: Root Ratio
Block	4							
Irrig. (I)	1	***	*	*	*	*	*	
Error (a)	4							6.89
KC1 (K)	1	1.68	0.79	0.90	5.60	4.12	1.35	4.54
I X K	1	0.75	1.24	0.71	2.02	0.49	0.31	11.20
Error (b)	8							
Species (S)	1	2.31	***	***	***	2.20	***	***
I X S	1	1.90	0.03	0.04	0.63	1.75	0.03	13.87
K X S	1	0.15	0.00	0.54	0.07	0.10	0.42	0.35
I X K X S	1	0.45	0.04	1.32	0.01	0.53	1.16	0.53
Error (c)	16							

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

1
 TABLE B-33. Summary of analysis of variance (F values) and significance levels of nutrient concentrations of foliage of 21 week-old conditioned Douglas-fir and jack pine container seedlings prior to out planting in the nursery experiment.

Source of variation	df	Nutrient					
		N	P	K	Ca	Mg	Cl ⁻
Block	4						
		*			*		*
Irrig. (I)	1	14.02	3.94	5.22	19.61	1.24	12.66
Error (a)	4						
				*			***
KCl (K)	1	0.96	0.30	9.91	0.03	1.33	173.28
I X K	1	2.24	1.23	0.07	8.69	0.05	3.97
Error (b)	8						
		**	***	***	***	***	*
Species (S)	1	9.29	385.98	21.33	41.64	23.63	5.24
		*			**		
I X S	1	6.64	0.45	0.04	9.64	1.05	0.18
							*
K X S	1	0.28	0.01	0.18	2.01	1.57	8.22
I X K X S	1	2.44	0.15	0.29	0.17	0.14	0.06
Error (c)	16						

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-34. Summary of analysis of variance (F values) and significance levels of nutrient concentrations of roots of 21 week-old conditioned Douglas-fir and jack pine container seedlings prior to out planting in the nursery experiment.

Source of variation	df	Nutrient					
		N	P	K	Ca	Mg	Cl ⁻
Block	4						
Irrig. (I)	1	0.68	**	***	2.02	1.69	*
Error (a)	4		27.63	270.44			12.06
KCl (K)	1	0.20	5.00	***	*	0.00	***
I X K	1	0.04	0.03	0.13	0.96	0.08	3.00
Error (b)	8						
Species (S)	1	2.57	***	*	***	***	***
I X S	1	*	*	0.46	0.80	8.48	0.64
K X S	1	0.00	0.00	0.22	1.57	2.63	0.09
I X K X S	1	0.08	0.92	0.01	0.00	1.10	0.13
Error (c)	16						

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-35. Summary of analysis of variance (F values) and significance levels of morphological parameters for Douglas-fir and jack pine seedlings in relation to soil type and conditioning treatment in response to a period of increasing soil water deficit during the nursery experiment.

Species / Morphological Parameter					
Source of variation	df	Douglas-fir		Jack pine	
		Epicotyl Length	Root Collar Dia.	Epicotyl Length	Root Collar Dia.
Block	1				
Soil (D)	1	2.18	18.26	8.79	0.79
Error (a)	1				
		*			
Irrig. (I)	1	24.80	15.17	10.44	10.83
D X I	1	0.96	2.21	0.84	0.01
Error (b)	2				
KCl (K)	1	0.90	0.10	0.21	0.48
D X K	1	2.24	2.10	0.22	0.23
I X K	1	0.45	0.04	0.86	2.16
D X I X K	1	3.22	2.03	0.07	0.06
Error (c)	4				
				*	
Time (T)	7	0.56	1.20	2.68	2.15

D X T	7	3.82	1.69	0.89	0.64
		*			
I X T	7	2.55	1.40	0.86	0.85
D X I X T	7	0.69	1.19	1.73	0.50
K X T	7	1.54	1.54	0.56	0.58
D X K X T	7	2.05	1.41	1.56	0.78
I X K X T	7	0.69	1.31	0.86	0.30
D X I X K X T	7	0.89	1.28	0.81	0.73
Error (d)	56				

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-36. Summary of analysis of variance (F values) and significance levels of morphological parameters of conditioned Douglas-fir and jack pine seedlings in response to increasing soil water deficits on two soil types the nursery experiment.

Source of variation	df	Soil Type / Morphological Parameter			
		Burnt Woods		River Sand	
		Epicotyl Length	Root Collar Dia.	Epicotyl Length	Root Collar Dia.
Block	1				
*					
Irrig. (I)	1	22.89	9.14	324.00	4.00
Error (a)	1				
KCl (K)	1	4.36	7.53	0.33	0.03
		*	*		
I X K	1	76.13	40.56	0.02	0.01
Error (b)	2				
		***		***	***
Species (S)	1	341.91	0.33	170.29	62.98
					*
I X K	1	5.63	0.00	0.20	10.50
					*
K X S	1	0.02	0.12	3.16	7.94
I X K X S	1	0.55	0.07	1.13	7.42
Error (c)	4				
Time (T)	7	1.69	1.79	1.69	1.01

I X T	7	0.59	0.22	3.87	1.61
K X T	7	0.94	1.81	1.33	0.98
I X K X T	7	0.26	0.42	1.25	1.70
				*	
S X T	7	1.92	1.85	2.92	0.65
I X S X T	7	0.66	0.50	1.77	2.00
				**	
K X S X T	7	0.96	0.66	3.17	0.48
I X K X S X T	7	0.61	0.74	1.59	0.81
Error (d)	56				

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-37. Progression of mean epicotyl length of conditioned Douglas-fir and jack pine seedlings during the nursery drought period on two soil types.

Soil	Sp.	Treat- ment	Sample time / Epicotyl length (cm)								Means	
			1	2	3	4	5	6	7	8	Irr.	Spec. Soil
Burnt Woods	Df	D0	21.00	22.00	27.50	20.50	23.50	23.50	23.00	23.25		
		D100	21.25	22.75	27.25	23.25	30.75	28.25	22.75	24.25	24.03	
		W0	19.25	22.50	21.25	20.25	20.25	19.75	22.50	21.75		
		W100	19.75	20.00	23.50	16.75	20.75	21.50	16.00	18.75	20.28	22.15
	Jp	D0	11.50	12.25	11.50	11.75	10.25	12.00	14.75	11.00		
		D100	13.50	15.25	16.50	10.50	9.75	11.00	13.75	13.50	12.42	
		W0	13.00	14.00	10.50	11.25	11.50	11.00	11.25	10.50		
		W100	11.75	12.50	13.50	11.25	10.25	10.00	10.00	8.75	11.31	11.86 17.01
River Sand	Df	D0	20.00	22.00	24.25	25.00	23.25	24.25	24.00	24.25		
		D100	19.50	24.25	21.50	22.75	21.25	19.25	18.00	21.00	22.15	
		W0	25.00	19.75	14.00	20.25	19.25	20.75	23.00	18.75		
		W100	19.75	23.00	16.50	21.50	18.25	13.75	19.00	21.75	19.64	20.90
	Jp	D0	15.00	17.75	17.00	16.00	13.00	14.50	9.00	7.75		
		D100	13.00	16.75	14.25	14.00	11.75	20.00	13.75	13.75	14.20	
		W0	13.75	11.00	13.25	10.75	13.25	12.25	11.25	12.50		
		W100	12.25	14.00	12.50	11.00	12.00	11.75	14.00	10.00	12.21	13.21 17.05

TABLE B-38. Progression of mean root collar diameter of conditioned Douglas-fir and jack pine seedlings during the nursery drought period on two soil types.

Soil	Sp.	Treat- ment	Sample time (wk) / Root collar diameter (mm)								Means	
			1	2	3	4	5	6	7	8	Irr.	Spec. Soil
Burnt Woods	Df	D0	2.78	2.63	3.10	2.78	2.83	2.93	3.33	3.00		
		D100	2.53	2.93	3.25	2.93	3.45	3.85	2.93	3.15	3.05	
		W0	2.33	2.65	2.60	2.45	2.60	2.80	2.83	2.88		
		W100	2.50	2.68	2.50	2.18	2.93	3.05	2.73	2.53	2.64	2.85
	Jp	D0	3.40	3.15	2.70	2.83	2.72	3.05	3.48	2.95		
		D100	3.33	3.35	3.53	2.88	2.90	3.15	3.30	2.90	3.10	
		W0	2.98	2.58	2.63	2.70	2.45	2.65	3.05	2.83		
		W100	2.43	2.73	2.80	2.65	2.40	2.73	2.80	2.50	2.68	2.89
River Sand	Df	D0	2.45	2.85	3.48	2.65	2.83	2.50	2.78	2.75		
		D100	2.55	2.80	2.58	2.58	2.50	2.55	2.18	2.90	2.68	
		W0	2.75	2.18	2.18	2.55	2.45	2.73	2.73	2.45		
		W100	2.63	2.80	2.35	2.48	2.35	2.43	2.58	2.33	2.50	2.59
	Jp	D0	3.40	3.18	3.15	3.28	2.68	3.00	2.60	2.50		
		D100	3.23	3.40	2.88	3.05	2.83	2.58	3.00	3.13	3.05	
		W0	2.60	2.63	2.60	2.58	2.43	2.68	2.95	2.78		
		W100	2.73	2.75	2.60	2.60	2.55	2.68	2.68	2.58	2.65	2.65

1
 TABLE B-39. Summary of analysis of variance (F values) and significance levels for total water potential (T.P.), osmotic potential (O.P.), pressure potential (P.P.), and relative water content (RWC), by species, in relation to soil type, conditioning treatment and increasing soil water deficits (time) during the nursery experiment.

Source of variation	df	Species / Water Relations Parameter							
		Douglas-fir				Jack pine			
		T.P.	O.P.	P.P.	RWC	T.P.	O.P.	P.P.	RWC
Block	1								
Soil (D)	1	***	***		***			*	
Error (a)	1	3595.17	332.09	74.68	2566.69	52.39	15.39	2945.96	133.47
Irrig. (I)	1	***	*	*	**				
D X I	1	45.43	23.74	12.42	23.08	0.58	0.01	2.29	0.31
Error (b)	2	28.01	31.42	3.47	19.92	0.13	0.77	0.08	0.20
KCl (K)	1	0.67	0.32	0.22	0.22	0.60	0.02	30.19	1.13
D X K	1	0.87	0.24	1.11	0.65	0.17	0.00	8.95	1.31
I X K	1	0.36	0.02	1.75	0.00	1.07	0.75	4.28	0.55
D X I X K	1	0.03	0.01	0.01	0.02	1.00	0.44	11.12	0.36
Error (c)	4								
Time (T)	7	***	***	***	***	***	***	***	***
D X T	7	***	*	*	***	*	*	*	***
I X T	7	25.06	11.69	23.36	13.79	21.17	12.13	18.95	24.49
D X I X T	7	3.58	2.29	2.58	4.01	2.97	2.95	2.22	6.76
K X T	7	*	*		*				
I X K X T	7	2.69	2.64	1.28	2.31	0.66	1.31	0.73	0.89
D X I X K X T	7	2.40	1.79	1.71	2.51	0.61	0.98	0.11	0.63
K X T	7	1.45	0.89	1.11	0.67	0.59	0.39	0.80	0.32
D X K X T	7	1.39	1.64	0.70	0.83	0.80	0.31	1.70	0.50
I X K X T	7	0.22	0.26	0.85	0.50	0.19	0.24	0.18	0.82
D X I X K X T	7	0.21	0.09	0.25	0.35	0.27	0.22	0.21	0.70
Error (d)	56								

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

1

TABLE B-40. Summary of analysis of variance (F values) and significance levels for total water potential (T.P.), osmotic potential (O.P.), pressure potential (P.P.), and relative water content (RWC) of conditioned seedlings, by soil type, in relation to increasing soil water deficits (time) during the nursery experiment.

		Soil Type / Water Relations Parameter							
		Burnt Woods				River Sand			
Source of variation	df	T.P.	O.P.	P.P.	RWC	T.P.	O.P.	P.P.	RWC
Block	1								
Irrig. (I)	1	1.01	22.35	2.14	43.71	7.27	14.78	4.37	1.85
Error (a)	1								
KCl (K)	1	0.12	0.07	0.06	0.24	0.56	0.12	6.06	0.88
I X K	1	1.26	0.61	0.81	0.14	0.40	0.12	2.93	0.13
Error (b)	2								
Species (S)	1	*	***	***	***	*	***	***	***
		11.54	311.50	446.54	212.68	0.78	14.47	112.28	85.95
I X S	1	0.16	2.86	0.77	0.02	9.02	3.49	15.78	0.29
K X S	1	0.91	0.00	2.53	0.06	0.13	0.60	0.54	0.55
I X K X S	1	2.08	0.13	4.19	0.00	0.89	1.03	0.11	0.73
Error (c)	4								
Time (T)	7	***	***	***	***	***	***	***	***
		211.91	61.11	43.17	26.03	20.94	12.55	17.86	22.52
I X T	7	0.92	2.91	1.04	1.49	2.51	2.82	1.42	1.68
K X T	7	0.82	2.56	3.30	0.53	0.33	0.25	0.40	0.35
I X K X T	7	0.64	0.49	0.95	0.72	0.15	0.90	0.27	0.50
S X T	7	***	***	*	***			*	***
		8.48	6.55	2.88	4.02	0.93	0.23	2.75	4.27
I X S X T	7	0.58	0.26	0.61	0.23	0.78	0.51	0.81	0.94
K X S X T	7	0.62	0.26	0.47	0.53	1.82	1.31	1.41	0.67
I X K X S X T	7	*		*					
		2.28	0.18	2.46	1.08	0.24	0.31	0.14	0.76
Error (d)	56								

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-41. Progression of mean total water potential of conditioned Douglas-fir and jack pine seedlings during the nursery drought period on two soil types.

Soil	Sp.	Treat- ment	Sample Time (wk)/ Total Water Potential								Means		
			1	2	3	4	5	6	7	8	Irr.	Spec.	Soil
----- - MPa -----													
Burnt Woods	Df	D0	0.34	0.35	0.53	0.58	0.83	1.03	1.47	1.75			
		D100	0.24	0.38	0.38	0.50	1.05	0.80	1.33	1.43	0.813		
		W0	0.33	0.25	0.43	0.52	0.68	0.71	1.24	1.33			
		W100	0.25	0.24	0.47	0.45	0.85	0.89	1.23	1.69	0.724	0.768	
	Jp	D0	0.30	0.37	0.59	0.83	1.07	1.22	1.41	1.24			
		D100	0.34	0.34	0.59	0.82	1.12	1.25	1.33	1.51	0.896		
		W0	0.26	0.36	0.55	0.67	1.05	1.10	1.34	1.33			
		W100	0.30	0.48	0.57	0.70	1.05	1.17	1.21	1.32	0.829	0.862	0.815
River Sand	Df	D0	0.32	0.62	1.22	0.62	1.05	2.17	3.34	3.25			
		D100	0.31	0.65	1.06	1.23	1.10	1.14	3.10	5.17	1.684		
		W0	0.26	0.39	0.74	0.54	0.96	1.03	0.81	1.59			
		W100	0.28	0.55	0.68	1.02	0.79	1.02	0.92	3.00	0.911	1.280	
	Jp	D0	0.41	0.48	0.76	0.85	1.31	1.95	2.14	4.12			
		D100	0.43	0.64	0.50	1.07	1.75	2.18	2.04	2.66	1.457		
		W0	0.34	0.47	0.71	0.47	1.45	1.58	1.36	2.34			
		W100	0.57	0.50	0.83	1.34	1.82	2.03	3.35	2.08	1.266	1.361	1.321

TABLE B-42. Progression of mean osmotic potential of conditioned Douglas-fir and jack pine seedlings during the nursery drought period on two soil types.

Soil	Sp.	Treat- ment	Sample Time (wk) / Osmotic Potential								Means		
			1	2	3	4	5	6	7	8	Irr.	Spec.	Soil
----- - MPa -----													
Burnt Woods	Df	D0	2.07	2.15	2.18	2.32	2.55	2.53	2.73	2.94			
		D100	2.16	2.26	2.28	2.28	2.48	2.39	2.61	2.81	2.421		
		W0	2.29	2.30	2.21	2.33	2.39	2.34	2.56	2.98			
		W100	2.41	2.41	2.36	2.31	2.51	2.44	2.57	2.73	2.447	2.434	
	Jp	D0	1.62	1.85	1.81	2.13	2.35	2.41	2.43	2.45			
		D100	1.80	1.88	1.86	2.12	2.30	2.32	2.34	2.32	2.126		
		W0	1.87	2.03	1.85	2.17	2.30	2.38	2.46	2.46			
		W100	2.00	2.05	1.96	2.17	2.30	2.33	2.47	2.37	2.203	2.164	2.299
River Sand	Df	D0	2.28	2.23	2.52	2.43	2.63	2.91	3.93	3.85			
		D100	2.27	2.19	2.41	2.75	2.66	2.49	3.59	5.48	2.915		
		W0	2.24	2.40	2.51	2.37	2.55	2.55	2.50	2.71			
		W100	2.42	2.46	2.24	2.60	2.62	2.54	2.46	3.60	2.548	2.731	
	Jp	D0	1.85	1.84	1.98	2.19	2.34	2.73	2.82	4.73			
		D100	1.77	1.95	1.81	2.20	2.46	2.82	2.72	3.70	2.495		
		W0	2.02	2.02	2.01	2.08	2.50	2.48	2.42	3.01			
		W100	2.01	2.07	2.10	2.44	2.55	2.55	3.22	2.98	2.404	2.450	2.590

TABLE B-43. Progression of mean turgor pressure of conditioned Douglas-fir and jack pine seedlings during the nursery drought period on two soil types.

Soil	Sp.	Treat- ment	Sample Time (wk) / Turgor Pressure								Means	
			1	2	3	4	5	6	7	8	Irr.	Spec. Soil
----- MPa -----												
Burnt Woods	Df	D0	1.73	1.80	1.64	1.74	1.71	1.50	1.25	1.19		
		D100	1.92	1.88	1.90	1.78	1.43	1.60	1.28	1.38	1.609	
		W0	1.96	2.05	1.78	1.81	1.70	1.63	1.32	1.65		
		W100	2.17	2.17	1.89	1.85	1.66	1.54	1.34	1.04	1.723	1.666
	Jp	D0	1.32	1.48	1.22	1.30	1.28	1.19	1.03	1.21		
		D100	1.46	1.53	1.27	1.30	1.17	1.07	1.02	0.82	1.230	
		W0	1.61	1.68	1.30	1.50	1.24	1.27	1.32	1.13		
		W100	1.70	1.57	1.39	1.46	1.34	1.16	1.26	1.05	1.374	1.302 1.484
River Sand	Df	D0	1.97	1.61	1.30	1.81	1.59	0.74	0.56	0.59		
		D100	1.96	1.54	1.34	1.51	1.56	1.36	0.49	0.31	1.265	
		W0	1.99	2.00	1.76	1.83	1.59	1.51	1.70	1.12		
		W100	2.14	1.91	1.56	1.58	1.83	1.52	1.54	0.61	1.637	1.451
	Jp	D0	1.44	1.36	1.23	1.34	1.03	0.77	0.68	0.62		
		D100	1.35	1.31	1.31	1.12	0.71	0.64	0.68	1.04	1.039	
		W0	1.68	1.55	1.30	1.61	1.05	0.90	1.07	0.66		
		W100	1.44	1.57	1.27	1.10	0.73	0.52	0.87	0.90	1.139	1.089 1.270

TABLE 8-44. Progression of mean relative water contents of conditioned Douglas-fir and jack pine seedlings during the nursery drought period on two soil types.

Soil	Sp.	Treat- ment	Sample Time (wk) / Relative Water Content								Means		
			1	2	3	4	5	6	7	8	Irr.	Spec. Soil	
----- % -----													
Burnt Woods	Df	D0	93.3	95.4	94.8	92.5	89.6	86.6	88.9	87.3			
		D100	95.8	94.0	89.4	94.6	92.4	90.6	88.0	89.3	91.5		
		W0	90.7	94.7	92.8	92.3	93.6	91.2	89.0	87.2			
		W100	92.7	92.7	95.7	92.9	92.1	91.4	86.9	89.4	91.6	91.5	
	Jp	D0	86.9	88.2	83.8	81.9	79.9	77.0	75.4	78.3			
		D100	92.1	87.7	84.3	81.9	78.3	77.2	77.5	75.9	81.6		
		W0	88.1	86.4	85.5	83.5	80.1	77.8	76.5	78.4			
		W100	85.7	87.0	85.0	84.1	80.4	79.6	75.8	77.8	82.0	81.8	86.7
River Sand	Df	D0	93.0	94.6	92.2	92.9	91.6	83.8	74.0	73.5			
		D100	89.3	91.1	93.4	89.9	90.9	91.8	67.3	65.2	85.9		
		W0	91.3	94.0	90.5	94.2	92.8	93.1	90.5	85.6			
		W100	92.4	94.3	92.0	90.0	92.7	92.0	90.4	75.6	90.7	88.3	
	Jp	D0	87.8	87.2	82.9	82.4	73.3	57.8	56.6	48.4			
		D100	83.1	85.7	85.3	81.8	68.5	51.0	61.4	46.0	71.2		
		W0	85.9	86.5	84.5	85.9	74.7	76.0	74.0	54.0			
		W100	84.3	85.6	83.1	74.1	69.7	63.7	46.9	58.4	74.2	72.7	80.5

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TABLE B-45. Summary of analysis of variance (F values) and significance levels of water relations parameters determined from the pressure-volume technique for Douglas-fir in response to conditioning treatment and soil type during a period of increasing soil water deficits in the nursery experiment. See Appendix A for definitions of abbreviations.

Source of variation	df	Plant Water Relations Parameter							
		OPFT	OPZT	RWC @		ME @		Dry Wt.	
				TLP	TLP	Ra	.995 RWC	turgid Wt.	WSFT Dry Wt.
Blocks	1								
Irrig. (I)	1	0.12	43.03	0.05	0.00	0.00	0.92	0.06	0.28
Error (a)	1								
KCl (K)	1	0.53	0.17	0.01	4.43	1.78	0.05	1.06	0.13
I X K	1	0.14	0.17	0.81	3.46	0.46	0.14	0.67	0.41
Error (b)	2								
Soil type (D)	1	0.69	0.02	0.14	1.44	0.73	0.03	1.82	20.41
I X D	1	0.39	5.79	0.00	1.31	10.12	0.00	0.54	0.04
K X D	1	0.21	1.41	0.07	0.06	3.29	0.20	1.67	2.60
I X K X D	1	0.03	0.08	0.05	0.02	2.29	0.01	1.73	4.17
Error (c)	4								
Time (T)	2	3.15	7.70	2.44	24.09	9.96	11.94	1.10	37.16
I X T	2	0.22	0.03	0.56	0.39	1.29	0.56	1.28	5.82
K X T	2	0.40	0.16	0.14	1.45	0.33	1.84	0.42	0.39
I X K X T	2	0.28	0.19	0.01	0.31	0.26	0.65	0.94	0.35
D X T	2	3.29	0.94	0.07	5.89	4.18	0.85	0.67	6.42
I X D X T	2	0.78	0.62	2.82	0.27	3.82	3.83	1.49	6.64
K X D X T	2	0.00	0.03	0.07	0.03	0.23	0.17	0.80	0.43
I X K X D X T	2	1.05	1.44	0.56	0.36	0.05	0.54	0.80	0.33
Error (d)	16								

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$

TABLE B-46. Summary of analysis of variance (F values) and significance levels of water relations parameters determined from the pressure-volume curve analysis for jack pine in response to conditioning treatment and soil type during a period of increasing soil water deficits in the nursery experiment. See Appendix A for definitions of abbreviations.

Source of variation	df	Plant Water Relations Parameter							
		OPFT	OPZT	RWC @ TLP	RSWC @ TLP	Ra	ME @ .995 RWC	Dry Wt. turgid Wt.	WSFT Dry Wt.
Blocks	1				*				
Irrig. (I)	1	2.78	0.41	0.55	491.45	1.92	0.19	30.99	14.10
Error (a)	1								
KCl (K)	1	6.88	0.56	0.04	8.81	8.64	0.51	6.33	0.94
I X K	1	3.34	3.33	0.04	0.15	0.31	1.06	0.98	0.05
Error (b)	2								
Soil type (D)	1	2.02	0.71	0.01	1.51	5.39	0.02	7.74	0.03
I X D	1	0.30	1.17	1.44	0.07	4.31	1.83	0.53	1.16
K X D	1	1.52	0.15	0.74	1.92	0.45	0.28	8.03	0.22
I X K X D	1	0.12	0.12	0.03	0.04	0.01	0.01	0.04	0.01
Error (c)	4								
Time (T)	2	0.11	2.14	1.12	5.60	3.64	2.90	1.56	5.81
I X T	2	1.59	1.63	0.34	0.47	0.34	0.15	0.39	0.64
K X T	2	1.89	2.95	0.39	0.84	0.03	0.86	1.36	0.12
I X K X T	2	0.65	0.28	0.30	0.64	1.19	0.66	2.03	0.05
D X T	2	2.06	0.45	0.53	2.47	1.39	0.62	0.05	0.07
I X D X T	2	0.78	1.15	0.34	0.94	0.57	0.39	1.33	0.92
K X D X T	2	0.56	0.21	0.45	0.43	0.29	2.33	0.90	0.20
I X K X D X T	2	0.39	1.24	0.13	0.14	0.02	0.74	1.30	0.08
Error (d)	16								

1

Significance levels

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.005$