EFFECTS OF WATER STRESS ON PHENOLOGY, PHYSIOLOGY, AND MORPHOLOGY OF CONTAINERIZED DOUGLAS-FIR (PSEUDOTSUGA MENZIESII (MIRB.) FRANCO) SEEDLINGS

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Signature redacted for privacy.

Abstract Approved –

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Approximately 3-4 month-old containerized Douglas-fir (Pseudotsuga

menziesii (Mirb.) Franco) seedlings (seed zone 262 and 271) were subjected to 6

moisture stress treatments (65, 53, 41, 29, 17 and 7% soil water content by volume

of dry soil) starting July 4 to September 22, 1991 at Forest Research Laboratory's

greenhouse at Oregon State University, Corvallis, OR. Seedlings were tested for

various phenological, physiological, and morphological parameters. All the

parameters were significantly affected by water stress treatments.

Moderate soil water content resulted in increased and earlier terminal bud

initiation and budset in seedlings whereas, too much and too little water content

caused decreased and delayed bud initiation, budset, and bud development. The

driest and wettest treatments apparently stressed these seedlings so severely and

kept them growing respectively that they took longer to set bud. A small

percentage of seedlings (13.1% of total 480 seedlings), after they had initiated bud

formation, resumed their growth with increasing soil water content.

Decreasing soil water content resulted in reduced total needle and root nutrient concentration and content (N, P, K, Ca, and Mg) except N concentration which was significantly higher at the lowest soil water content (7%). On the other hand, shoot nutrient concentration and content, measured at day 0 and 43, remained unaffected. Moisture stress treatments had also a profound effect on starch reserves in needles and roots. A significant decrease was found in starch concentration in roots (measured at day 0, 43, and 81) and in needles and roots (measured at day 81) with decreasing soil water content. Further analysis of needle:root starch concentration ratios showed a higher concentration in needles than that of roots, indicating that less starch was translocated from needles to roots due to severe moisture stress.

Seedlings treated with the lowest soil water content were most stressed and experienced the greatest plant moisture stress (22.34 and 23.95 bars pre-dawn and mid-day PMS, respectively). There was an approximately 398 and 211% increase in pre-dawn and mid-day PMS respectively from the wettest to driest treatments. Similarly, water stress treatments had the greatest effect on various morphological attributes. Shoot height, caliper, fresh and dry weights of shoots and roots (measured at day 0, 43, and 81), total shoot height and caliper, shoot and caliper growth, and total fresh and dry weights of needles, stems, branches and roots (measured at day 81) decreased significantly with decreasing soil water content. Most drastic effect was found at the driest treatment (7% soil water content), where, seedlings decreased approximately by 66, 44, 25, 25, and 69% in shoot height and caliper growth, total fresh weight of needles, stems and roots from the

wettest to driest treatments. This effect was also prominent in terminal bud development. Both terminal bud length and diameter were reduced approximately by 35 and 29% at the lowest soil water content. Severe moisture stress resulted in complete cessation of growth and breakdown of metabolic system of a few seedlings, thus, causing their mortality.

Effects of Water Stress on Phenology, Physiology,
and Morphology of Containerized Douglas-fir
(Pseudotsuga menziesii (mirb.) Franco) Seedlings

by

Shafiqur Rehman Khan

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THE EFFECTS OF WATER STRESS ON PHENOLOGY, PHYSIOLOGY, AND MORPHOLOGY OF CONTAINERIZED DOUGLAS-FIR (PSEUDOTSUGA MENZIESII (MIRB.) FRANCO) SEEDLINGS.

1. INTRODUCTION

1.1. BACKGROUND

The global human population has rapidly increased during the past several decades. It was recorded as 4 billion in the year 1975 and is estimated to rise up to 6.3 billion in the year 2000 (Peterson, 1969). Consequently demand for timber, fuelwood, and fodder and forage for animals is also greatly increased resulting in deforestation at an accelerated rate. Tropical forests are currently cleared at the rate of about 70,000 km^2 / year (National Press Academy, 1980). The earth's surface had a rich cover of forests covering about 6.2 billion ha, about 10,000 years ago, before the dawn of agriculture. These forests have shrunk to about 4.2 billion ha as a result of commercial timber harvesting, fuelwood collection and grazing. A large block of tropical forest, about 11.3 million ha, were cleared in the early 1980s while only 1.1 million ha were planted. The United States of America had about 385 million ha of forested area in 1630, but with the growing needs of an increasing population, the area had shrunk to 249 million ha by 1920 (Postal and Reise, 1988).

This alarming situation has necessitated and greatly emphasized the need for successful and cost effective reforestation programs. These programs will be

dependent on the production of vigorous and high quality seedlings that survive and grow well once planted. Foresters have relied for decades on stocktype designation, height and stem diameter to grade seedlings. However, the Nursery Technology Cooperative (NTC) at Oregon State University has developed a new concept of assessing seedling performance and quality called "the Target Seedling Concept" (TSC). The TSC means "to target specific physiological and morphological seedling characteristics that can be quantitatively linked with reforestation success" (Rose et al., 1990). and the target seedling is one that has a high probability of survival (Carlson and Miller, 1990).

It was also reported that, until recently, seedling quality was mainly judged and defined on the basis of morphological characteristics or physical appearance. Now, however, silviculturists have recognized the need for a greater understanding and knowledge of those aspects of seedling physiology that are critical to field performance (Brissettee and Carlson, 1987). Because morphological parameters do not indicate vitality and vigor of the seedlings, they are not considered good predictor for seedling performance (Mexal and Landis, 1990). Therefore, in addition to keeping morphological parameters of seedlings in view, it is also important to examine physiological parameters, (e.g.), carbohydrate reserves, root desiccation resistance, low temperature tolerance, and plant moisture stress (Ritchie and Tanaka, 1990).

Seedlings in the proper stage of dormancy with high carbohydrate reserves and nutrient contents are considered to be of high quality and perform better

when outplanted. These parameters are closely related to water stress. Duryea (1984) has pointed out that conifers growing in the Pacific Northwest PNW) complete their height growth in spring and early summer when there is adequate soil moisture available to them through seasonal precipitation. However, they set bud during summer and cease their growth when there is high evaporative demand and associated plant moisture stress (PMS) which prevents second flushing. It's at this stage that seedlings begin dormancy initiation. It is, therefore, crucial to closely monitor plant moisture stress throughout the growing season because too much or too little watering can harm seedling quality and subsequent field performance. So it is important to determine an optimal level of water stress at which container grown Douglas-fir seedlings can be induced to set their terminal buds (dormancy initiation) without depleting much of their carbohydrate reserves, nutrient contents and still maintain their vigor.

This study is a desegregated sub-unit of a larger research program which is currently being conducted by Oregon State University's Nursery Technology Cooperative. Other studies in this research program include: effect of root volume on field performance of 2+0 Douglas-fir and ponderosa pine, transplant shock in Douglas-fir seedlings, dormancy and cold hardiness, variable chlorophyll fluorescence as a use of cold hardiness and freezing stress, the influence of antidesiccants on physiology of 2+0 ponderosa pine, and effects of Moisturin™ on seedling performance relative to target seedlings. All studies aim at improving quality, vigor and performance potential of the seedlings.

In this study about 3-4 month old containerized Douglas-fir seedlings, grown in the Bureau of Land Management-Colton greenhouse near Portland, OR., were brought to a greenhouse at Oregon State University's Forest Research Laboratory in Corvallis in July 1991. These seedlings were subjected to 6 water stress treatments (65, 53, 41, 29, 17 and 7% soil water content by dry volume of soil) for about 12 weeks starting July 4, 1991 to September 22, 1991. A total of 1,680 randomly selected seedlings were destructively harvested at day 0, 43, and 81 (initial, middle, and final harvests respectively) to measure various morphological and physiological parameters. Seedlings were also monitored regularly for phenological parameters (e.g., terminal bud initiation, budset, resumption of growth after initial bud formation, and bud development) throughout the study. All the data were analyzed using SAS software while mean separation was accomplished using Fisher's Protected Least Significant Difference (FPLSD) at 5 and 1% significance levels. In this thesis, means refer to the "sample means" and not the "population means". Results are presented in graphical as well as tabulated form.

This study was conducted in cooperation with Nursery Technology Cooperative (NTC) of Forest Science Department, College of Forestry, Oregon State University, Corvallis, OR., Bureau of land Management (BLM), Portland, Pakistan Participant Training Program, (PPTP), and United States Agency for International Development (USAID), Washington, D. C.

1.2. JUSTIFICATION OF THE STUDY

Water stress is considered an important factor in a seedling's life cycle to induce early budset (dormancy initiation), cold hardiness, greater tolerance to exposure during handling of seedlings and increased field survival potential. The question arises as to how much water stress is enough. A moderate frequency of irrigation and nutrients has been reported to cause an increased shoot height, stem diameter and dry weight of styro-plugs 2 and 8 of lodgepole pine and interior spruce in a plastic covered frame shelter in British Columbia, Canada and New Mexico (Van Eerden, 1974). Too much watering promotes growth and seedlings continue to grow. As a result of this, delayed bud set may occur which inhibits completion of the subsequent phases of dormancy which are necessary for vigorous field growth of the seedlings (Duryea, 1984). Similarly, too little watering (high moisture stress) causes premature bud set and seedlings will be too small to meet minimum size standards (Zaerr et al., 1981 in Duryea, 1984). It also adversely affects nutrient contents and photosynthesis which results in depletion of carbohydrate reserves. Subsequently, all such negative interactions result in production of poor quality planting stock and may badly affect seedling field performance when outplanted. It means that the production cost of seedlings and cost per acre of reforestation will increase because of inferior quality seedlings and repeated planting of the area due to plantation failures. This cost would be very hard to justify and may result in low funding by various agencies and governments. It may also compel these funding agencies to change their priorities

resulting in the forestry sector being put on low priority on national as well as state or provincial level programs. Moreover, repeated reforestation failures and unjustified high costs can also be subjected to political criticism by public representatives. If it happens, it would be a misfortune for the forestry sector.

Therefore, it is, of immense importance to determine a level of water stress at which seedlings set terminal bud at the desired time without reducing their carbohydrate reserves, and nutrient contents. This can help produce high quality vigorous seedlings. In summary water stress plays a key role in quality control but it should not be at the expense of vigor and performance potential of seedlings

1.3. OBJECTIVES OF THE STUDY

The objectives of this study were to evaluate the effects of water stress on A) phenology: 1) terminal bud initiation, budset and bud development; 2) resumption of growth after initial budset; B) physiology: 3) nutrient concentration and content (N, P, K, Ca, Mg) in shoots, needles, and roots; 4) starch reserves in needles and roots; 5) pre-dawn and mid-day plant moisture stress (PMS); C) morphology: 6) various morphological parameters showing soil water content/measurement time interaction; 7) various final morphological parameters; 8) terminal bud dimensions, 9) and fresh and dry matter allocation. An additional objective was to identify an optimal level of water stress in order to provide practical guidelines to container seedling nursery managers.

1.4. HYPOTHESES TESTED

Keeping the above objectives in view, it is hypothesized that: (1) decreasing soil water content does not result in increased and earlier terminal bud initiation, budset, and bud development; (2) increasing water content does not cause resumption of growth after initial bud formation; (3) decreasing water content does not reduce nutrient concentration and content; (4) decreasing water content has no effect on starch reserves; (5) pre-dawn as well as mid-day PMS is not affected by decreasing soil water content; (6) decreasing soil water content does not cause any moisture stress by measurement time interaction effect on seedling morphology; (7) decreasing water content does not reduce final morphological parameters; (8) decreasing soil water content does not result in reduced terminal bud length and diameter; (9) decreasing soil water content does not reduce fresh and dry weights of seedlings

2. LITERATURE REVIEW

2.1. PLANT MOISTURE STRESS (PMS)

The importance of water to the growth of container grown seedlings can't be neglected. It is considered to be a principal limiting factor for the growth of seedlings especially in a greenhouse environment and is undoubtedly one of the most difficult environmental factors to effectively maintain at optimum level (Larson, 1974). It plays a key role in the physiological processes of the seedlings. For example, photosynthesis decreases drastically as moisture stress increases, (Landis, 1989b). It is reported in another study that rate of photosynthesis decreased for loblolly pine (Pinus taeda) at plant water potential of -6 bars (Brix, 1962), and for Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) at -10 bars (Cleary, 1971). Similarly Brix (1978) has reported that rate of photosynthesis for Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), western hemlock (Tsuga heterophylla (Ref.) Sarg.), white spruce (Picea glauca (Moench) Voss) and lodgepole pine (Pinus contorta Dougl.) seedlings decreased when plant water potential decreased from -10.0,

-10.7, -12.4 and -6.6 bars respectively and became zero with water potentials of -53.9, -39,7, -28.6 and -22.4 bars respectively.

Moisture stress during late summer and early autumn promotes early dormancy induction in Douglas-fir seedlings (Lavender et al., 1968) as well as cold hardiness (Blake et al., 1979). As soil moisture stress develops, growth of seedlings

is reduced long before there is any reduction in photosynthesis (Hsiao, 1973).

Consequently, starch increases sharply under mild water stress but as the water

stress increases and becomes severe, photosynthesis is reduced thus reducing

starch reserves in the seedlings (Vartanian, 1981).

Use of water stress has been a common practice to induce dormancy in

seedlings in Pacific Northwest (PNW) nurseries. Approximately 95% (20 of 21) of

PNW nurseries reduce watering to harden seedlings in fall (Duryea and Landis,

1984). About 50% of them monitor plant water potential to schedule watering

regimes while the other 50% stop watering on a certain date or when a target

height is achieved. But no consensus could be obtained due to variations in

nursery sites, climatic conditions, and difference of opinions of nursery managers

(McDonald, 1984).

Plant moisture stress (PMS) is a measure of water availability for seedlings

just as soil moisture stress is a measure of water availability in the soil. Plants

absorb water through their roots and at the same time lose it (transpiration) to

the air through their foliage (Greaves et al., 1988). Thus stress arises through

plant's inability to maintain adequate cell turgor in conditions of high atmospheric

evaporative demands or low soil water potential (Livingston and Black, 1987).

This phenomenon results in water deficit only when water loss exceeds rate of

absorption, leaving plant cell and tissue less than fully turgid (Kramer, 1969, and

Lopushinsky, 1990). This imbalance between the rate of absorption through roots

and the rate of transpiration through shoots can be mathematically explained as:

$$W = (A - T + S)$$

whereas:

W = seedling water status,

A = rate of absorption,

T = rate of transpiration, and

S = quantity of water of stored inside the seedling itself.

When T exceeds A, (typically during the day but sometimes at night) water inside the seedling (S) comes under tension or "stress". When this stress is sufficiently great or prolonged, growth and photosynthesis cease, the metabolic system breaks down and the seedling is threatened with mortality (Ritchie, 1984b).

Pre-dawn plant water potential (Ψ), which is indirectly a measure of soil water potential, is a reliable and stable measure of seedling moisture status while mid-day measurements are the second most stable measures. Therefore, pre-dawn readings should be preferred over mid-day readings. Generally when, mid-day plant water potential decreases to -12 to -15 bars, moisture stress begins to impair growth of seedlings (McDonald and Running, 1979 in McDonald, 1984). Moderate water deficits can result in stomatal closure and reduced photosynthesis

while more severe water deficit can damage whole photosynthetic machinery of seedlings (Lopushinsky, 1990).

Seedling water status can be expressed either by plant water potential (PWP) or PMS. PWP is a measure of chemical potential or free energy of water which controls water movement through soil-plant-atmosphere system. Water potential is defined as "the ability of water to do work in comparison to free pure water at standard pressure and temperature whose water potential is zero". PWP is usually expressed in megapascals (1 megapascal = approximately 10 bars) and bars (Lopushinsky, 1990 and Krizek, 1985). PWP (Ψ_w) is the sum of osmotic (Ψ_s), pressure or turgor (Ψ_p), matric (Ψ_m) and gravitational (Ψ_g) potentials (Lopushinsky, 1990). The effect of matric potential is usually negligible while gravitational potential becomes important only in tall plants, therefore, the equation for PWP can be expressed as:

$$\Psi_w = \Psi_s + \Psi_p$$

In this equation, Ψ_s is a negative number resulting from the effect of dissolved solutes such as sugars, salts and other materials while Ψ_p is a positive force exerted (but small) inward on the cell contents by the rigid cell wall, so that PWP in most cases is a negative number. PWP becomes lower (more negative) as rate of transpiration increases, thus increasing water deficit or PMS (Ritchie, 1984b and Lopushinsky, 1990). The second term used to indicate seedling water

status is PMS, which is dimensionally equivalent to PWP except it differs in sign (measured in positive number). Thus PMS increases as PWP decreases that is a high PMS of 20 bars (2.0 MPa) is equivalent to a low PWP of -20 bars (-2.0 MPa) (Lopushinsky, 1990).

Temperature and moisture are the main factors which should be given a greater attention and consideration in nursery production. Moisture stress has a great bearing on seed management and reduces seed germination (Bonner, 1984). Dunlap and Barnett (1984) found that low water potentials (more negative) had a considerably large effect on loblolly pine seed germination. Soil water potential can be augmented by high temperature, low humidity and wind which play a key role in nursery production. Although, it is difficult to control temperature and moisture stress in large production systems, conditions can be optimized with improved technology and better understanding of biological responses of plant species. Water is the main constituent of plant cells and plays a key role in a plant's life cycle. It is an extremely good solvent. The mineral nutrients needed for plant growth and photosynthates produced as a result of photosynthesis are transported throughout the plant in aqueous solution (Nobel, 1991). Irrigation can have a great influence on growth of nursery stock by affecting mineral nutrition, therefore nursery personnel should effectively manipulate plant moisture and protect seedlings from severe PMS (Lavender, 1984). As movement of certain nutrients, especially phosphorous, is mostly dependent on water movement within soil (Mengel and Kirkby, 1982), too little watering can affect uptake and exchange

of mineral nutrients, necessary for a plant growth (Lamont, B. 1982, and Cordell et al., 1987). It can be reasonably assumed that irrigation practices can alter nutrient absorption by plant root system and thus retard growth of seedlings. Besides, low water content can restrict elongation and development of new roots (Day and MacGillivrary, 1975). Therefore, influence of decreased available moisture on tree responses has been probably investigated more than any other operational factor (Crafts, 1968 in Hobbs, 1984). It was found that rate of photosynthesis in loblolly pine seedlings was decreased rapidly at xylem pressure potentials less than -6 bars (Brix, 1962) whereas, in Douglas-fir, this point was reached at -10 bars (Cleary, 1971). It was also reported that prolonged periods of moisture stress can cause the cessation of cambial activity and inhibit cell division (Kramer, 1969). While, on the other hand, rate of photosynthesis may also be slowed down with excess watering (Zaerr, 1983).

Water deficit affects every aspect of plant growth including anatomy, biochemistry, physiology and morphology. The most profound and obvious effects of water stress are reduction in plant size, leaf area, stomatal closure and carbon fixation. It results in reduced photosynthesis, dark respiration, translocation and partitioning of metabolites and crop yield. The quantity and quality of a plant growth depend on cell division, enlargement and differentiation which are all greatly affected by water stress, thus leading to decreased productivity. In addition, the activity of some important enzymes involved in dark reaction of photosynthesis such as ribulose-1, 5-biphosphate carboxylase, ribulose-5-phosphate

kinase and phosphoenolpyruvate carboxylase is highly reduced by water stress, thus leading to decreased photosynthetic activities (Kramer, 1983). However, it is often assumed that effects of water stress are temporary and maximum growth resumes when seedlings are rewatered. But, water stress has long term effects and damages root system to absorb water from soil (Warkentin, 1984). Similarly, Zaerr and Holbo (1976) have reported in a study with Douglas-fir seedlings that recovery from strees in seedlings, exposed to lower plant water potential, was at a lower rate than those that had higher starting values of plant water potential.

Water constitutes more than 80% of fresh weight of actively growing shoots of woody plants and a change of 15% to 20% in water content may result in cessation of all growth processes while a loss of 1% to 2% of tissue water can accelerate marked changes in physiological activities. Virtually all aspects of seedling growth are highly sensitive to water stress; leaf anatomy, shoot growth, leaf expansion, bud formation, cambial growth and root growth are affected even by a mild level of internal stress (Joly, 1985). Therefore, stresses of any kind, including moisture stress, should be avoided as they interfere with physiological process that in turn affects frost hardiness processes (Glerum, 1985). Blake et al. (1979) have reported that mild plant water potential values (-0.5 to -0.1 MPa) during mid-summer can lead to cold hardiness in plants. Similarly Zaerr et al., (1981) reported that moderate moisture stress can be used to induce seedling dormancy during early to mid-summer. Davey (1990) is of the point of view that adequate irrigation schedules are seldom detrimental to mycorrhizae formation or

function. In general, seedlings suffer more severely and quickly from inadequate or excessive moisture than the mycorrhizal fungi.

It has been reported that too much watering during seed germination is not desirable. An excessive amount of water promotes pre-emergence damping-off and growth of certain seed-borne fungi in nurseries (Peterson, 1974, and Thompson, 1984). However, uppermost portion of the media should be kept wet at all times which help keep entire media moist. Thereafter, the watering regime should be gradually reduced to promote cold and drought resistance in seedlings (Barnett, 1974). A judicious use of water can reduce pre-emergence damping-off by accelerating seed germination and germinant emergence. Adequate use of water can also diminish certain fusaria-cause root rots (Sutherland, 1984). Once germination has peaked, watering schedule should be changed. Pre-dawn PMS can be allowed to increase between 12 bars to 15 bars before rewatering to induce and promote budset (Thompson, 1984). Hamm (1990) has associated Fusarium Hypocotyl Rot, a fungal diseases occurring primarily on Douglas-fir and to a lesser extent on Shasta red fir, western larch, sugar pine, white pine and ponderosa pine in the Pacific Northwest, with water stress caused by high soil temperatures and inadequate watering regimes. Similarly many other researchers such as Hansen (1990), Kliejunas (1990), James (1990), Sutherland (1990) and Campbell (1990) have related many nursery diseases with too much or too little water, either causing high water stress or saturated conditions, thus exposing young seedlings to different disease problems.

Although water is widely used culturally to alleviate stress caused by high summer temperatures, too much water saturates soil and inhibits oxygen supply to roots and symbiotic fungi (Cordell et al., 1987 , and Hansen et al., 1990) thus allowing soil borne fungi to reproduce and multiply. Likewise, water accumulation on foliage for a longer time also promotes pathogens on stem and needle (Hansen et al., 1990). Therefore, it is recommended that irrigation needs should be coordinated with summer cooling requirements and pesticide application schedule. Both the total amount of water used and the frequency and duration of the times the foliage is wet, should be kept in mind. Efforts should be made to use controlled watering to avoid any water stress or saturation to help seedlings grow healthy.

Duryea (1984) has concluded that either wet irrigation regime or a high moisture stress may adversely affect seedling survival and growth. A general recommendation is that when seedlings have reached their proper height and caliper, they should be exposed to moderate moisture stress (8 to 12 bars pre-dawn PMS). But because, nurseries differ in soil type, climatic conditions, seedling species and so forth, exact irrigation regimes have to be defined for individual nurseries.

2.2. PHENOLOGY

Dormancy may be defined as "any case in which a tissue predisposed to elongate does not do so". A perennial material is said to be dormant when buds

have formed on terminals of the shoots (Doorenbos, 1953 in Lavender, 1985). It can also be loosely defined as the opposite of shoot growth when it is not visible due to presence of terminal buds (Burr, 1990). Burdett and Simpson (1984) have defined dormancy as a state of growth inactivity in the absence of environmental constraints to plant growth.

Dormancy can be induced either by controlling environmental factors or by internal physiological functions of plant itself. Therefore, a terminal bud can be either quiescent or at rest. A bud is said to be quiescent when dormancy is imposed by environmental factors like drought stress and temperature. "Summer dormancy" is a synonym for quiescence. On the other hand, a bud is considered to be in rest when dormancy is maintained by agents within bud itself (Romberger, 1963 in Lavender, 1985). A resting bud is unable to grow and elongate under even favorable conditions. "Winter dormancy" is synonymous to rest (Lavender, 1985). The level of dormancy in coniferous seedlings can be assessed by days to bud break (Ritchie, 1984a and Ritchie et al., 1985). This procedure measures the time it takes for buds to break with the higher level of dormancy (Lavender, 1985). This method has been used by some other researchers. Carlson (1985) has reported in an experiment that intensity of bud dormancy in loblolly pine seedlings was reduced rapidly in cold storage as in nature. Mean days to terminal bud break ranged from 16 days to 33 days when seedlings were lifted on November 23 with a total of 207 chilling hours.

Macey and Arnott (1986) found that both periodic moisture stress and nutrient withdrawal (N, P and K) were effective in inducing bud formation in container-grown white spruce seedlings under nonlimiting photoperiods. No evidence of bud formation was found in unstressed seedlings. Similarly Tinus (1974) has reported that appropriate moisture stress and removal of nitrogen help initiate budset promptly and in this way seedling growing cycle can be shortened as much as possible.

While discussing effects of water stress on photosynthesis, Ritchie and Dunlap (1980) reported that although little work has been done on irrigation effects on root growth potential, it is hypothesized that water stress in late summer influences dormancy so that it results in lower photosynthesis, slowed translocation and a reduction in metabolic substrate for root production. Root growth potential is greatly influenced by some physiological processes of the seedlings such as photosynthesis, bud dormancy and carbohydrate availability. As dormancy deepens as a result of water stress, growth inhibitors accumulate in buds and bud scales and root growth potential reaches a low level but as dormancy weakens, auxins and gibberlins (promoters) are exported downward from the buds and shoots through the phloem to initiate root activity.

Burr et al., (1987) and Burr, et all., (1989) have pointed out that there is a relationship between dormancy, root growth potential (RGP) and cold hardiness. Information on cold hardiness can be used to estimate bud dormancy and RGP. They found in a study that during cold acclimation, the lag period in container-

grown Douglas-fir (<u>Pseudotsuga</u> <u>menziesii</u> Var. Glauca (Beison) Franco),

ponderosa pine (<u>Pinus</u> <u>ponderosa</u> Var. Scopulorum Engelm) and Engelmann

spruce (<u>Picea</u> <u>engelmannii</u> (Pary) Engelm) seedlings in the development of cold

hardiness at approximately -15 ^{0}C, was an indicator of bud dormancy status and

low RGP in all three species.

2.3. MINERAL NUTRITION

Good mineral nutrition is a basic and fundamental requirement for

producing target seedlings. It is as basic as light and water. Seedlings rich in

mineral nutrition show good physical characteristics such as color, height and

diameter. There are 16 commonly accepted elements that constitute the essential

nutrients, amongst which N, P, K, Ca, Mg, Fe and other micronutrients play an

important role in a plant's life. Seedlings having poor mineral nutrition usually

show poor and stunted growth and depict many deficiency symptoms (Bigg and

Schalau, 1990). However, the key point should be synchronization of all essential

elements (Whitcomb, 1987). Seedling photosynthesis and other metabolic activities

depend on an adequate and balanced supply of nutrients. Besides carbon,

hydrogen and oxygen, seedlings require N, P, K, Ca, Mg and S and other trace

elements in the form which plants can assimilate. Seedlings markedly deficient or

imbalanced in one or more of these nutrients usually show at least one symptom

of deficiency such as foliage discoloration (usually red or yellow), death of part or

all of the needles or shoot, reduced needle length and reduced height growth (Cleary et al., 1988).

Nutritional status of seedlings can largely be altered by application of organic or inorganic fertilizers. However, the motive should be to achieve a target seedling size rather than to obtain an increased nutrient concentration (Armson and Sadreika, 1979 in Duryea and McClain, 1984). It was found that as nitrogen was increased in 1+0 and 2+0 Douglas-fir seedlings from 0 to 100 kg/ha, 1+0 shoot nitrogen concentration was increased from 1.09% to 2.01%, whereas phosphorous decreased from 0.17% to 0.12%. In 2+0 needles, nitrogen concentration increased dramatically from 0.71% to 2.7% at 200 kg/ha while phosphorous and potassium concentration decreased with increasing nitrogen supply from 0.17% to 0.09% and 0.56% to,0.26% respectively. Increase in nitrogen concentration also resulted in an increase in shoot dry weight of 2-year old Douglas-fir seedlings (Van den Driessche, 1990).

The deficiency of a mineral nutrient occurs when plant's growth rate is limited by the availability of a certain nutrient. Seedling nutritional disorders can occur without predisposing stress factors, however, some environmental factors may indirectly inhibit nutrient uptake. When a seedling is unable to obtain enough of an essential nutrient, the first effect it shows is the reduction in growth rate. If this deficiency is not corrected, the seedling may exhibit clear deficiency symptoms, indicating stunted growth and sometimes mortality (Landis, 1990). Similarly, Landis and Steinfeld (1990) have reported that imbalance concentration

of soluble salts in soil can cause injuries to plants in four different ways: 1) causing an osmotic effect, thus reducing water availability to plants, 2) reducing permeability and infiltration rate of water, 3) causing toxicity directly to plants as high levels of boron, chlorine and sodium, and 4) deficiency or imbalance of salts as calcium can reduce availability of other mineral nutrients such as iron or phosphorous. The authors have defined soluble salts as " those inorganic chemicals that are more soluble than gypsum ($CaSO_4$) and include cation salts as sodium (Na^+), calcium (Ca^{++}) and magnesium (Mg^{++}) and anion salts as chlorine (Cl^-), sulphate (SO_4^-) and bicarbonate (HCO_3^-).

Nutrient status of the seedlings can be affected by irrigation patterns, both negatively as well as positively. Excessive irrigation or heavy rainfall can cause leaching of soluble nutrients such as nitrate - nitrogen and potassium from the root zone of the seedlings and produce a nutrient deficiency. Eastern white pine (Pinus strobus L.) seedlings showed reduced foliar concentrations of N, P, and K with increasing frequency of irrigation but Ca and Mg were unaffected (Schomaker, 1969). On the other hand, moisture stress caused by reduced irrigation can limit seedling growth and change foliar nutrient levels (Pharis and Kramer, 1964). Similarly, Timmer and Armstrong (1989) reported that moisture stress significantly decreased nutrient uptake of red pine (Pinus resinosa Ait.) seedlings. It was also documented by Schomaker (1969) that less frequent irrigation resulted in lower uptake of total N uptake by white pine seedlings.

On the other hand, some researchers have associated some negative effects

of excessive and inappropriate mineral nutrition with reduced growth and survival, frost damage and reduced drought resistance (Filer Jr, and Cordell, 1987). Van den Driessche (1984) has also pointed out that excessive use of phosphorous has been related to decrease hardiness in some species. Similarly, if nitrogen is applied in summer before the shoot height has stopped growing, it can retard dormancy development and delay onset of hardiness.

Landis (1989c) has stated that environmental factors play a major role in maintaining good health of seedlings. Any environmental stress can cause diseases when it affects seedling growth. Several of these factors such as heat, water and mineral nutrients are required for normal seedling growth but can induce physiological stress in plants when they reach extreme ends, thus rendering seedlings to diseases and insect attack. Similarly, Russel (1990) has pointed out that germinating seed and new germlings store sufficient food in their endosperms to get them well on their way and thus do not need too much early nitrogen application. Too much early nitrogen applications promote damping-off, a fungal disease caused by Pythium and Fusarium species of fungi, in seedlings.

Nitrogen is commonly used in nursery soils to increase size of seedlings. Many researchers have found a positive correlation between nitrogen fertilization and many timber species like Douglas-fir, white spruce, lodgepole pine, and loblolly pine. Once the target height is achieved, fertilization is usually stopped and watering decreased to induce dormancy (Fisher and Mexal, 1984 and Brix and Van den Driessche, 1974). Although, potassium is used to promote cold hardiness

in seedlings, there is sufficient evidence that potassium fertilization has little, if any, effect of cold hardiness (Pellett and Cater, 1981. However, it is likely that potassium is required for outplanting success through regulation of plant water status (Bradburry and Malcolm, 1977). Usually potassium regulates stomatal control and drought tolerance of transplanted seedlings, thus low levels of potassium in foliage may result in loss of stomatal control during the critical period of seedling establishment. It is very mobile in the soils and can cause deficiency levels, especially in sandy soils, thus in that situation, addition of more potassium would be required (Fisher and Mexal, 1984). Crapo and Ketellapper (1981) have demonstrated in a study that root growth of tomato, barley and wheat plants was severely inhibited under conditions that did not significantly favor the active uptake of potassium or total respiration. As photosynthesis was restricted, root growth was completely halted.

Landis (1985) has concluded that seedling nutrient status is closely related to subsequent growth after outplanting rather than survival because a large quantity of nutrient supply is no guarantee of seedling vitality. However, a balanced and adequate nutrient supply is essential for further growth until the seedling root system is fully developed and established on the field. Foliar nitrogen level appears to be a very good indicator of growth after outplanting but is poorly correlated with initial survival of seedlings because seedling survival is strongly affected by other operational factors like handling, storage, planting techniques and site characteristics.

The importance of mineral nutrition on both quality and quantity of growth of container grown seedlings can not be overemphasized. The beneficial effects of mineral nutrients to improve plant growth have been known for more than 2,000 years. Thirteen elements have been identified as being essential for the growth of higher plants. These are classified in to 6 macronutrients (nitrogen, phosphorous, potassium, calcium, magnesium and sulfur) and 7 micronutrient (iron, zinc, copper, boron, chlorine and molybdenum). Macronutrients are used by plants in large amounts while micronutrient in small quantities (Landis, 1989a).

Soil pH has a great role on availability of nutrients to plants. Macronutrients (N, K, Ca and Mg) are most readily available at soil pH values above 6 and 7 (alkaline soils) but P is restricted between 6 and 7. On the other hand, micronutrient are most available in acid soils that is pH values below 5.5. Therefore, extremely acid soils (pH < 4.5) are infertile because they do not retain nutrient cations such as NH_4^+, Ca^{++} and Mg^{++} to any extent (Van den Driessche, 1984).

Godbold et al., (1988) conducted an experiment to find out the influence of aluminum (Al) and nitrate on root growth and mineral nutrition of Norway spruce (Picea abies) seedlings and found that over 7 days, the rate of root elongation was severely reduced by Al, irrespective of nitrate concentration. Root elongation was inhibited within 12 hours of exposure and this was associated with a displacement of Ca and Mg by Al in the roots. It was further found that after 35 days, Ca and Mg contents of roots and needles were significantly reduced by Al. Similarly,

Gleason et al., (1990) have reported in a study that 2+0 ponderosa pine seedlings supplied with ammonium nitrate ($NH_4.NO_3$), at a rate of 46 kg N/ha, plus potassium nitrate (KNO_3), at a rate of 37 kg K/ha, showed a significantly higher N concentration (1.55%) than that of control, no fertilizer, (1.47%). Similarly, seedlings provided with $NH_4.NO_3$, at a rate of 46 kg N/ha, showed an increase of foliar N concentration from 1.47% to 1.53%.

2.4. CARBOHYDRATE RESERVES

Carbohydrates constitute about 75% of total dry weight of trees, and are an extremely important component of their life. Carbohydrates are principally classified into three major groups: monosaccharides (for example glucose and fructose), disaccharides (for example sucrose and maltose) and polysaccharides (for example cellulose and starch). Photosynthesis is a primary source of production of carbohydrates. These food reserves are primarily used to maintain respiration and growth or are consumed to synthesize other important organic compounds and structural parts of trees during periods when photosynthates are not produced by photosynthesis. Carbohydrates are stored only when rate of photosynthetic production exceeds the rate of consumption (Kramer and Kozlowski, 1979).

It was reported that starch does not vary enough throughout the year to guard differentiation between dormant and non dormant seedlings (Krueger and Trappe, 1967). Furthermore, variation in starch concentration among plants is

fairly high but it seems to be a good food reserve to play a role in plant's ability to grow when outplanted (Zaerr, 1985). Furthermore, poor seedling survival has been attributed to depleted carbohydrate reserves during cold storage in radiata and mugo pines (McCracken, 1979). Webb (1981) has reported in a study that starch content of Douglas-fir and white fir twigs provided a good basis for predicting mortality of trees in two tussak moth outbreaks, one in British Colombia, Canada and other in New Mexico. Trees that had been defoliated by insects, with a detectable level of carbohydrate reserves (starch) recovered whereas those lacking starch did not. Similarly, Parker (1974) has demonstrated that defoliation of sugar mapple trees resulted in depleted starch content in roots compared to trees either girdled or severed. This indicates that trees under any kind of stress condition deplete their carbohydrate reserves.

Tree seedlings primarily accumulate their food reserves in the form of starch and sucrose but also in the form of cellulose, fats, proteins and other compounds (Kramer and Kozlowski, 1979) of which starch is stored within special structures (e.g., amyloplasts and chloroplasts) inside the cells (Marshall, 1985). Because starch is immobile and can not pass from cell to cell, it must be synthesized and broken down in place where it is found and then transported from leaves and stems to roots which are non-photosynthetic organs of a plant (Kramer and Kozlowski, 1960, and Ritchie and Dunlap, 1980). Silvius and Snyder (1979) have explained that sucrose is transported from the shoot to tap root in sugarbeat plants where it is either metabolized in cellular growth and maintenance or

further translocated to fibrous roots. Similarly, Rose (1992) has reported in a study with loblolly pine seedlings that overall mean percentage of starch was found higher in seedlings that produced roots than in those that did not, but no relation of percentage of starch initially, in lateral roots, was found with root growth potential (RGP). However, Marshall (1985) has described starch as a "savings account" from which seedlings can use stored starch material during the period when respiratory or growth expenses exceed photosynthetic income.

McNabb (1985) has reported that both sugar and starch concentrations are affected by water stress. Slash pine (Pinus elliottii) seedlings subjected to intensive water stress (watering once every 8 weeks) were found to have higher sugar but lower starch concentration compared to the seedlings receiving more water. Total carbohydrate levels were found to be lower in heavily stressed seedlings. Hermann (1990) has pointed out that insufficient irrigation results in reduced accumulation of carbohydrate reserves in seedlings, thus contributing to lowered frost resistance and may also result in freezing injury during dormancy period.

2.5. MORPHOLOGY

"Morphology is defined as the form and structure of an organism or any of its parts" (Thompson, 1985, and Barnett, 1984). It includes a long list of physical attributes of seedlings such as height, stem diameter, weight, stomate number, bark thickness and number of root tips. Height is one of the easiest morphological traits to measure. Many studies have suggested that height is a good indicator of

subsequent growth but shows an unpredictable relationship with survival, especially on droughty sites. On the other hand, stem diameter is generally accepted as a better measure of both growth and survival (Thompson, 1985 and Barnett, 1984). Bud height is also considered a good indicator of field growth potential. It is usually used to refine prediction of field growth between lots of seedlings rather than within a lot. When seedlings have equal heights and stem diameters, those with larger buds are preferred and selected (Thompson, 1985). Similarly dry weight of seedlings at the time of outplanting was correlated with height in field over several years but not closely related to survival (Barnett, 1984). Zaerr and Lavender (1976) have found in a study with 2-0 Douglas-fir seedlings that larger and vigorous seedlings tend to have increased survival and growth when outplanted.

Ritchie (1984b) has summarized various morphological characteristics of seedlings as shoot height and weight, root system weight or volume, root fibrocity, stem diameter at root collar, bud set, foliage color and various rates such as shoot:root, weight or top height:stem diameter (sturdiness ratio). Because they are relatively easy to control and measure, morphological attributes have been extensively used for the last several decades to define seedling quality (Sutton, 1979). Therefore, some European nations have passed and adopted legislation to enforce and establish morphological grading standards for tree seedlings. (Schmidt-Vogt, 1981 in Ritchie, 1984b).

3. MATERIALS AND METHODS

3.1. PLANT MATERIAL

Seed of Douglas-fir (seed zones 262 & 271) was stratified by immersing in cold water for 24 hours and then placed in cold storage at 1 ^{0}C for a period of 63 days (Jan 11 to March 14, 1991) at Colton greenhouse of Bureau of Land Management (BLM) near Portland OR. Two to three viable seeds were sown in 49.17 cm^3 Ray Leach Single Cell containers filled with a 50% Fison brand sphagnum peat, 30% # 13 grade W.R. Grace Horticulture vermiculite and 20% perlite. The mix was pasteurized with aerated steam at 65 to 71 ^{0}C for 30 minutes prior to being bagged. No nutrients were added in the mix, however, after germination seedlings were supplied nutrients weekly such as N, P, K, Ca, Mg and some trace elements mixed in the irrigation water. Sowing began on March 14, 1991 and was completed on March 15, 1991. Ninety percent of the seed germinated by March 29, 1991 and the rest by April 4, 1991. Seedlings were grown at Bureau of Land Management's greenhouse in Colton, near Portland until June 30, 1991 when they were brought to the Forest Research Laboratory's greenhouse at Oregon State University, Corvallis on July 1, 1991 to carry experimental activities.

3.2. METHODS

3.2.1. GENERAL

The study was conducted in the Forest Research Laboratory's greenhouse under climate controlled conditions. Twenty-four trays (6 treatments * 4 blocks), each consisting of 200 seedlings, were randomly arranged on four benches (blocks) so that all in a block had uniform environmental conditions. Twenty randomly selected seedlings per treatment per block (a total of 480 seedlings) were measured at day 0 (before the start of water stress treatments) for their initial shoot height, stem diameter, fresh and dry weight of shoot and root, nutrient concentration and content (N, P, K, Ca, Mg) of shoots and starch concentration in roots. Similarly, another 480 seedlings were randomly selected at day 0 from all 6 treatments (120 from each block) to observe for terminal bud initiation and budset throughout the course of study. These seedlings were tagged and were not destructively harvested. However, they were used for a final destructive harvest for recording other morphological and physiological measurements as described above. Based on a pilot study conducted in May, 1991, in the Forest Research Laboratory's greenhouse, 6 water stress treatments (65, 53, 41, 29, 17 and 7% soil water content by dry volume of soil) were started on July 4, 1991 by watering all trays to their field capacity and then letting them dry down to predetermined percent water contents. Because of small size of seedlings, trays were weighed daily to assess their weights and were rewatered once they had

dried down to their predetermined percent water contents. Seedlings were closely examined to observe terminal bud initiation, budset and any mortality.

Seedlings were harvested approximately halfway through the study (August 14-16, 1991). Four hundred eighty (480) seedlings randomly selected from all 6 treatments (120 from each block) were measured for shoot height, stem diameter, fresh and dry weight of shoots and roots, nutrient concentration and content (N, P, K, Ca, Mg) of shoots and starch reserve in roots. Similarly, an additional 240 seedlings were randomly selected to measure their pre-dawn and mid-day plant moisture stress (PMS).

A final harvest was made on September 22-24, 1991 using the same 480 seedlings which were tagged and observed for bud initiation and budset throughout the study. As usual, seedlings were measured for the same morphological parameters except that seedlings were severed into needles, branches, stems and roots to measure fresh and dry weight of individual parts. Similarly, needles and roots from the final harvested seedlings were measured for total nutrient content and starch concentration.

Since the study was conducted in summer, fans and coolers were operated to cool the greenhouse on the hot days and maintain temperature at about 28 ^{0}C.

3.2.2. DATA COLLECTION AND METHODS OF MEASUREMENTS

3.2.2.1. Terminal budset: Twenty randomly selected seedlings in each block and treatment (a total of 480 seedlings) were tagged and only those seedlings were

examined each time for tetminal bud initiaton, budset, and bud development throughout the course of study. Physical development of terminal buds was classified in to 5 different developmental stages, as explained below. A 0-5 rating system was used to keep track of these developmental stages of terminal buds and capture the exact time of bud initiation and bud set (Figure 1):

0 = seedlings actively growing, no sign of bud initiation,

1 = terminal bud formation initiated, i.e. when scales on terminal buds turned light brown,

2 = development in size of buds, bud scales and turning brown,

3 = development in size progresses, bud scales fully developed, more brown and larger in size than stage 2,

4 = same as of stage 3 except larger in size, and

5 = same as of stages 3 and 4 except larger in size.

The rating system used in this study is similar to one, reported by many other researchers. For example, a scoring system of 0-5 was adopted to evaluate frost hardiness and stress resistance in coniferous planting stock (Hermann and Lavender, 1979), a rating system of 1-3 to keep track of bud development in white and red spruce (Blum, 1988), and a numerical grouping of 1-4 to evaluate the effect of high temperature on bud morphology in blue spruce (Deal, et al., 1990).
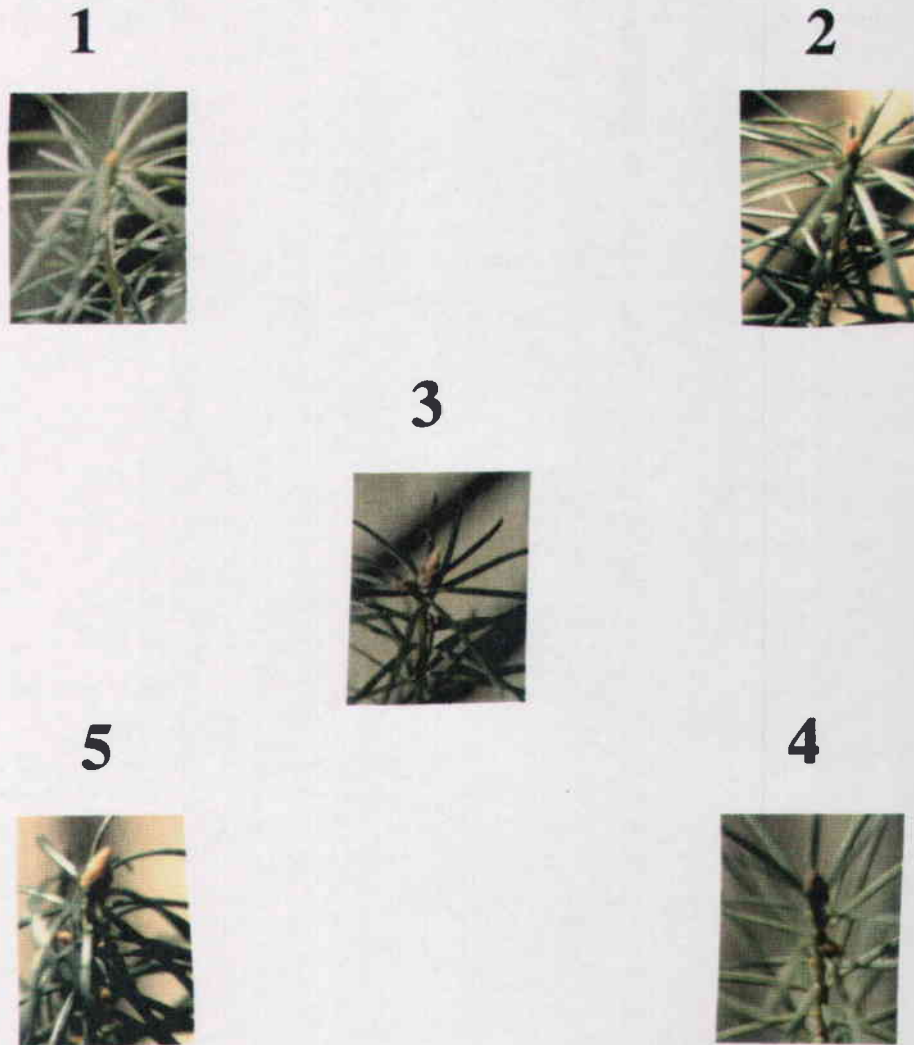
Figure 1. A 0-5 rating system used to monitor and evaluate physical developmental stages of terminal buds of containerized Douglas-fir seedlings: (0) seedlings actively growing, no sign of bud formation (picture not shown); (1) terminal bud formation initiated, 1.e, when bud scales turned light brown; (2) development in size of buds, bud scales and turning brown; (3) development in size progresses, bud scales fully developed, more brown and larger in size than stage 2; (4) same as of stage 3 except larger in size; and (5) same as of bud developmental stages 3 and 4 except larger in size.

Seedlings were regularly observed throughout the course of study and were assigned a code number representing their stage of bud development as explained above. In the beginning, seedlings were observed daily or at a short interval to capture the exact time of bud initiation. When it was realized with experience gained during the past few weeks that bud development was not taking place rapidly, the interval of observing buds was extended to almost one week. This practice is similar to that adopted by Tung and Deyoe (1991) in a study to observe the effects of moisture stress on dormancy induction in nobel and shasta red fir seedlings.

3.2.2.2. Nutrients

3.2.2.2.1. Lab analyses: Because container grown seedlings are often small, tissue samples are usually submitted as a composite of individual seedlings (Landis, 1985). About 60 g of fresh or 10 g of dried tissue is required for nutrient analysis, therefore, a composite tissue should consisted of a minimum of 20 to 50 seedlings (Youngberg, 1984). Similarly Ritchie (1982) and Cannell et al., (1990) adopted the same methodology and pooled seedlings per replicate to estimate carbohydrate concentrations. Therefore, keeping these guidelines in view, oven dried shoots (from initial and middle harvests at day 0 and 43 respectively), and needles and roots (from the final harvest at day 83) from 20 seedlings in each treatment and block were combined as per measurement time and ground in a Wiley mill to pass through a 40 mesh sieve. The ground material was stored in a freezer at about -22 to -25 ^{0}C (Rose, et al., 1991) for analyses of nutrient concentrations. All

analyses were performed by department of Soil Science's Plant Analysis Laboratory located at Oregon State University, Corvallis, OR.

3.2.2.2.2. Vector analyses: Besides analyzing nutrient elements for their concentration and content, total needle nutrients (N, P, K, Ca, and Mg) were also diagonized using a non-statistical analysis technique named "vector analysis or vector diagnosis". This technique has been successfully used by many other researchers such as Timmer and Stone (1978), Timmer (1979), Timmer and Morrow (1984), and Timmer and Armstrong (1989). To facilitate interpretation, changes in relative values of concentration, content and dry weight are displayed on Y, X and Z axis of the same single graph respectively (see Figures 16-19 in results section). For this purpose, 41% soil water content by volume is taken as central point which has a relative values of 100% concentration, content and dry weight. The relative values for rest of the water stress treatments (65, 53, 29, 17, and 7% soil water content) are calculated by dividing the absolute values of concentration, content and dry weight for 65, 53, 29, 17, and 7% soil water content by the absolute values for 41% soil water content and then multiplying by 100 (Table 1, 2).

TABLE 1. Absolute values of total needle nitrogen, phosphorous, calcium and magnesium concentration and content and total needle dry weight as affected by 6 different water stress treatments

trmt	dry weight (g)	N conc	N cont	P conc	P cont	Ca conc	Ca cont	Mg conc	Mg cont
65%	7.02	1.29	90.04	0.72	50.05	0.25	17.11	0.26	18.12
53%	7.18	1.26	89.13	0.76	53.78	0.23	16.34	0.25	17.86
41%	6.73	1.23	81.44	0.70	46.46	0.23	15.39	0.24	16.10
29%	6.98	1.21	83.26	0.68	47.18	0.21	14.69	0.22	14.92
17%	6.80	1.19	80.25	0.65	43.63	0.20	13.25	0.21	13.92
7%	5.44	1.39	75.33	0.66	35.55	0.17	9.08	0.19	10.32

TABLE 2. Relative values of total needle nitrogen, phosphorous, calcium and magnesium concentration and content and total needle dry weight as affected by 6 different water stress treatments

trmt	dry weight (g)	N conc	N cont	P conc	P cont	Ca conc	Ca cont	Mg conc	Mg cont
65%	104	105	111	103	108	109	111	108	113
53%	107	102	110	109	116	100	106	104	111
41%	100	100	100	100	100	100	100	100	100
29%	104	98	102	97	101	91	95	92	93
17%	101	97	99	93	94	87	86	88	86
7%	81	113	93	94	76	74	59	79	64

This will be more clear by the following calculation made for 65% soil water content.

Relative N concentration = $\dfrac{\text{absolute N conc (\%) for 65\%}}{\text{absolute N conc (\%) for 41\%}}$ x 100

$$= \dfrac{1.29}{1.23} \text{ x } 100 \quad = \quad 105$$

It means that N concentration of seedlings treated with 65% soil water content was 105% of those treated with 41% soil water content. Rest of the calculations were done using the same formula.

3.2.2.3. Starch: Similarly roots (from initial, middle and final harvests at day 0, 43 and 81 respectively) and needles (from final harvest only) from 20 seedlings in each treatment and block were combined as per measurement time and ground together for the analysis of starch concentration. The ground material was stored in a freezer at about -22 to -25 ^{0}C. Starch analysis of 72 root and 24 needle tissue samples (a total of 96 samples) was carried out in Physiological Laboratory located in Peavy Hall, College of Forestry, Oregon State University, Corvallis, OR., using enzymatic method as detailed by Rose et al., (1991) and Omi and Rose, (1991). Ground material was extracted with methanol:chloroform:water (MCW), 12:5:3:, solution (3 times for root and 5 times for needle tissues) to remove soluble sugars, phenolics and other compounds hindering starch

determination. The starch was hydrolyzed with 1 ml of α-amylase and amuloglucosidase enzymatic digestion solution and incubating samples for 24 hours and then analyzed for glucose concentration. Each sample was analyzed twice. Glucose concentration was corrected to starch concentration (% dry weight) using 0.9 as a hydrolysis factor (Pasternack and Danbury, 1968).

3.2.2.4. Plant moisture stress (PMS): PMS was determined with a pressure chamber apparatus (Scholander, et al., 1965 and Waring and Cleary, 1967). The methodology and operating guidlines are discussed in detail by Cleary and Zaerr (1980 and 1984), however, a high instrument reading means high PMS in the seedlings being measured (Edgren, 1984). Shoots of 240 randomly selected seedlings from all 6 treatments (60 from each block) were cut with a sharp blade and each 240 were measured for their pre-dawn and mid-day PMS respectively. Pre-dawn as well as mid-day measurements were made about 45 minutes before sunrise and from noon to 1.0 pm respectively. Necessary arrangements (turning lights off, using small battery for minimal light, avoiding any delay in measurements, and measuring seedlings on spot in the greenhouse) were made to maintain uniformity and accuracy in the measurements.

3.2.2.5. Shoot height: Shoot height is usually measured from the root color to the base of terminal bud, but if no terminal bud is present, measurement is done either to the highest point (often to the tip of needles) or to the approximate growing point (Thompson, 1985). As seedlings under observation were small and actively growing during initial destructive harvest, there were no terminal buds

present on them. Therefore, seedling height was measured to the nearest 0.1 cm from immediately below the cotyledons to the tip of the leaves. This methodology was also kept consistent in middle and final destructive harvests.

3.2.2.6. Terminal bud length: Length of terminal buds, on the same seedlings measured for terminal bud set and final harvest, was measured with a digital caliper and recorded to the nearest 0.01 mm at the end of the study.

3.2.2.7. Terminal bud diameter: Diameter of terminal buds of the same seedlings (as for bud length) was measured with a digital caliper and recorded to the nearest 0.01 mm.

3.2.2.8. Stem diameter: Stem diameter was measured with a digital caliper and recorded to the accuracy of 0.01 mm immediately above the point marked for shoot height.

3.2.2.9. Fresh weight: After measuring for height and diameter, seedlings were cut at the point marked for shoot height. Then root and shoot of individual seedlings from initial and middle harvests were separately weighed for their fresh weight to the nearest 0.01 g. However, final harvest seedlings were partitioned into needles, branches, stems and roots and each of them was measured for fresh weight.

3.2.2.10. Dry weight: After measuring for their fresh weight, 20 shoots and roots (from initial and middle destructive harvests) from each treatment and block were combined and put together in separate paper bags and were oven-dried for 48 hours at about 65-70 $^{\circ}$C (Feret, 1982, and Rose, 1992). The samples were taken out from the bags and reweighed to get their composite dry weight to the accuracy

of 0.01 g. Later on, dry weight of individual shoot and root was calculated using following formula:

dry weight of ind shoot or root =

$$\frac{\text{total dry wt of 20 shoots/roots}}{\text{total fresh wt of 20 shoots/roots}} \times \text{fresh wt of ind shoot/root}$$

Seedlings from the final harvest, after measuring for their fresh weight as mentioned above, were measured for dry weight of needles, branches, stems and roots of individual seedling. All the samples were stored at about -22 to -25 °C in a freezer until they were ground for nutrient and starch analyses later on.

3.2.2.11. Mortality: Whole trays of the seedlings (200 in number) were monitored for mortality. Seedlings were considered dead when the foliage of the seedlings had turned brown or the needles were brittle to touch and fell even they were green.

Data were recorded for each parameter, as mentioned above, on data sheets designed for the purpose as required and then put in the computer.

3.2.3. DESTRUCTIVE HARVESTS

3.2.3.1. Initial harvest (day 0): After moving the seedlings to the Forest Research Laboratory's greenhouse, a total of 480 seedlings were randomly selected from all 6 treatments (120 from each block) i.e, 24 samples (6 treatments x 4 blocks x 20 seedlings per sample). They were measured for shoot height, stem diameter, fresh

and dry weight of root & shoot separately, nutrient content (N, P, K, Ca and Mg) and starch concentration in roots before subjecting them to 6 moisture stress treatments. Also, another 480 seedlings were randomly selected from all treatments (120 from each block) and tagged to observe their terminal bud initiation, budset and bud development throughout the course of the study. All measurements were recorded as explained earlier.

3.2.3.2. Middle harvest (day 43): A destructive harvest was made approximately halfway through the study (August 14 - 16, 1991). Four hundred eighty (480) randomly selected seedlings for all 6 treatments (120 for each block) were measured for all the parameters as described above. In addition to these measurements, 240 more seedlings were randomly selected (6 treatments x 4 blocks x 5 seedlings per sample) and leading shoots of each 120 were used to measure their pre-dawn and mid-day PMS with a pressure chamber as explained before. Further, a close monitoring was continued on 480 seedlings (randomly selected at day 0), for terminal bud initiation, and budset. In addition, all 24 trays, consisting of a total of 4,800 seedlings, were regularly observed for any mortality or disease problem.

3.2.3.3. Final harvest (day 81): A final harvest was made at the end of the study (Sept 22-24, 1991) using the same seedlings tagged and marked for terminal bud initiation and budset at day 0. These seedlings were severed at the point of shoot height measurement (section 3.2.2.5) to measure their shoot height, and stem diameter. The shoots were partitioned into needles, branches, and stems to

measure fresh and dry weight of each individual seedling. Needles and roots of individual seedlings were oven dried for 48 hours at about 65-70 $^{\circ}$C for nutrient (N, P, K, Ca and Mg) and starch analysis. Similarly length and diameter of terminal buds was measured on 120 seedlings randomly selected from all 6 treatments (30 from each block).

3.2.4. MOISTURE STRESS TREATMENTS

Moisture-stress treatments consisted of watering all 24 trays to field capacity and letting them dry down to their predetermined percent water content and re-watering to field capacity (Margolis and Waring, 1986a). This cycle was repeated for about 12 weeks. These moisture-stress treatments were selected on the basis of a pilot study conducted in the Forest Research Laboratory's greenhouse in May, 1991. Moisture content may be expressed either by weight or volume of dry soil.

Soil water content by weight (Pw) was determined by using the following equation.

$$Pw = \frac{TW - (T + DS + S + C)}{DS} \qquad \text{equation (1)}$$

whereas

Pw = percent water content by weight for desired treatment,

TW = total weight of tray + water + soil + seedlings + containers,

T = weight of empty tray,

DS = average weight of dry soil for 200 seedlings,

S = average weight of 200 seedlings, and

C = average weight of Ray Leach Single Cell containers for 200

seedlings.

Water content by volume (Pv) was calculated as water content by weight (Pw) multiplied by bulk density (Db). Because the soil material was very light in weight and not always filled tightly to their brims, the average volume of soil in each Ray Leach Single Cell container was estimated to be 39 cm^3, about 20% less of the total volume of container (49.17 cm^3). Bulk density of soil was calculated as follows (Kling, 1991 personal communication and Warkentin, 1984):

$$\text{bulk density (Db)} = \frac{\text{av. dry weight of soil}}{\text{av. dry vol. of soil}}$$

water content by vol (Pv) = Db x Pw

Soil water content was also determined at saturation point and field capacity and is given as below:

soil water content at saturation point = Pw = 668%, Pv = 87%

soil water content at field capacity = Pw = 598%, Pv = 78%

Therefore, after working out the maximum limits of water content in the soil material used in this study, following 6 water stress treatments were decided to be applied on the experimental material:

Treatment #	Soil Water Content (%)	
	Pw	Pv
1	498	65
2	406	53
3	314	41
4	222	29
5	130	17
6	38	7

Soil water content was monitored by weighing the trays and using equation (1).

By rearranging the equation (1), the weight of the trays at the desired soil water content was determined as follows:

$$TW = (Pw * DS) + T + DS + S + C \qquad \text{equation (2)}$$

Trays were weighed daily to assess water content and were rewatered once they had dried down to their predetermined weights. Total weight gained by seedlings during the course of study was added to recalculate the total weight of the trays at which they were to be rewatered after they had dried down. This technique used for controlling soil water content in this study is not a new one rather it has been commonly used by many other researchers in this field of study. This technique is now the most popular moisture monitoring technique used in container tree seedling nurseries, since water is relatively heavier to other components of the container and thereafter, the moisture content of a tray or block can be easily monitored. The weight of container decreases as water is lost through evapo-transpiration. Seedlings are rewatered when container weight reaches some predetermined level (Landis, 1989b). This technique was also used by some other researchers to control soil moisture content, (e.g.) Tanaka and Timmis, (1974) in a study with Douglas-fir, Heinrich and Patric (1986) with Eucalyptus pilularis Smith, Becker, et al., (1987) with red pine and O'Reilly et al., (1989b) with western hemlock seedlings.

3.2.5. EXPERIMENTAL DESIGN

A split-plot design (Figure 2) was used in this study with water stress treatments being the whole-plot and measurement time being the sub-plot (Figure 3). Because of variations in environmental conditions and other heterogeneous conditions inside the greenhouse (e.g., placement of heating system, position of light fixtures and fans), blocking was considered necessary to give more precise estimates than in a completely randomized design (Peterson, 1985). Therefore, each bench in the greenhouse was considered a block (a total of 4 blocks). Six trays, each representing an independent treatment (experimental unit), were randomly arranged in each block to reduce variation due to positioning of the trays. During the course of the study, intra-block shifting of the trays was also regularly done after 2 - 3 days to further reduce position effects of the trays. Water stress treatments were randomly applied to the experimental material. Each tray of the seedlings was an experimental unit with each of the 200 seedlings in each tray being the sampling unit, such that there were a total of 4,800 seedlings in this study (4 blocks * 6 treatments * 200 seedlings per experimental unit).

3.2.6. CONSTANT VARIANCE ASSUMPTIONS

"Violations of one or more of the assumptions made in analysis of variance (ANOVA) or linear regression analysis may lead to erroneous results. Often data will not confirm to the assumptions implicit in the analysis, but transforming the
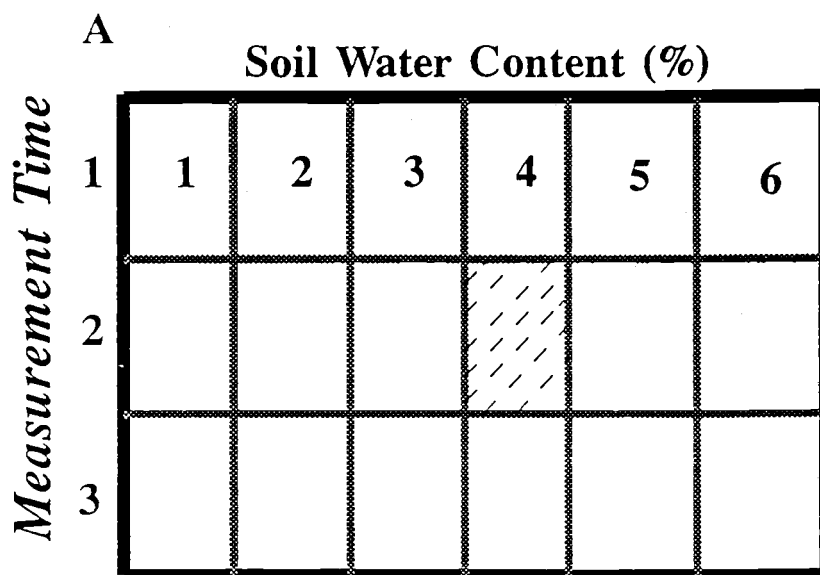
Figure 2. A split-plot design used in the study: Numbers in columns show water stress treatments: 65, 53, 41, 29, 17, and 7% soil water content by volume of dry soil, respectively, while, numbers in rows show measurement times: initial, middle, and final harvests, respectively, (Day 0, 43, and 81 respectively). The shaded cell represents a water stress treatment by measurement time interaction effect, averaged over all blocks.

A1

Whole-plot
Unit

A2

Sub-plot Unit

A3

1,2,3,....20
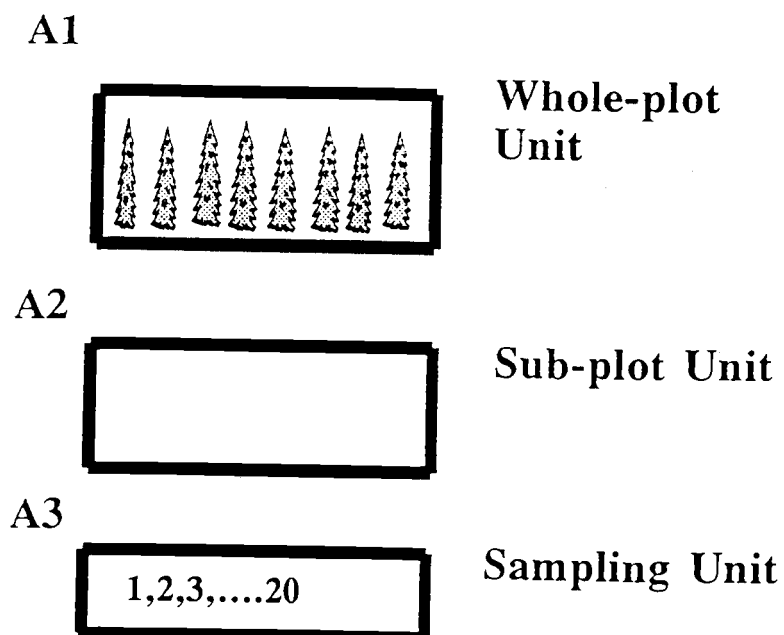
Sampling Unit

Figure 3. A split-plot design used in the study: (A) whole-plot unit (water-stress treatment) representing an experimental unit (each tray consisting of 200 seedlings); (B) sub-plot unit (measurement time); (C) a sampling unit (each of 200 seedlings in an experimental unit shows a sampling unit).

data to a different scale may lead to an appropriate model. Before determining what transformation should be used, an investigator must first determine if the assumptions are valid, and if they are not valid, how they are being violated" (Sabin and Stafford, 1990). Therefore, keeping these guidelines in view, all the data were tested for normality, linearity and constant variance to ensure the validity of these necessary assumptions. These tests showed that there was a need for transforming shoot height, caliper, shoot and root fresh and dry weights (measured at initial, middle and final harvests), fresh and dry weights of needles and roots (measured at final harvest), and pre-dawn and mid-day PMS data. Therefore, data were log transformed to achieve a normal and homogenous distribution of the variance. Means presented anywhere in the Thesis or used in graphical or tabulated presentation of the data were retransformed from the log.

3.2.7. STATISTICAL ANALYSES

3.2.7.1. Analysis of phenological data: Randomly selected seedlings were assigned a rating code of 0-5 corresponding to the developmental status of terminal buds (see section 3.2.2.1). However, the question arises as to which stage should be considered and referred to as representative budset stage. Different approaches were applied to decide upon this very basic but sensitive question. The first approach was to determine the percentage of seedlings reversing from their different stages to zero (i.e., breaking their buds and re-starting active growth). Buds were considered to have been broken when bud scales parted and needles

extended to grow (Margolis and Waring, 1986b, and Grossnickle, 1989). This provided valuable information about the behavior of the seedlings. Because, if some seedlings break their buds during bud developmental stages 1, 2 or any other stage, and start regrowing actively, those stages, obviously, can not be considered as budset stages. The statistical analysis showed that seedlings in bud developmental stages 1 and 2 were not stable stages since 13.1 and 0.83% (1.e., 63/480 and 4/480 seedings respectively: based on a total of 480 seedlings for all 6 treatments) of seedlings broke their terminal buds. Whereas, bud developmental stages 3, 4 and 5 were found to be quite stable, since none of these seedlings resumed growth after reaching these stages. The second approach applied was to determine the percentage of seedlings reaching different bud developmental stages (see section 3.2.2.1 for detail). Likewise, this approach furnished an important information about growth response of terminal buds to water stress treatments. Statistical analysis showed that 97, 96, 86, 44 and 13% (i.e., 465/480, 463/480, 415/480, 210/480, and 63/480 seedlings: based on a total of 480 seedlings for all 6 treatments) of seedlings reached bud developmental stages 1, 2, 3, 4 and 5 respectively. Stages 1 and 2 were not considered as representative budset stage because of nonstability in growth of terminal buds (i.e., resuming growth after reaching these stages). Therefore, rest of three bud developmental stages (3, 4 and 5) were considered for this purpose. These two approaches provided sufficient statistical evidence to deal with the question as to which bud developmental stage should be considered a complete budset stage. Therefore,

based on the stable behavior and number of the seedlings in each stage, bud developmental stage 3 was chosen to be representative of complete budset. The methodology used in this study is similar to that reported by Lavender et al., (1968) in a study to examine the effects of various dormancy induction treatments on dormancy initiation and growth of Douglas-fir seedlings.

The first day, the seedlings reached stage 3, was considered as day (i.e., time) to budset. SAS programming was done in a way that made it possible to pick up the first day, seedlings reached stage 3. For example, seedling # 1 in block 1, subjected to treatment 1 (65% soil water content), reached stage 3 (i.e., set bud). on day 37 from the start of the study (i.e, day 0). It stayed at the same stage unto day 73, before it shifted to developmental stage 4. But the program picked up the first day of reaching stage 3 (day 37) which was considered the time of budset for that particular seedling. All the data were analyzed based on this methodology.

All the data were analyzed using the General Linear Model (GLM) procedures for a randomized complete block design. Statistical Analysis System (SAS Institute, 1982) software was used for analysis of all data. Fisher's Protected Least Significant Difference (FPLSD) (Steel and Torrie, 1980) was used to determine significant differences among treatment means at the 1% significance level unless stated otherwise.

3.2.7.2. Analysis of physiological, morphological, PMS and terminal bud

dimensions data: Data, from total needle and root nutrients, total needle starch, pre-dawn and mid-day PMS, total shoot height, caliper, shoot and caliper growth, shoot:root ratio, length and diameter of terminal buds, and fresh and dry weights of roots, needles and stems, were analyzed for randomized complete block design using SAS software (SAS Institute, 1982). Fisher's Protected Least Significant Difference (FPLSD) was used to accomplish mean separation at 1% significance level, unless stated otherwise.

3.2.7.3. Analysis of soil water content/measurement time interaction:

Data, from shoot height, caliper, fresh and dry weights of shoots and roots, and root starch, measured at initial, middle and final harvests (day 0, 43, and 81 respectively), and shoot nutrients, measured at initial and middle harvests, were analyzed and tested for a split-plot design using SAS software. The hypotheses for interaction were tested at 1% significance level. Interaction between whole plot and sub plot can be presented in two ways; either 1) different levels of factor A (water stress treatments) at the same level of factor B (measurement time) or 2) vice versa. A least square means (LSMEANS) procedure was used in SAS to determine significant differences among different levels of factor B (measurement time) at the same level of factor A (water stress treatments). Whereas, it was not possible to get LSMEANS for different levels of factor A at the same level of

factor B, Fisher Protected Least Significant Difference (FPLSD) was calculated to accomplish mean separation as follows:

a) calculate standard error (SE)   (Stafford and Sabin, 1992 unpubl)

$$SE = \sqrt{\frac{2[(b-1)(E_b)+(E_a)]}{rbn}}$$

where:

E_a = whole plot error "A" (block *treatment *time),

E_b = sub plot error "B" (block * treatment),

r = number of blocks;

b = factor B "sub plot" (measurement time), and

n = sub-sampling (20 seedlings in each block and treatment).

b) calculate degrees of freedom (df)   (Peterson, 1985)

$$df = \frac{a(r-1)(a-1) \ [(b-1)(E_b) + (E_a)]^2}{[(a-1)(b-1)(E_b)^2] + [(a)(E_a)^2]}$$

where

a = factor A "whole plot" (water stress treatments), rest are explained above.

c) find out t-value

$$t_{\text{tab } \alpha(df)}$$

d) calculate Fisher's Protected Least Significant Difference (FPLSD)

$$\text{FPLSD} = t_{\text{tab } \alpha(df)} * SE$$

E_a typically should be greater than E_b. When E_a occasionally is less than E_b, it means that variation between subunits has been maximized at expense of variation among whole plots, which is contrary to the purpose of split-plot design (Stafford and Sabin, 1992 unpubl). In this situation, E_a should be dropped from the model (Sabin, 1992, personal communication). This happened in case of root fresh weight, measured at day 0, 43, and 81. E_a was dropped from the model and hypotheses of whole plot, sub plot and their interaction were all tested with the same error term (E_b). The exact same situation was found in root starch concentration, therefore, E_a was dropped from the model. However, there was no sub-sampling in this case, all the hypotheses were tested using total error in the model.

4. RESULTS

4.1 PHENOLOGICAL PARAMETERS

4.1.1 THE PERCENTAGE OF SEEDLINGS REVERSING FROM DIFFERENT STAGES TO ZERO

Moisture stress treatments had a highly significant effect on bud activity (Appendix I. 1-5). Figure 4A shows that seedlings in bud developmental stages 1 and 2 reversed by 13.1% and 0.83% (see section 3.2.7.1 for details) whereas, stages 3, 4 and 5 were found to be stable since none of these seedlings resumed growth after reaching these bud developmental stages. The percentage of seedlings reversing from stage 1 to 0 decreased significantly (P= 0.0418) with decreasing soil water content. Seedlings grown in the driest soil (7% water content) were most stressed resulting in about 84% decrease of seedlings reversing from stage 1 to 0 compared to seedlings grown in the wettest soil (65% soil water content) (Figure 4B).

4.1.2. THE PERCENTAGE OF SEEDLINGS REACHING DIFFERENT STAGES

Figure 4C shows that 97, 96, 86, 44 and 13% of the total 480 seedlings (see section 3.2.7.1 for detail) reached bud developmental stages 1, 2, 3, 4 and 5 respectively. As expected, decreasing soil water content resulted in higher percentage of seedlings reaching more advanced stages except in the severely stressed seedlings (7% soil water content).
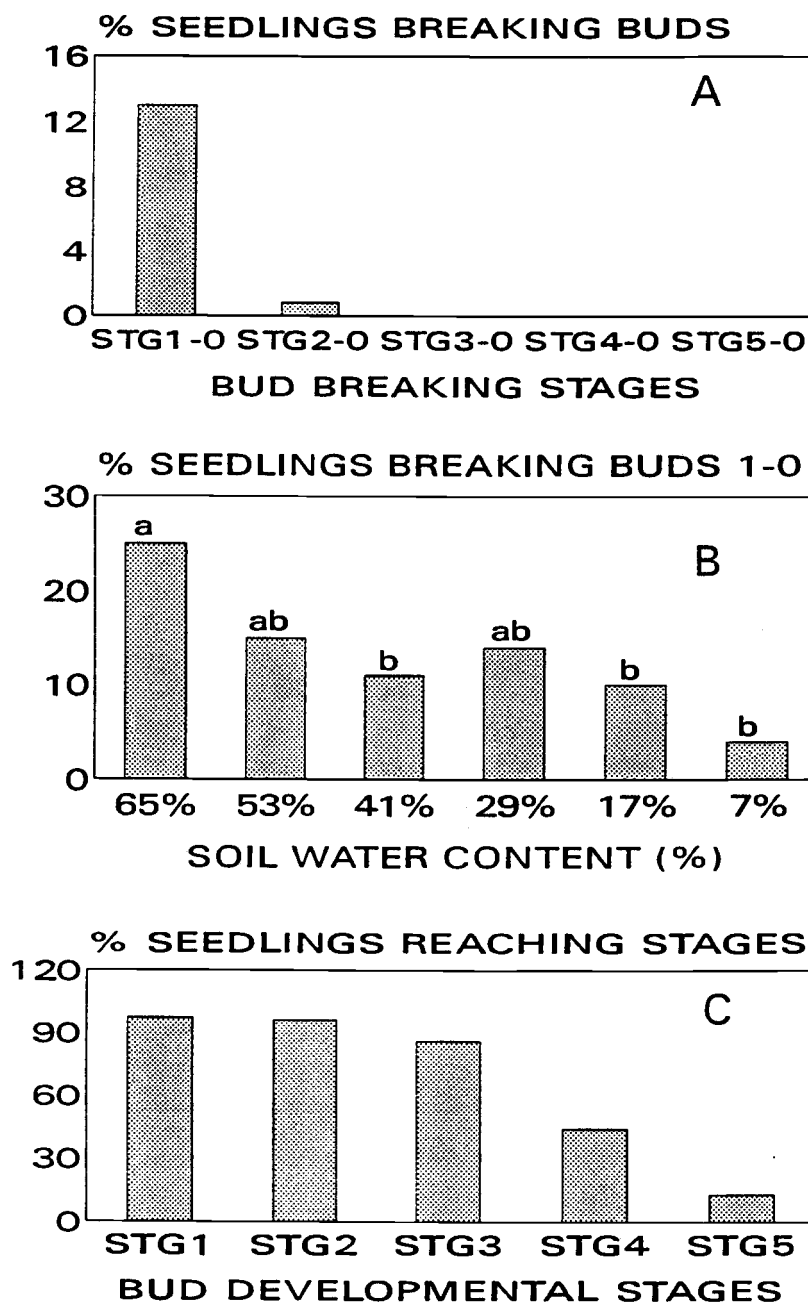
Figure 4. Effect of soil water content on terminal bud activity: (A) % of seedlings breaking buds from different bud developmental stages; (B) % of seedlings breaking buds, after seedlings had initiated bud formation; (C) % of seedlings reaching different bud developmental stages. Bars with the same letters are not significantly different at $\alpha = 0.05$ level.

4.1.2.1. Stage 1 (bud initiation): Water stress treatments were successful in initiating bud formation in seedlings (P= 0.0007). Five water stress treatments (65, 53, 41, 29 and 17% soil water content) were effective in resulting in 100% bud formation (i.e., 80 out of 80 seedlings for each treatment). However, 19% of seedlings (15 out of 80 seedlings for each treatment) were unable to initiate terminal buds at the lowest soil water content (7%) (Figure 5A). Seedlings subjected to lower soil water contents took significantly less time (P= 0.0012) to initiate bud formation except the wettest and driest treatments (65% and 7% soil water contents) which delayed bud formation (Figure 5B).

4.1.2.2. Stage 2 : A similar trend to this was found in seedlings reaching stage 2. However, there was a decrease of 19% (P= 0.0017) in seedlings reaching bud developmental stage 2 from the 65% to 7% soil moisture content. Days to reach bud developmental stage 2 decreased with decreasing soil water content (P= 0.0079), except those grown in the driest soil, which took considerably longer to reach stage 2 (Figure 5C).

4.1.2.3. Stage 3 (budset): Moisture stress treatments were found to be quite successful in inducing budset in seedlings (P= 0.0073). The percentage of seedlings setting buds increased with decreasing soil water content. However, when moisture content dropped beyond 29%, percentage of seedlings setting buds also decreased. Similarly, the wettest treatment (65% soil water content) also resulted in reduced percentage of seedlings setting buds (Figure 6A). As expected, seedlings treated with decreasing soil water content took considerably

% SEEDLINGS INITIATING BUDS

DAYS TO BUD INITIATION

DAYS TO REACH STAGE 2
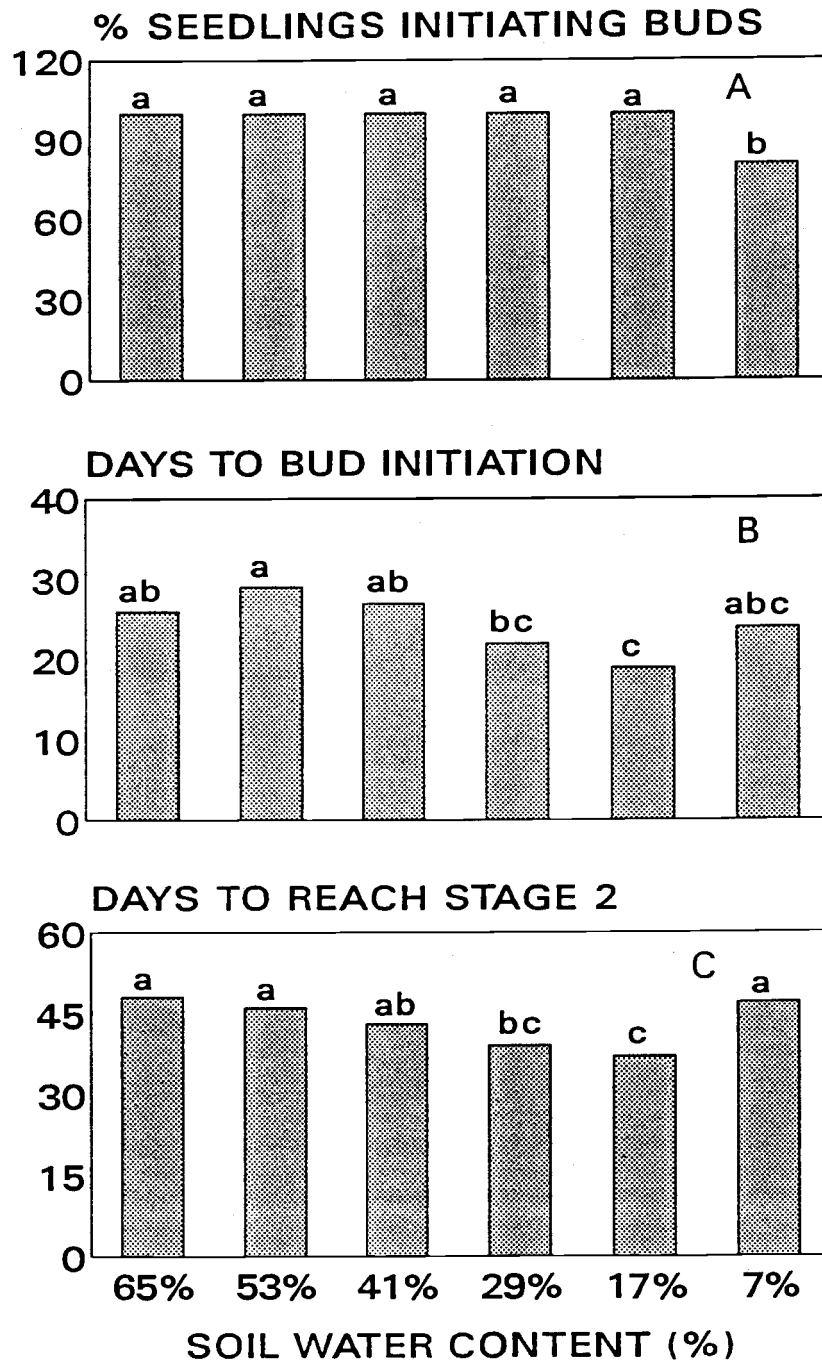
SOIL WATER CONTENT (%)

Figure 5. Effect of soil water content on terminal bud activity: (A) % of seedlings initiating buds; (B) average days to bud initiation; (C) average days to reach stage 2. Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

less time (P= 0.0072) to set buds except 7% which took significantly longer days) to set terminal buds (Figure 6B). It was also found that seedlings grown in the driest soil (7% soil water content) took significantly longer (P= 0.0106) to shift to budset stage (stage 3) after initiating bud formation (Table 3)

4.1.2.4. Stage 4 and 5: Analysis showed that the percentage of seedlings reaching stage 4 increased significantly (P= 0.0006) with decreasing soil water content, reaching maximum at 17% soil water content. But too much and too little watering reduced percentage of seedlings since only 29% and 10% (i.e., 23 out of 80 and 8 out of 80 seedlings respectively for each treatment) of seedings could reach stage 4 (Figure 7A). Although, small differences appeared in percentage of seedlings reaching the most advance stage (stage 5) of bud development (P= 0.0853), decreasing soil water content resulted in higher percentage of seedlings. Consistent with the results of other bud developmental stages, seedlings subjected to the lowest soil water content (7%) were so drastically stressed that none of them could reach the most advance bud developmental stage (stage 5) (Figure 7B). The percentage of seedlings reaching stage 5 was also reduced at the wettest treatment (65% soil water content). Although statistically not significant, seedlings treated with the wettest and driest treatments (65% and 7% soil water contents) took relatively longer (P= 0.6129 and 0.8917 respectively) to reach stages 4 and 5 (Table 3).

% OF SEEDLINGS SETTING BUDS

DAYS TO BUD SET
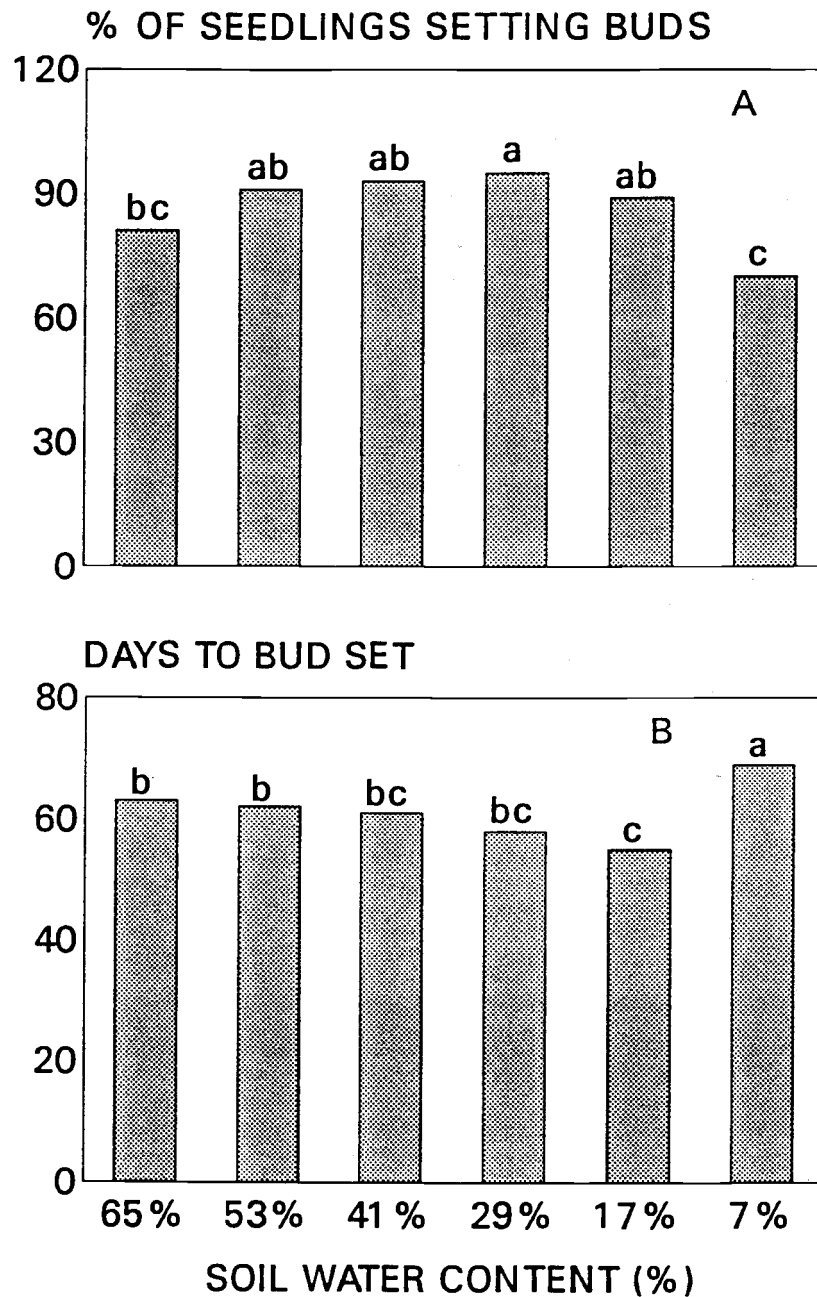
SOIL WATER CONTENT (%)

Figure 6. Effect of soil water content on terminal bud activity: (A) % of seedlings setting buds; (B) average days to budset. Bars with the same letters are not significantly different at $\alpha = 0.01$ level.
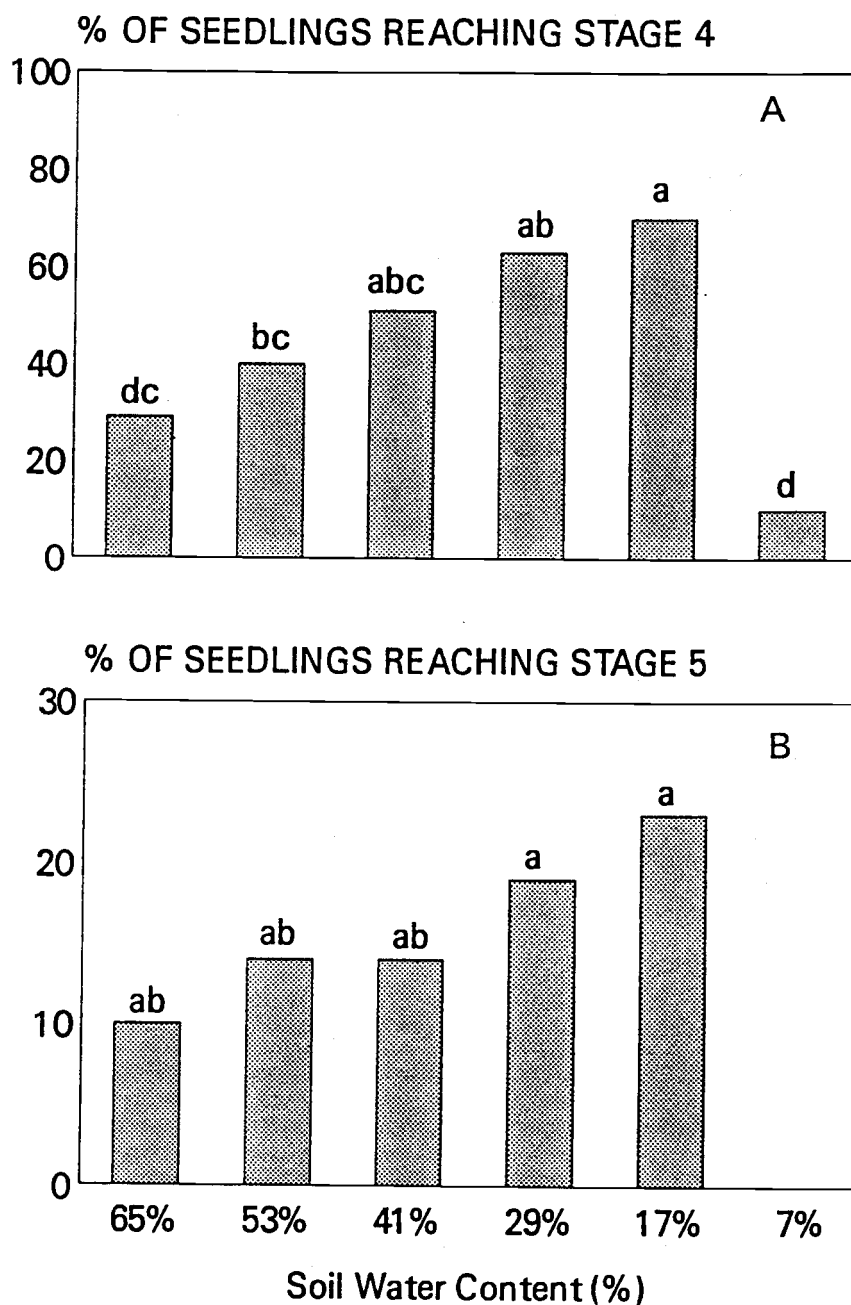
Figure 7. Effect of soil water content on terminal bud activity: (A) % of seedlings reaching stage 4; (B) % of seedlings reaching stage 5. Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

TABLE 3. Means of selected phenological parameters as affected by water stress treatments. Mean days within each column with same letters are not significantly different at 1% significance level, numbers within parentheses are number of seedlings.

soil water content	days to budset after bud initiation	days to reach stage 4	days to reach stage 5
65%	38b (65)	68b (23)	78a (08)
53%	34b (73)	70b (32)	75a (11)
41%	35b (74)	72ab (41)	78a (11)
29%	36b (76)	72b (50)	78a (15)
17%	38b (71)	72ab (56)	76a (18)
7%	48a (56)	78a (08)	00 (00)

4.2. PHYSIOLOGICAL PARAMETERS

4.2.1. NUTRIENTS

4.2.1.1. Total needle nutrient concentration and content: Total needle nutrient concentration (%) and content (mg) were significantly influenced by soil water content (Appendix IIA. 6-14). Decreasing soil water content resulted in lower nutrient concentration and content.

Although, treatment effect was highly significant (P = 0.0093) on total nitrogen (N) concentration, multiple mean comparison suggested that 65 to 17% soil water content had the same effect. However, in general, total N concentration tended to decrease with decreasing soil water content except at 7% soil water content at which N concentration was found significantly higher (Figure 8A). On the other hand, N content decreased with decreasing soil water content (P=0.0388). The greatest reduction was at the lowest moisture content (7%) (Figure 8B).

Total needle phosphorous (P) concentration and content decreased significantly (P= 0.0274 & ≤ 0.0001 respectively) with decreasing soil water content. There was a decrease of approximately 8% and 29% in P concentration and content from the highest to lowest soil water content (Figure 9A and B). P concentration and content also decreased at the wettest treatment (65% soil water content).

Analysis showed that total needle potassium (K) concentration was unaffected by moisture stress treatments (P= 0.2812). However, a trend of

NEEDLE NITROGEN CONCENTRATION

NEEDLE NITROGEN CONTENT (mg)
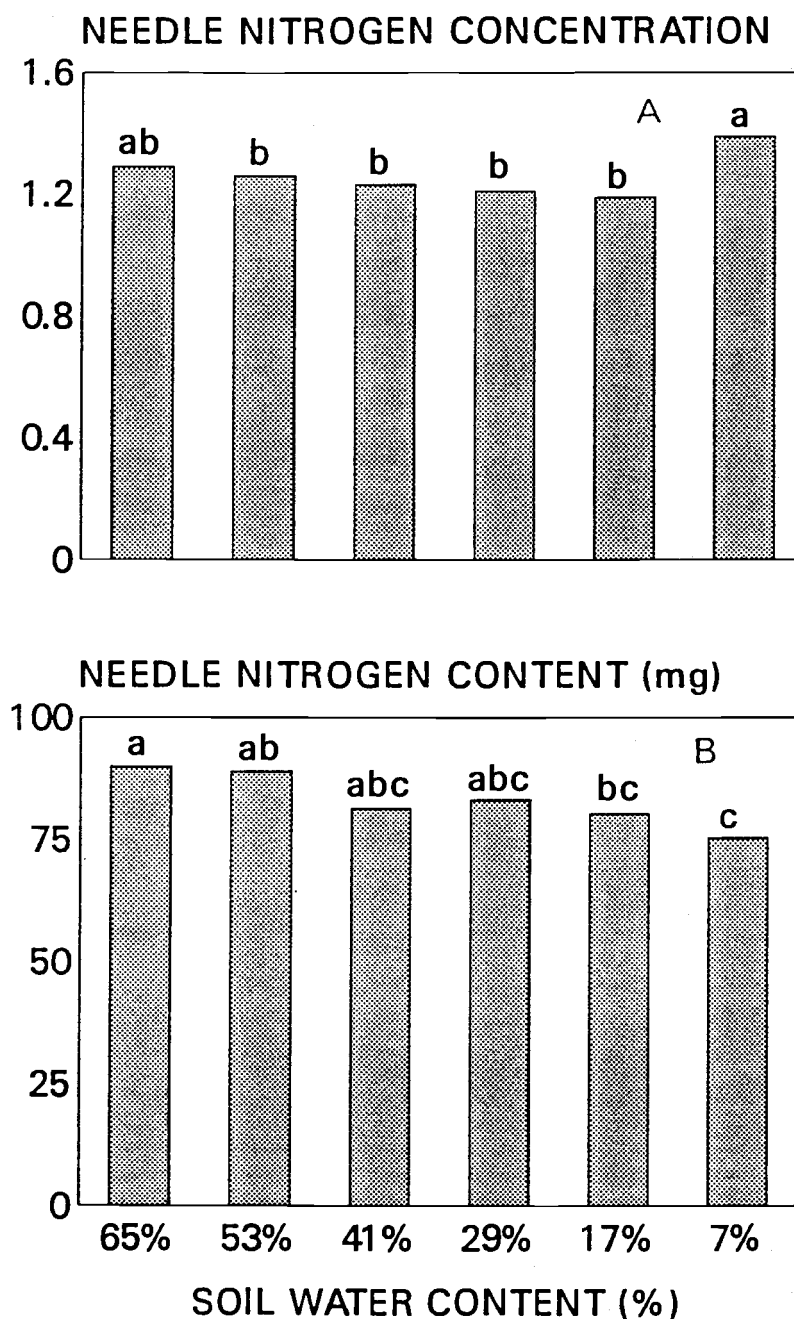
Figure 8. Effect of soil water content on total needle nutrient status (% dry weight): (A) nitrogen concentration (%); (B) nitrogen content (mg). Bars with the same letters are not significantly different at $\alpha = 0.05$ level.

NEEDLE PHOSPHOROUS CONC (%)

NEEDLE PHOSPHOROUS CONTENT (mg)
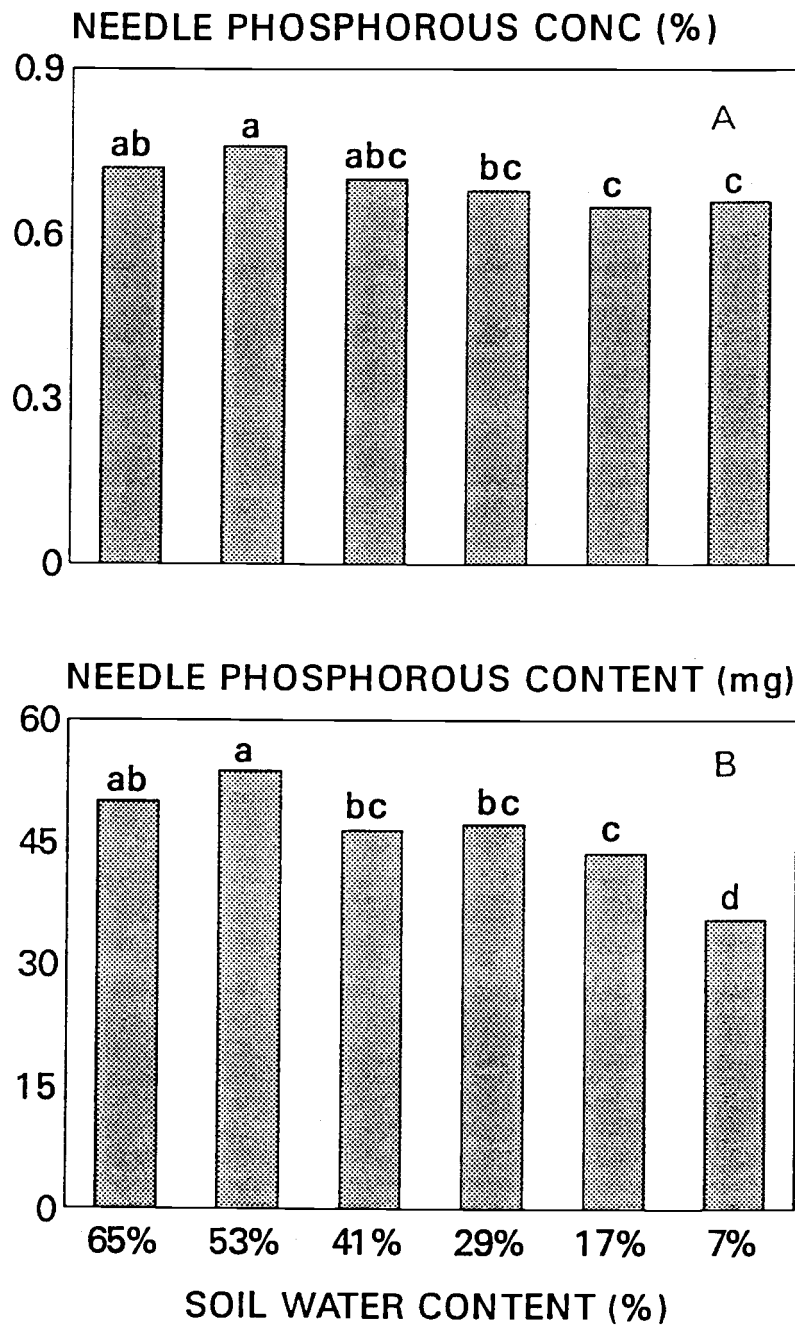
SOIL WATER CONTENT (%)

Figure 9. Effect of soil water content on total needle nutrient status (% dry weight): (A) phosphorous concentration (%); (B) phosphorous content (mg). Bars with the same letters are not significantly different at $\alpha = 0.05$ level.

decreasing K concentration with decreasing soil water content can be observed in Table 4. On the other hand, total K content was significantly decreased (P = 0.0036) at 7% soil water content. Multiple mean comparison procedure revealed a significantly low mean (about 34% lower than that of 65% soil water content) for K content at 7% soil water content, which caused overall significant treatment effect. The rest of the treatments did not significantly differ from one an other (Table 4).

Total needle calcium (Ca) concentration and content were also significantly decreased (P ≤ 0.0001 for both) with decreasing soil water content. There was a drastic decrease of about 32% and 47% for Ca concentration and content, respectively, from the highest to lowest soil water content (Figure 10A and B). A similar trend was found in total needle magnesium (Mg) concentration and content (P ≤ 0.0001 for both). Mg concentration and content decreased by about 27% and 43% respectively from the highest to lowest soil water content (Figure 11A and B).

4.2.1.2. Shoot nutrient concentration and content: Analysis of data showed no significant water stress treatments/measurement times interaction for shoot nutrients (measured at day 0 and 43) except for Ca content (Table 5 for P-values). Further testing of hypotheses for main effects (water stress treatments) revealed a significant effect of water stress treatments on P content and Ca concentration (Table 6). This effect on P was quite irregular and not clearly related to water

TABLE 4. Means of total needle and root potassium concentration (%) and content (mg). Means within same column with same letters are not significantly different at 1% significance level, (Fisher's Protected LSD).

soil water content	total needle potassium		total root potassium	
	%	mg	%	mg
65%	1.85a	129.56a	0.87a	59.77b
53%	1.82a	129.69a	0.95a	69.99a
41%	1.80a	117.16a	0.86a	56.89c
29%	1.75a	120.32a	0.82a	54.28c
17%	1.72a	122.06a	0.85a	53.31c
7%	1.59a	085.93b	0.86a	41.17d

NEEDLE CALCIUM CONCENTRATION

NEEDLE CALCIUM CONTENT (mg)
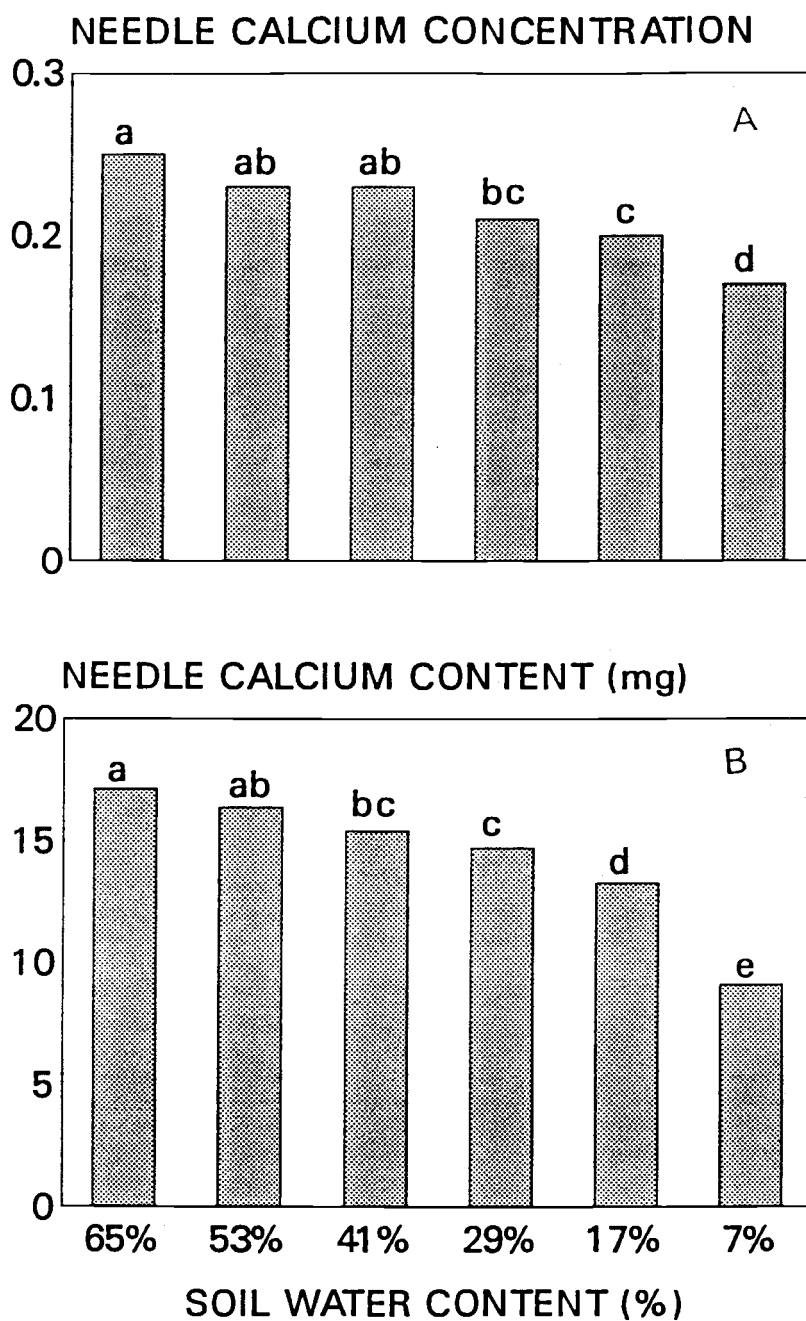
SOIL WATER CONTENT (%)

Figure 10. Effect of soil water content on total needle nutrient status (% dry weight): (A) calcium concentration (%); (B) calcium content (mg). Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

NEEDLE MAGNESIUM CONC

A

NEEDLE MAGNESIUM CONTENT

B

SHOOT CALCIUM CONTENT

C

65%   53%   41%   29%   17%   7%
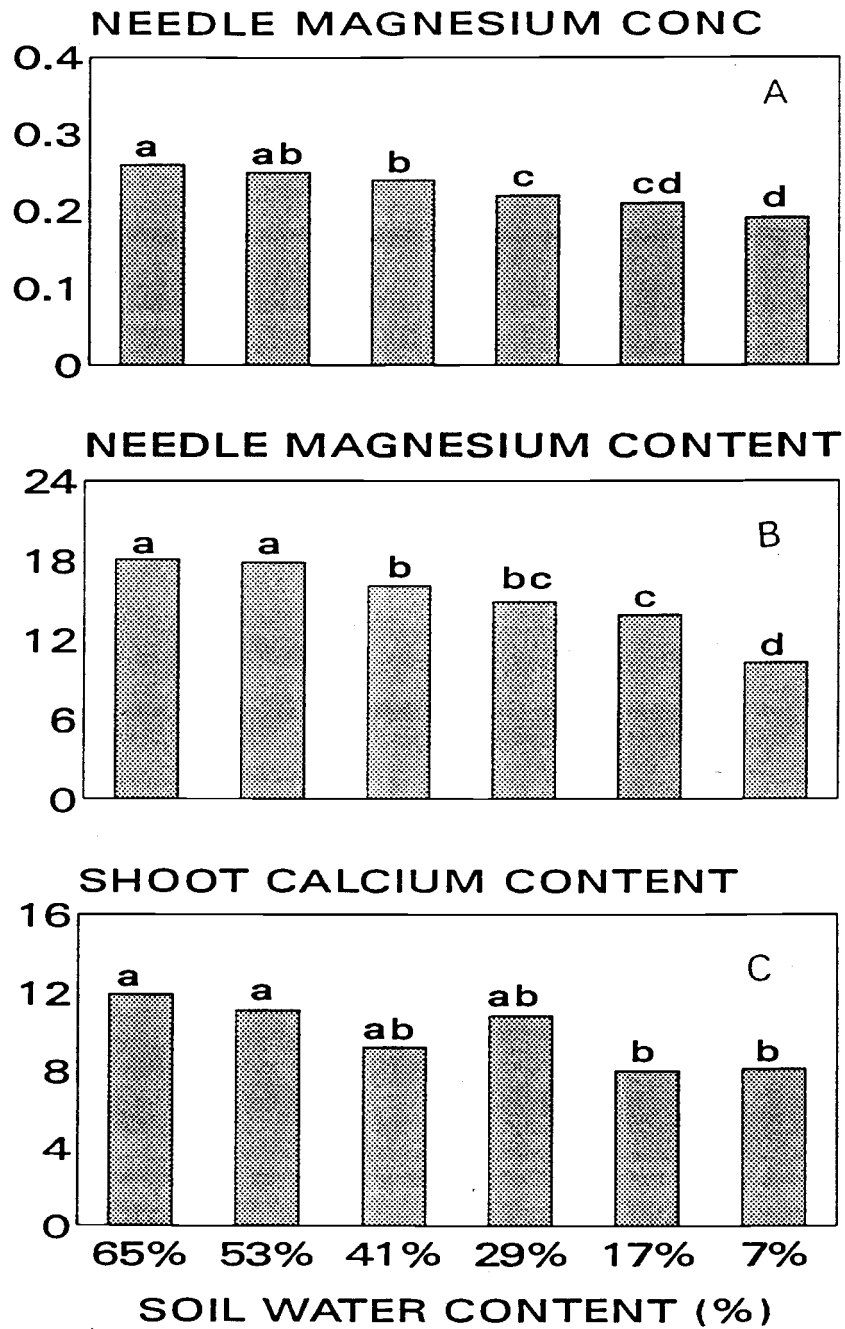
SOIL WATER CONTENT (%)

Figure 11. Effect of soil water content on total needle nutrient status (% dry weight): (A) magnesium concentration (%); (B) magnesium content (mg); (C) shoot calcium content. Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

TABLE 5. P-values for shoot nutrient concentration a (%) and content (mg) showing water stress treatment/measurement time interaction or no interaction and significance of main effect (water stress treatments)

| nutrients | P-values | | |
	interaction	water stress treatments	measurement time
N %	0.1084	0.0893	0.0001
mg	0.4602	0.2598	0.3241
P %	0.4104	0.8261	0.0001
mg	0.0655	0.0450	0.0001
K %	0.9620	0.5477	0.001
mg	0.1697	0.0778	0.0001
Ca %	0.1450	0.0091	0.0006
mg	0.0159	0.0173	0.0001
Mg %	0.1959	0.4982	0.2411
mg	0.1237	0.1164	0.0001

TABLE 6. Means of shoot phosphorous contents (mg) and calcium concentration (%) showing irregular effect of water stress treatments (main effect). Means within same column with same letters are not significantly different at 1% significance level. (Fisher's Protected LSD).

soil water content	phosphorous mg	calcium %
65%	34.35ab	0.18a
53%	36.27a	0.16b
41%	30.35bc	0.16b
29%	33.07abc	0.16b
17%	28.32c	0.14b
7%	28.77bc	0.15b

stress treatments. However, calcium content decreased significantly with decreasing soil water content (Figure 11C).

4.2.1.3. Total root nutrient concentration and content: Total root nutrient concentration and content also significantly decreased (Appendix IIB. 15-24) with decreasing soil water content (65% to 7%).

Although, treatment effect was significant (P= 0.0106) for total root N concentration, multiple mean comparison showed an irregular effect of treatments (Figure 12A). Conversely, total root N content significantly decreased (P ≤ 0.0001) with decreasing soil water content. It decreased approximately by 27% from the highest to lowest soil water content (Figure 12B).

Total root P concentration and content decreased significantly (P ≤ 0.0001 for both) with decreasing soil water content. There was a drastic decrease of about 31% and 51% for total root phosphorous concentration and content from the wettest to driest soil water content (65% to 7%) (Figure 13A and B).

In contrast, total root potassium concentration remained relatively unaffected (P= 0.1061) by water stress treatments, however, it showed a decreasing trend with decreasing soil water content (Table 2). K content, however, decreased significantly (P ≤ 0.0001) with decreasing soil water content. Seedlings grown in the driest soil (7% soil water content) experienced a major decrease (about 31%) in total K content compared with seedlings grown in the wettest soil (65% soil water content) (Figure 13C).

ROOT NITROGEN CONCENTRATION (%)

ROOT NITROGEN CONTENT (mg)
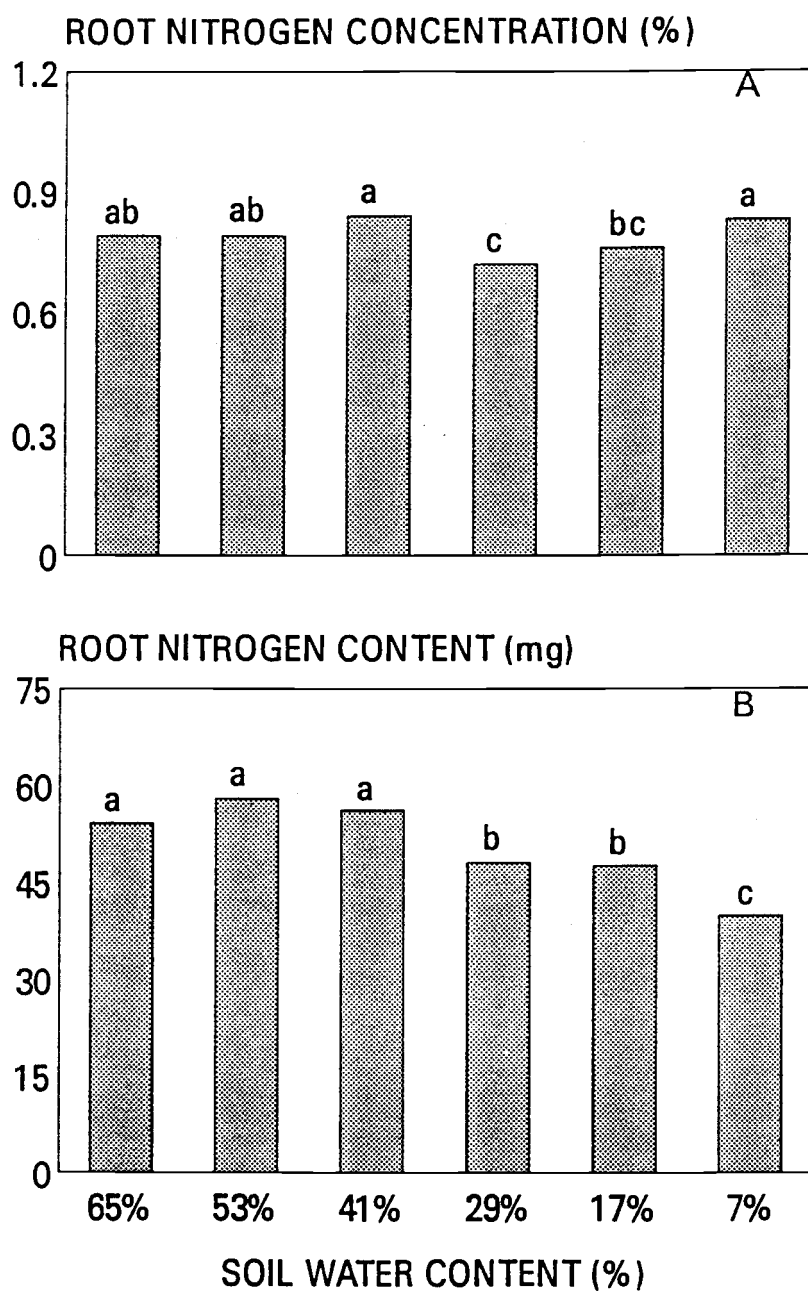
Figure 12. Effect of soil water content on total root nutrient status (% dry weight): (A) nitrogen concentration (%); (B) nitrogen content (mg). Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

ROOT PHOSPHOROUS CONC (%)

ROOT PHOSPHOROUS CONTENT

ROOT POTASSIUM CONTENT (mg)
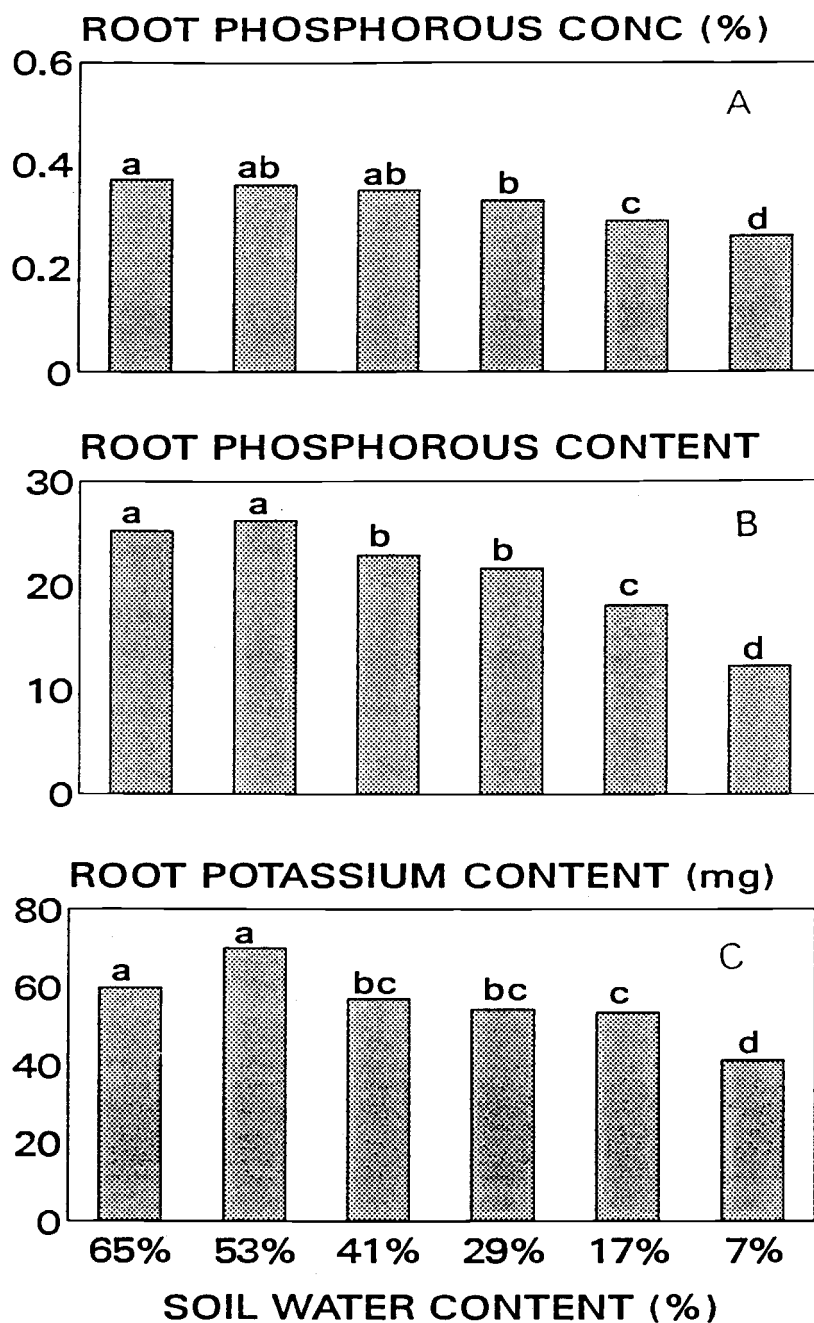
SOIL WATER CONTENT (%)

Figure 13. Effect of soil water content on total root nutrient status (% dry weight): (A) phosphorous concentration (%); (B) phosphorous content (mg); (C) potassium content. Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

Decreasing soil water content resulted in decreased total root Ca concentration and content (P= 0.0059 & ≤ 0.0001 respectively). There was a tremendous decrease of about 38% and 53% in Ca concentration and content from the wettest to driest treatments (65% to 7%) (Figure 14A and B). Similarly, total root Mg concentration and content decreased significantly (P ≤ 0.0001 for both) with decreasing soil water content. This decrease was as much as 58% and 70% for magnesium concentration and content, respectively, from the wettest to driest soils (65% to 7% moisture content) (Figure 15A and B).

Both needle and root nutrients were also analyzed on an N= 100 basis (i.e., its ratio to N) (Appendix IIC. 25-28). P/N, Ca/N and Mg/N ratios in needles of seedlings decreased significantly with decreasing soil water content. There was a huge reduction of about 15%, 36% and 32% for P/N, Ca/N and Mg/N ratios respectively from the wettest to driest treatments (65% to 7% soil water content) (Table 7). P/N, Ca/N and Mg/N ratios in roots of seedlings also decreased significantly (Appendix IID. 29-32) with decreasing soil water content (Table 8). The K/N ratio in both needles and roots, remained relatively unaffected by soil water content.

4.2.2. VECTOR ANALYSES

Vector analysis is done by comparing the vector shift between 41% soil water content and other water stress treatments (65, 53, 29, 17, and 7% soil water content) (Figures 16-19). Possible interpretation of directional shifts in total

ROOT CALCIUM CONCENTRATION (%)

ROOT CALCIUM CONTENT (mg)
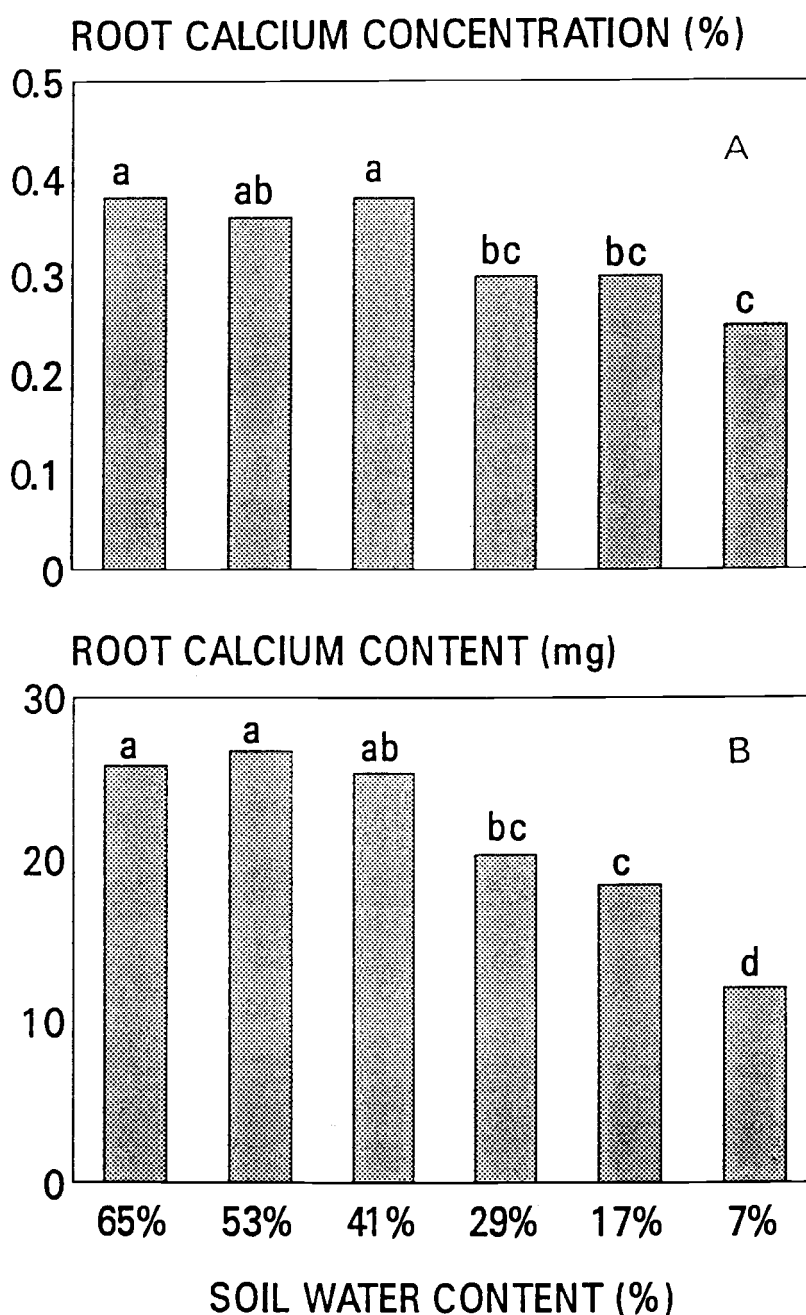
SOIL WATER CONTENT (%)

Figure 14. Effect of soil water content on total root nutrient status (% dry weight): (A) calcium concentration (%); (B) calcium content (mg). Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

NEEDLE MAGNESIUM CONC

A

NEEDLE MAGNESIUM CONTENT

B

SHOOT CALCIUM CONTENT

C

65% 53% 41% 29% 17% 7%
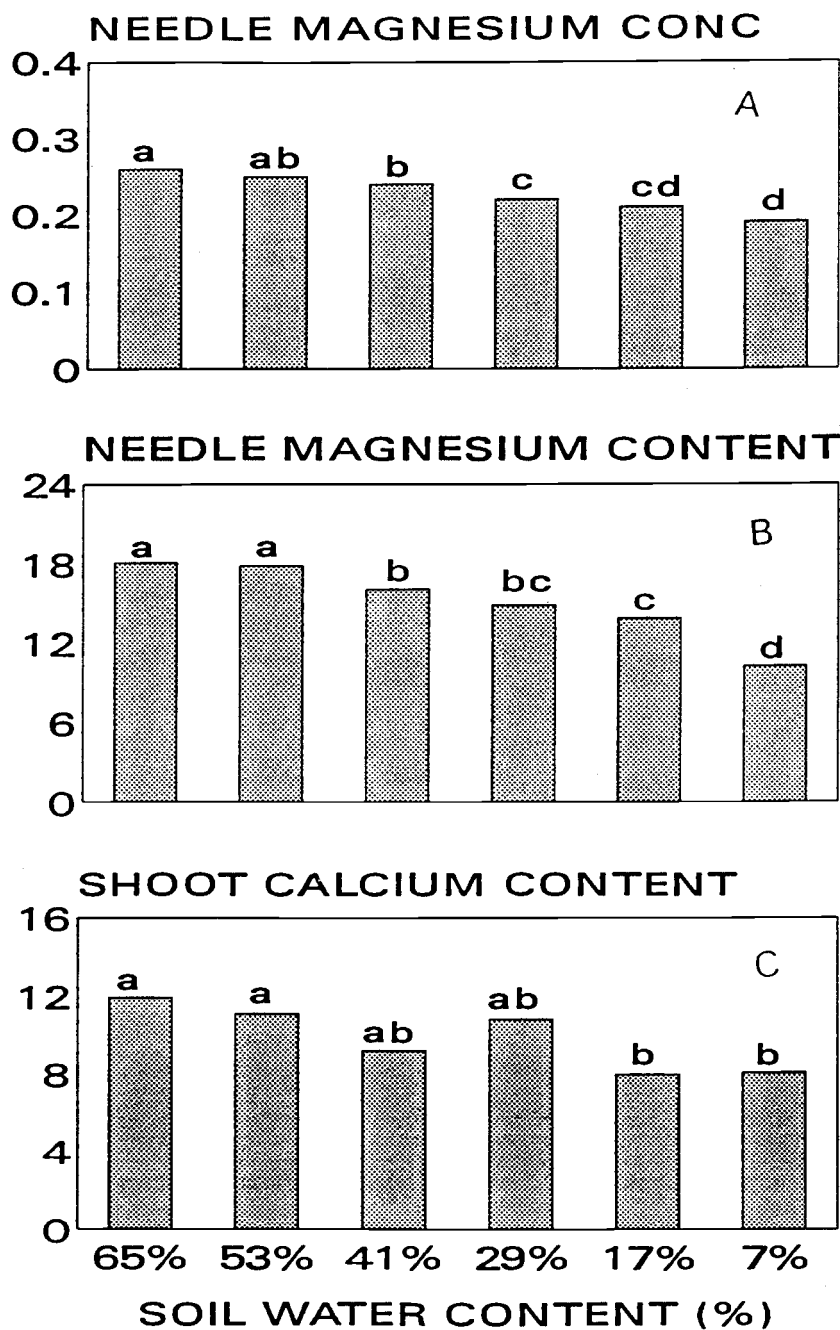
SOIL WATER CONTENT (%)

Figure 15. Effect of soil water content on total root nutrient status (% dry weight): (A) magnesium concentration (%); (B) magnesium content (mg). Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

TABLE 7. Mineral nutrient ratios to N of final needle tissue. Means within same column with same letters are not significantly different at 1% significance level. (Fisher's Protected LSD).

soil water content	nitrogen	phospho-rous	potassium	calcium	magnesium
65%	100	55.60b	143.70ab	19.05a	20.17a
53%	100	60.58a	145.93a	18.43ab	20.10a
41%	100	57.13ab	143.65ab	18.88a	19.73ab
29%	100	56.81ab	144.11a	17.73ab	17.95ab
17%	100	54.41b	155.87a	16.64b	17.54b
7%	100	47.34c	114.24b	12.11c	13.73c

TABLE 8. Mineral nutrient ratios of final root tissue. Means within same column with same letters are not significantly different at 1% significance level. (Fisher's Protected LSD).

soil water content	nitrogen	phospho- rous	potassium	calcium	magnesium
65%	100	46.70a	110.80ab	47.91a	75.75a
53%	100	45.21ab	120.56a	45.78a	87.50a
41%	100	41.34bc	103.44b	44.87a	55.95b
29%	100	45.14ab	113.39ab	42.16a	40.44bc
17%	100	38.13c	112.41ab	38.89ab	39.77bc
7%	100	30.93d	103.43b	30.37b	30.66c
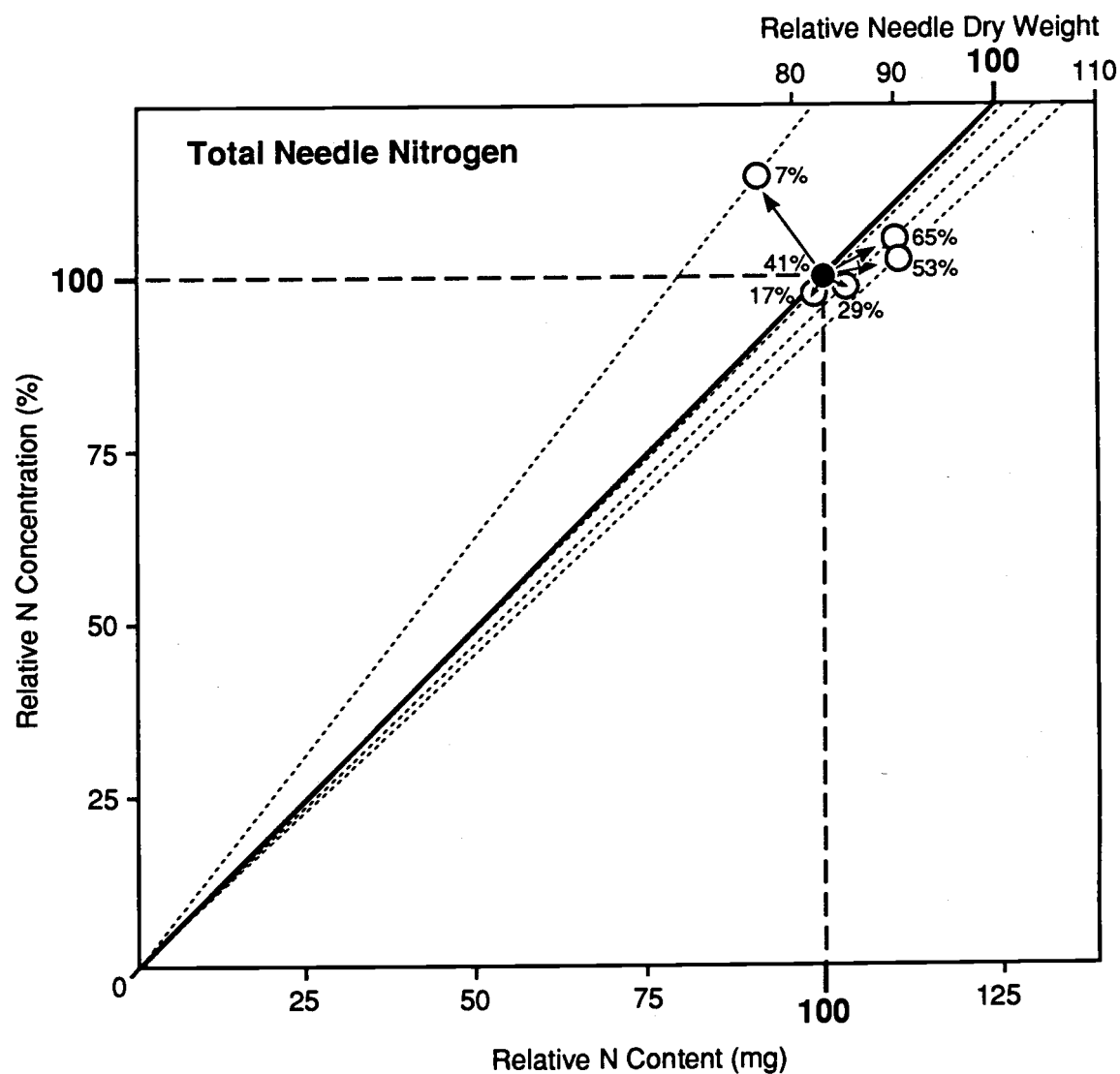
Figure 16. Interpretation of directional differences (Vectors) in total needle nitrogen concentration (%), content (mg), and dry weight (g) between 3-4 month old containerized Douglas-fir seedlings grown under 6 different water stress treatments (65, 53, 41, 29, 17, and 7% soil water content by volume). The filled circle representing 41% soil water content, is used to calculate absolute values of concentration, content, and dry weight. Vectors described by different water stress treatments are interpreted in Table 9.
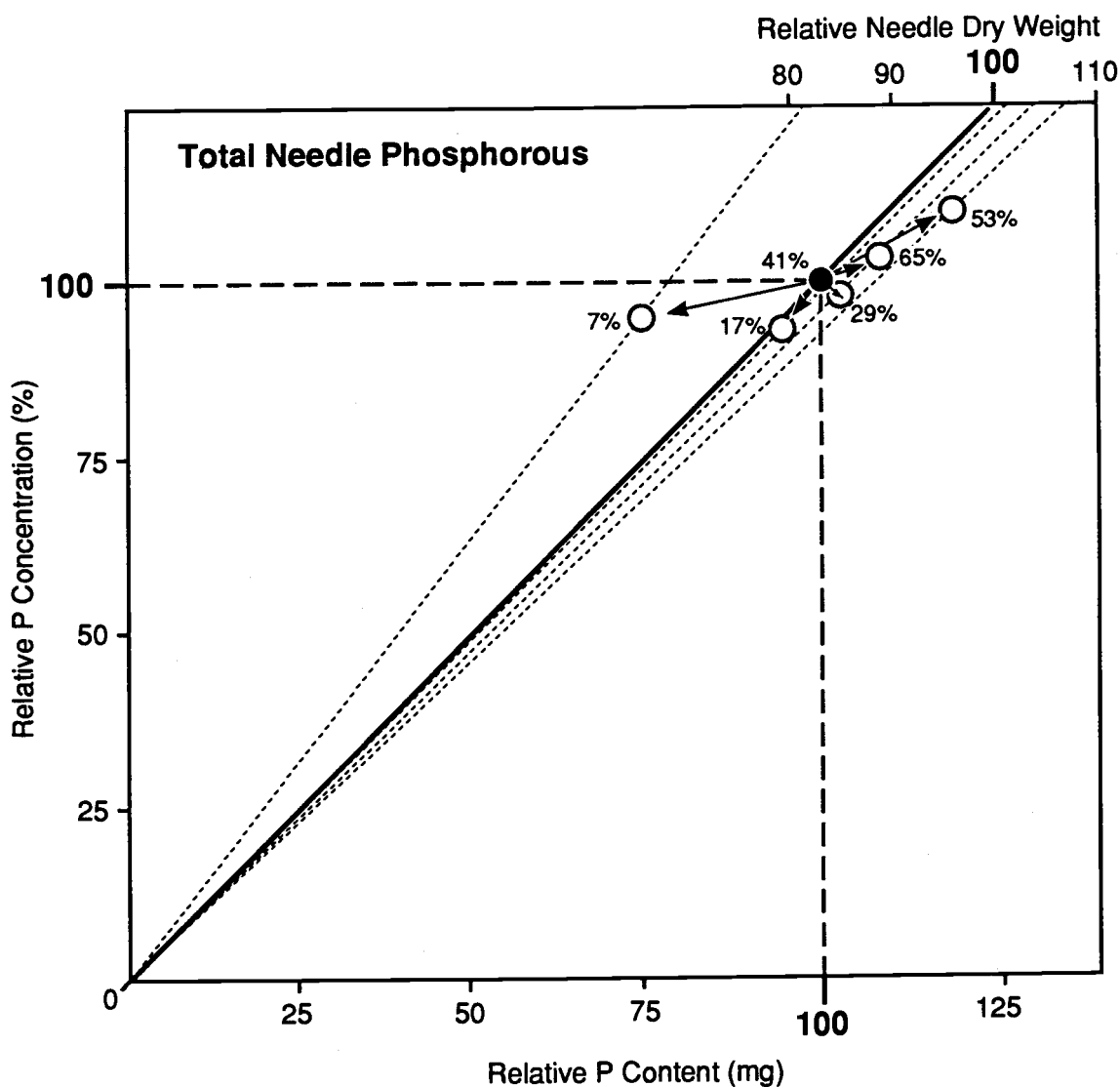
Figure 17. Interpretation of directional differences (Vectors) in total needle phosphorous concentration (%), content (mg), and dry weight (g) between 3-4 month old containerized Douglas-fir seedlings grown under 6 different water stress treatments (65, 53, 41, 29, 17, and 7% soil water content by volume). The filled circle representing 41% soil water content, is used to calculate absolute values of concentration, content, and dry weight. Vectors described by different water stress treatments are interpreted in Table 10.
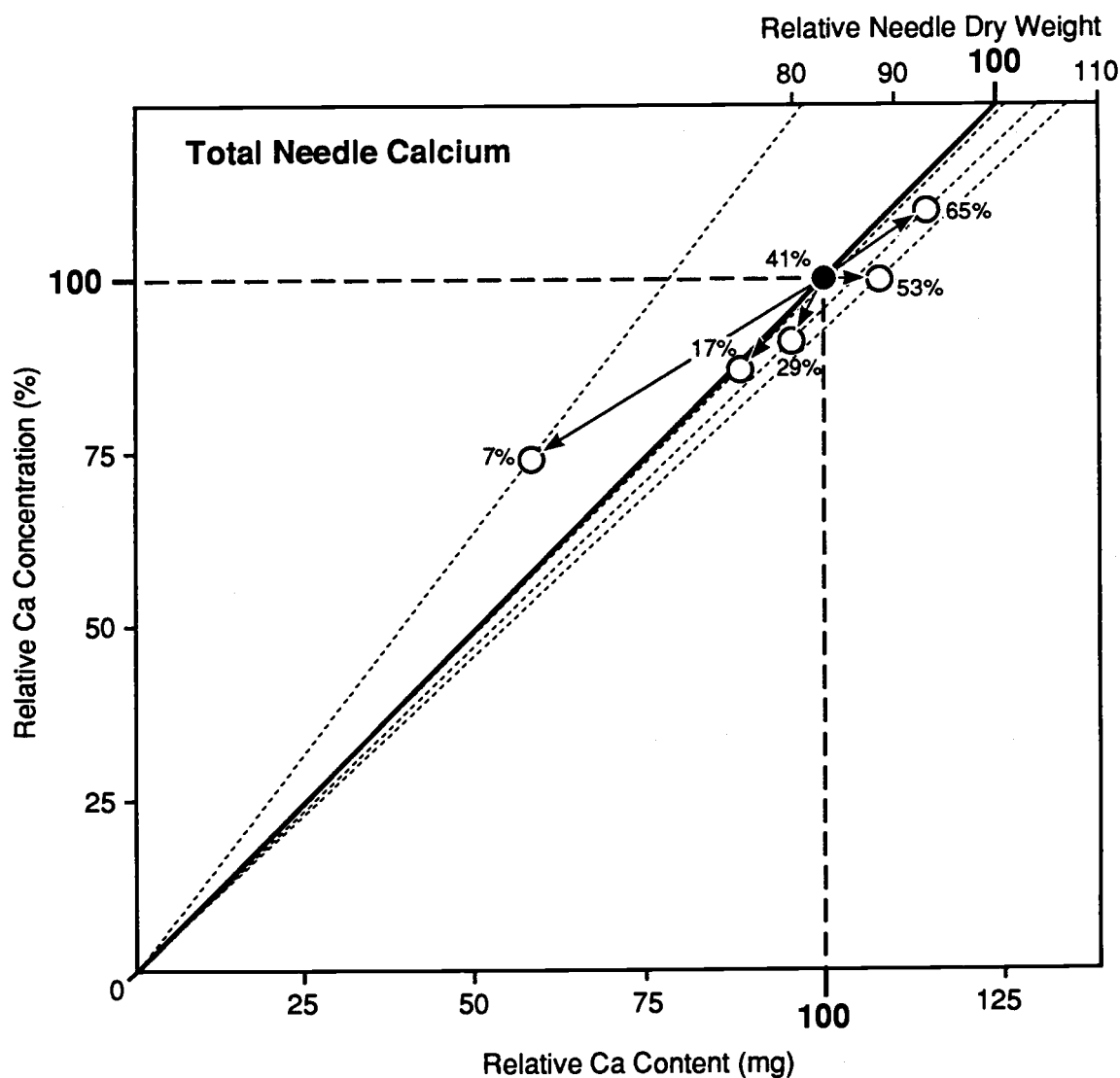
Figure 18. Interpretation of directional differences (Vectors) in total needle calcium concentration (%), content (mg), and dry weight (g) between 3-4 month old containerized Douglas-fir seedlings grown under 6 different water stress treatments (65, 53, 41, 29, 17, and 7% soil water content by volume). The filled circle representing 41% soil water content, is used to calculate absolute values of concentration, content, and dry weight. Vectors described by different water stress treatments are interpreted in Table 11.
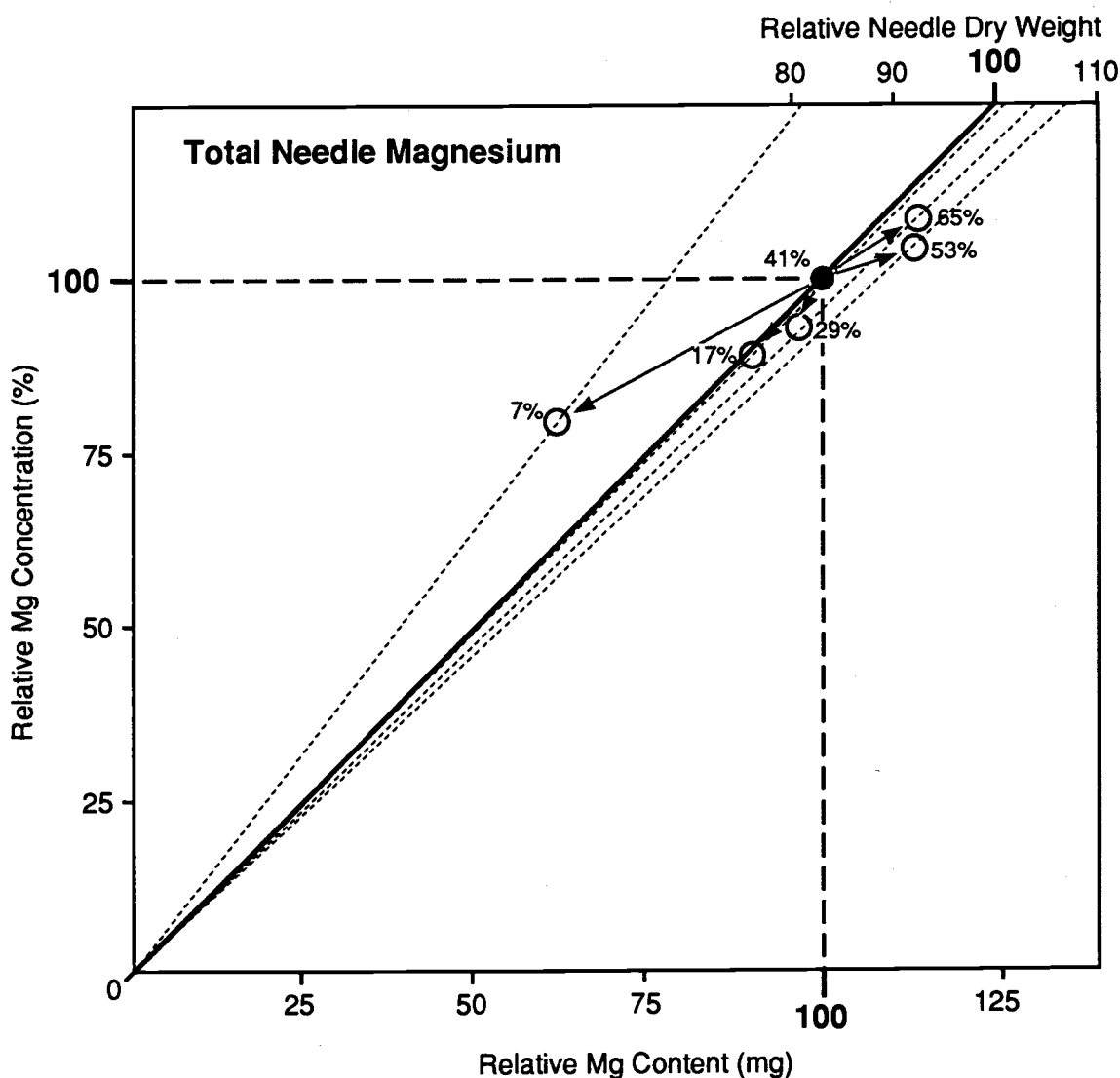
Figure 19. Interpretation of directional differences (Vectors) in total needle magnesium concentration (%), content (mg), and dry weight (g) between 3-4 month old containerized Douglas-fir seedlings grown under 6 different water stress treatments (65, 53, 41, 29, 17, and 7% soil water content by volume). The filled circle representing 41% soil water content, is used to calculate absolute values of concentration, content, and dry weight. Vectors described by different water stress treatments are interpreted in Table 12.

needle N, P, Ca, and Mg concentration and content and dry weight is discussed in Tables 9-12. All the elements have one aspect in common that as water availability becomes limiting to seedlings (29% soil water content and below), it results in downward shift in these elements except N. Total N concentration increased at the lowest soil water content (7%) which might be due to toxicity. Relative to 41% soil water content, all other water stress treatments (except 7%) resulted in upward shift in total needle dry weight. Figures 16-19 show that 65 and 53% soil water content resulted in increased concentration and content of the elements which is interpreted as deficiency of these elements. While on the other hand, 7% soil water content caused a toxic effect for total N and an antagonism effect for P, ca, and Mg.

4.2.3. CARBOHYDRATE RESERVES

4.2.3.1. Total needle starch concentration: Analysis of variance (Appendix III. 33) showed a highly significant effect (P= 0.0104) of water stress treatments on total needle starch concentration of container-grown Douglas-fir seedlings. Total needle starch concentration consistently decreased with decreasing soil water content (Figure 20A). Seedlings grown in the driest soil (7% soil water content) had the lowest concentration (4.69%) while those grown in the wettest soil (65% soil water content) had the highest concentration (11.59%). This is a decrease of approximately 60% in total needle starch concentration from the highest to lowest soil water content.

TABLE 9. Possible interpretation of directional shifts in total nitrogen concentration, content and needle dry weight as displayed in figure 16

soil water content	dry weight	change in relative nutrient		possible interpretation of vector
		conc	cont	
65%	increase	increase	increase	deficiency
53%	increase	increase	increase	deficiency
29%	increase	decrease	increase	dilution
17%	increase	decrease	decrease	*?*
7%	decrease	increase	decrease	toxicity

TABLE 10. Possible interpretation of directional shifts in total phosphorous concentration, content and needle dry weight as displayed in figure 17

soil water content	dry weight	change in relative nutrient		possible interpretation of vector
		conc	cont	
65%	increase	increase	increase	deficiency
53%	increase	increase	increase	deficiency
29%	increase	decrease	increase	dilution
17%	increase	decrease	decrease	
7%	decrease	decrease	decrease	antagonism

TABLE 11. Possible interpretation of directional shifts in total calcium
concentration, content and needle dry weight as displayed in figure 18

soil water content	dry weight	change in relative nutrient		possible interpretation of vector
		conc	cont	
65%	increase	increase	increase	deficiency
53%	increase	increase	increase	deficiency
29%	increase	decrease	decrease	
17%	increase	decrease	decrease	
7%	decrease	decrease	decrease	antagonism

TABLE 12. Possible interpretation of directional shifts in total magnesium concentration, content and needle dry weight as displayed in figure 19

soil water content	dry weight	change in relative nutrient		possible interpretation of vector
		conc	cont	
65%	increase	increase	increase	deficiency
53%	increase	increase	increase	deficiency
29%	increase	decrease	decrease	
17%	increase	decrease	decrease	
7%	decrease	decrease	decrease	antagonism

NEEDLE STARCH CONCENTRATION

ROOT STARCH CONCENTRATION

Figure 20. Effect of soil water content on seedling's total carbohydrate status (% dry weight): (A) needle starch concentration (%); (B) root starch concentration (%). Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

4.2.3.2. Root starch concentration: Analysis of variance showed a significant interaction (P= 0.0131) between water stress treatments and measurement times for root starch (measured at day 0, 43, and 81), indicating that effect of soil moisture content was dependent on measurement times (Appendix III. 34). Root starch concentration decreased with decreasing soil water content at the same levels of middle and final measurements made at day 43 and 81.

Total root starch concentration (measured at day 81) also decreased significantly (P= 0.0286) with decreasing soil water content. Seedlings at the lowest soil water content (7%) showed approximately 50% decrease in starch concentration than those at the highest soil water content (65%) (Figure 20B).

Data were also analyzed for total needle:root starch concentration ratio to find out allocation pattern from needles to roots (Appendix III. 35). Although the statistical differences were small (P= 0.0558), among water stress treatments, the ratio showed a decreasing trend when moisture content dropped beyond 53%. In general, needles had much higher starch concentration that roots (Table 13).

4.2.4. PLANT MOISTURE STRESS

Analysis of data (Appendix IV. 36-37) showed that both pre-dawn and mid-day plant moisture stress (PMS) were significantly affected (P≤ 0.0001 for both) by water stress treatments. Multiple mean comparison suggested that such a high P-value was primarily driven by the 7% soil water content. However, decreasing soil water content resulted in higher pre-dawn and mid-day PMS. Seedlings grown

TABLE 13. Means of total needle and root starch concentration (%) and needle:root starch ratios. Means within same column with same letters are not significantly different at 5% significance level (Fisher's Protected LSD).

soil water content	tot starch concentratio (%)		tot needle:root ratios
	needles	roots	
65%	11.59a	2.35a	5.18b
53%	10.16ab	2.13ab	4.89b
41%	9.87ab	1.23c	8.05a
29%	9.57ab	1.79abc	5.18b
17%	8.02bc	1.57bc	4.88b
7%	4.69c	1.19c	4.03b

in the driest soil (7% soil water content) had the highest pre-dawn and mid-day PMS readings (22.34 and 23.95 bars respectively) and thus experienced the most severe stress (Figure 21A and B). The severity of stress which seedlings experienced at the lowest soil water content (7%) can be well realized by the fact that there was a tremendous increase of approximately 398% and 211% for pre-dawn and mid-day PMS, respectively, from the highest to lowest soil water content (65% to 7%). Consequently, it resulted in unrecoverable damage to seedlings.

4.3. MORPHOLOGICAL PARAMETERS

4.3.1. INITIAL, MIDDLE AND FINAL MORPHOLOGY

On considering Analysis of Variance (Appendix VA. 38-43) of all morphological parameters measured, it was seen that there was a highly significant interaction ($P \leq 0.0001$ for all) between soil moisture content and measurement time (day 0, 43 and 81) for shoot height, shoot fresh weight, stem caliper, root fresh and dry weight. This indicates that effect of soil water content on all variables dependend on time. On the other hand, effect of soil water content on shoot dry weight did not depend on time i.e., no significant interaction ($P = 0.3591$) existed between them.

Seedlings measured at day 0 (initial measurement) showed no differences for any variable. This can be explained by the fact that seedlings were fairly homogenous in size and had not been subjected to water stress treatments at that

PRE-DAWN PMS (BARS)

MID-DAY PMS (BARS)
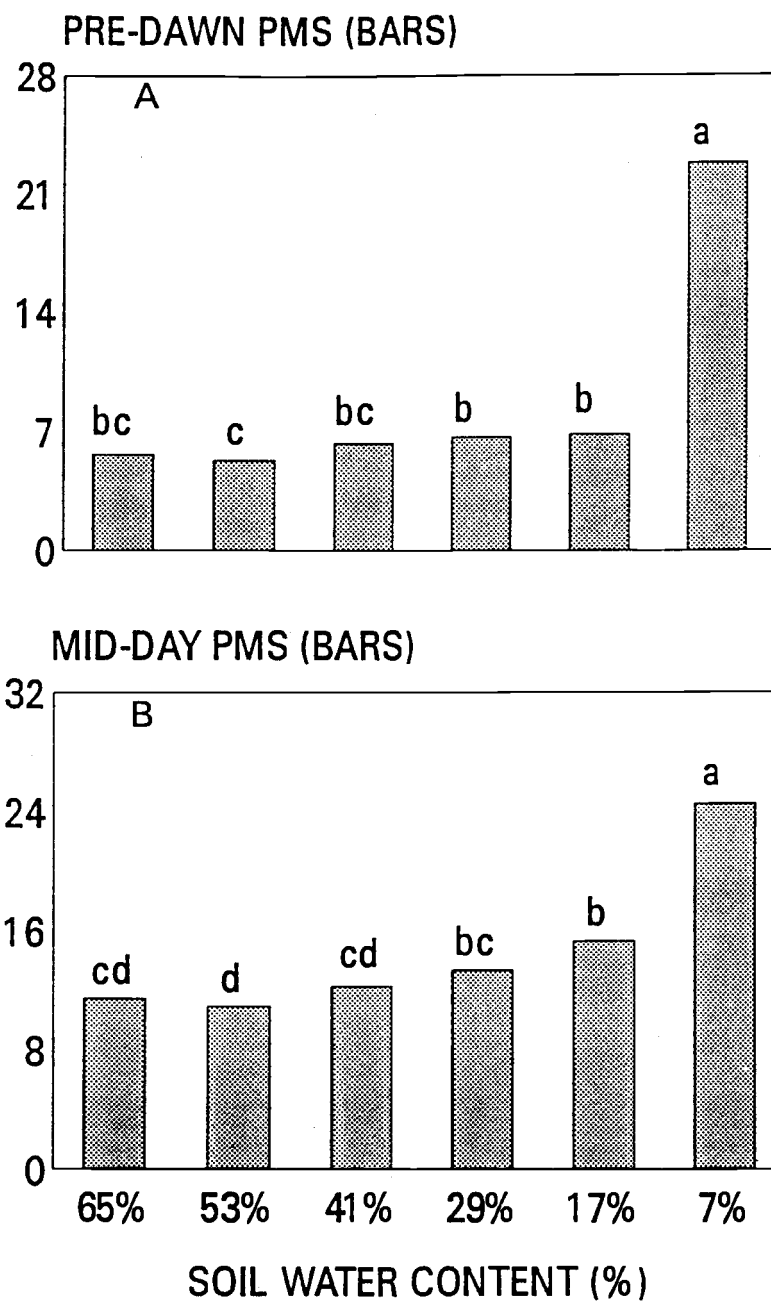
SOIL WATER CONTENT (%)

Figure 21. Effect of soil water content on plant moisture stress (PMS): (A) pre-dawn PMS (bars); (B) mid-day PMS (bars). Means are back-transformed from log. Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

time. The assumption of minimal initial variability in experimental material is, therefore, valid and does not create any confounding effect in the experiment. The treatment effect could be examined and evaluated clearly and freely (Figure 22A, B and C, and 23A and B).

Interestingly, there were no significant increases in shoot height and shoot fresh weight of seedlings measured on days 43 and 81 at the same level of each moisture stress treatment. This indicated that growth in these parameters did not depend on time over this interval but they significantly differed from initial measurements (day 0) (Figure 24A and B). But on the other hand, significant differences were found in caliper, root fresh and dry weight measured at days 0, 43 and 81 (initial, middle and final measurements respectively) at the same level of each moisture stress treatment (Figure 25A, B, and C).

Significant moisture stress treatment/measurement time interaction suggested that at the same level of middle and final measurements (day 43 and 81 respectively), growth of all morphological parameters decreased significantly with decreasing soil water content (figure 22A, B and C, and 23A and B). Most drastic reduction was found in seedlings grown in the driest soil (7% soil moisture content).

Shoot height significantly decreased with decreasing soil water content. Similarly, total shoot height also decreased significantly (P≤ 0.0001) with decreasing soil moisture content (Appendix VB. 44). There was a decrease of approximately 15% for total shoot height from the wettest to driest treatment
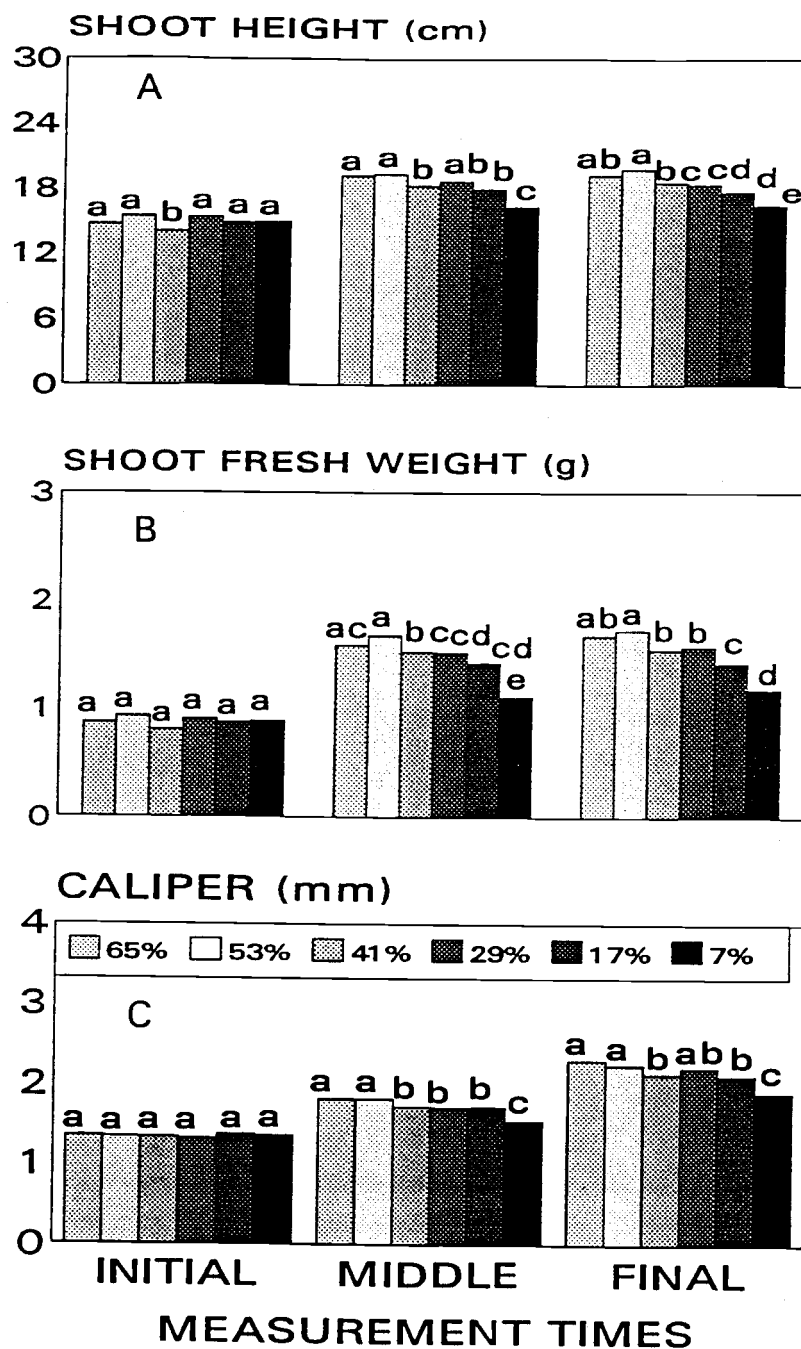
Figure 22. Effect of soil water content on seedling's morphology at the same levels of measurement time. (there was a significant soil water content by measurement time interaction): (A) shoot height; (B) shoot fresh weight; (C) caliper. Means are back-transformed from log. Within each time, bars with the same letters are not significantly different at $\alpha = 0.05$ level.

ROOT FRESH WEIGHT (g)

ROOT DRY WEIGHT (g)
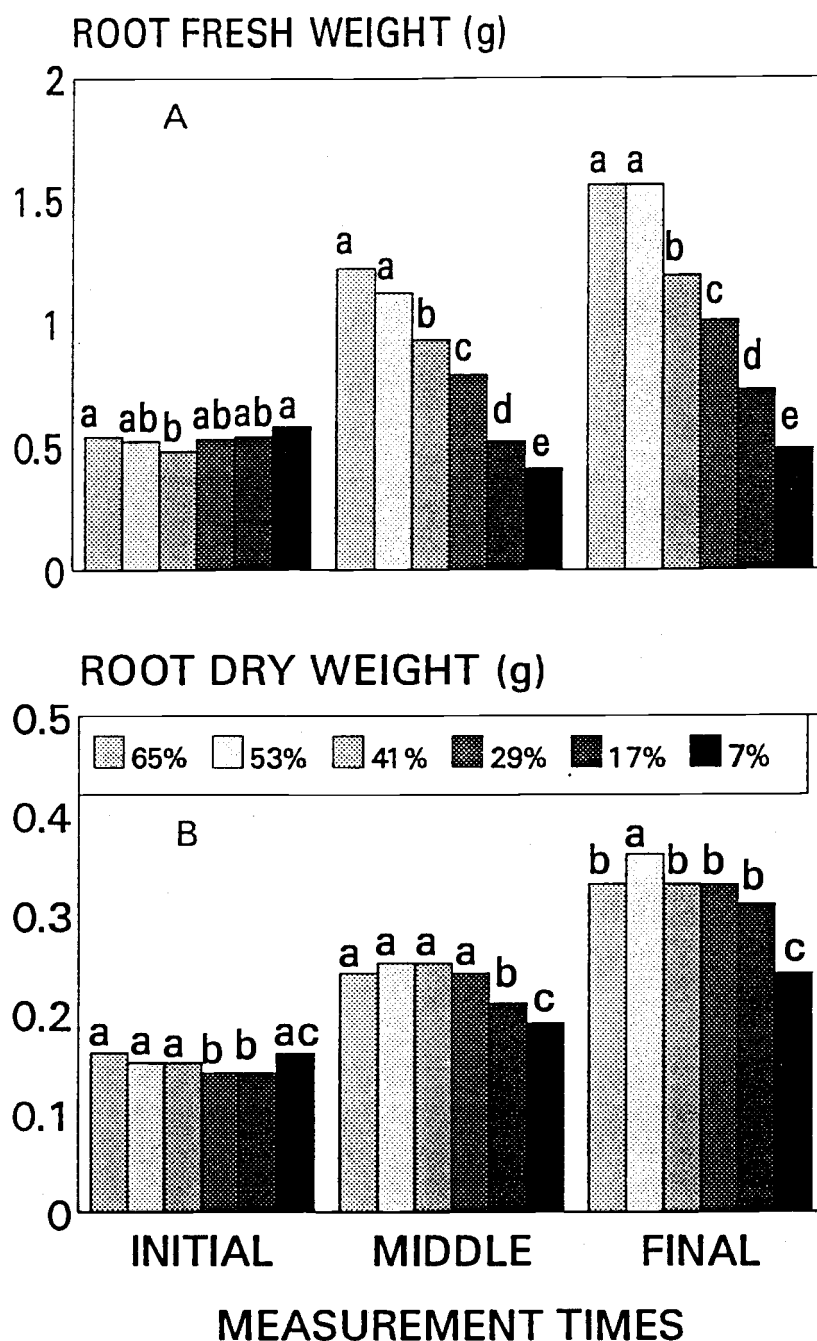
MEASUREMENT TIMES

Figure 23. Effect of soil water content on seedling's morphology at the same levels of measurement time. (there was a significant soil water content by measurement time interaction): (A) root fresh weight; (B) root dry weight. Means are back-transformed from log. Within each time, bars with the same letters are not significantly different at $\alpha = 0.05$ level.

SHOOT HEIGHT (cm)

SHOOT FRESH WEIGHT (g)
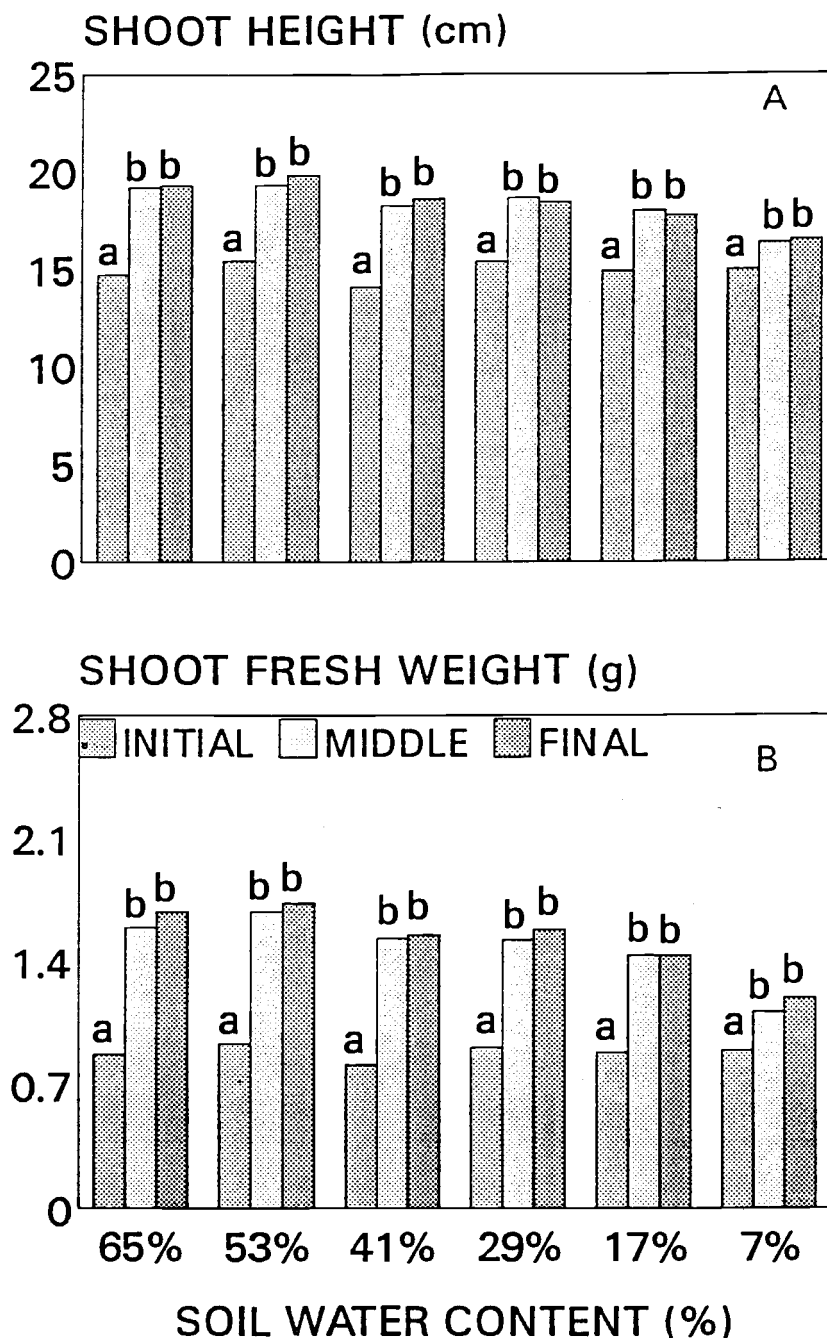
SOIL WATER CONTENT (%)

Figure 24. Effect of soil water content on seedling's morphology at the same levels of soil water content. (there was a significant soil water content by measurement time interaction): (A) shoot height, (B) shoot fresh weight. Means are back-transformed from log. Within each time, bars with the same letters are not significantly different at $\alpha = 0.05$ level.

CALIPER (mm)

A

ROOT FRESH WEIGHT (g)

B

ROOT DRY WEIGHT (g)

□ INITIAL □ MIDDLE ▨ FINAL C

65% 53% 41% 29% 17% 7%
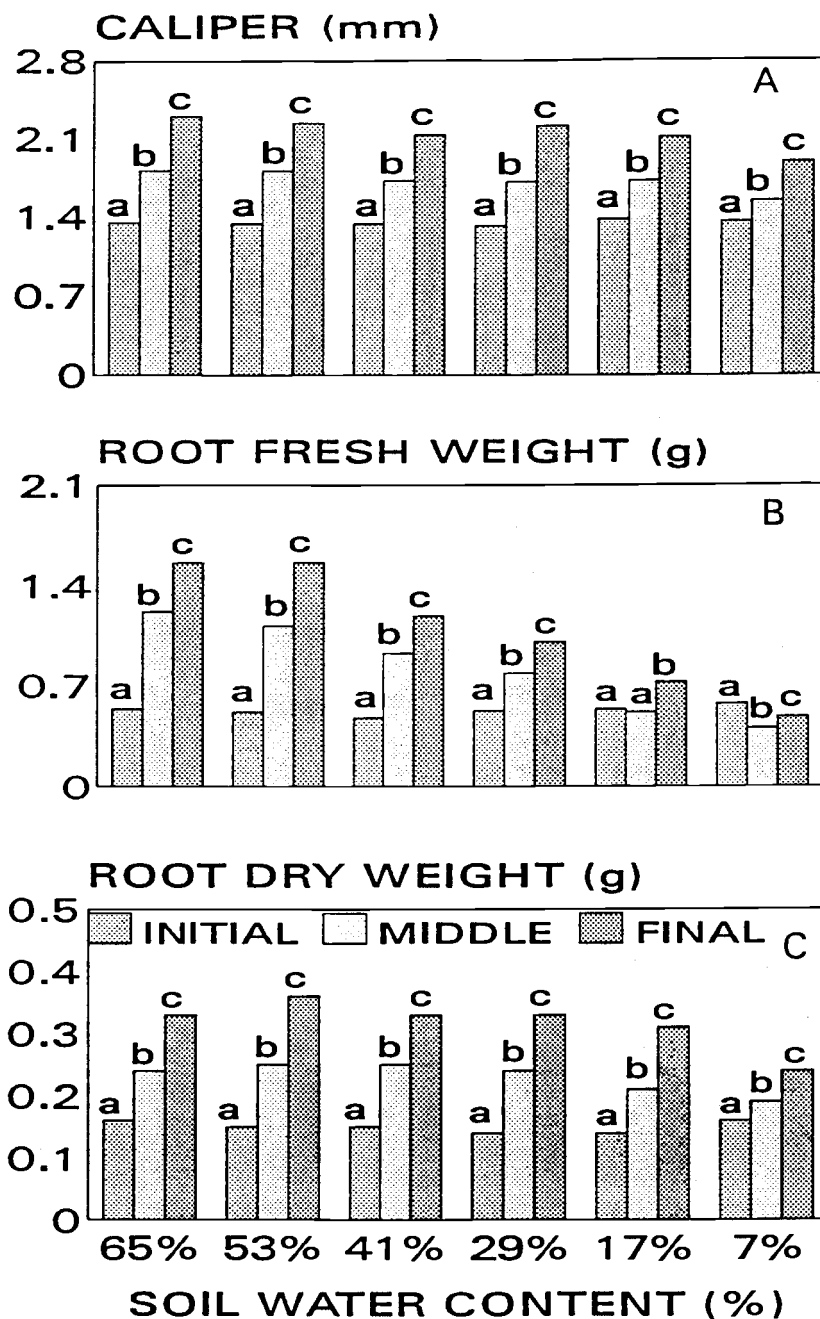
SOIL WATER CONTENT (%)

Figure 25. Effect of soil water content on seedling's morphology at the same levels of soil water content. (there was a significant soil water content by measurement time interaction): (A) caliper; (B) root fresh weight; (C) root dry weight. Means are back-transformed from log. Within each time, bars with the same letters are not significantly different at $\alpha = 0.05$ level.

(Figure 26A). Water stress treatments also had a highly significant effect (P ≤ 0.0001) on shoot height growth (Appendix VB. 45). A 66% decrease was found in shoot height growth from the wettest to driest treatments (Figure 26B). In all cases, there was a significant decrease in shoot height with decreasing soil water content.

A similar trend was found in caliper measured at initial, middle and final harvests (day 0, 43 and 81 respectively). It significantly decreased with decreasing soil water content at the same level of measurement time. Total stem caliper also decreased significantly (P ≤ 0.0001) with decreasing soil water content (Appendix VB. 46). This decrease was about 18% from the highest to lowest soil water content (65% to 7%) (Figure 27A). Similarly caliper growth decreased approximately 44% (P ≤ 0.0001) from the wettest to driest treatment (Figure 27B) (Appendix VB. 47).

4.3.2. TERMINAL BUD DIMENSIONS

The effect of water stress was also pronounced (P ≤ 0.0001) in the terminal bud development (Appendix VC. 48-49). Both length and diameter of terminal buds were significantly reduced at the lowest soil water content (Figure 28A and B). An approximately 35% and 29% decrease was found for length and diameter of terminal buds from the highest to lowest soil water content (65% to 7%). When water stress treatments were plotted against number of needle primordia per mm of terminal bud length, it can be seen that smaller buds, resulting from

TOTAL SHOOT HEIGHT (cm)

SHOOT GROWTH (cm)
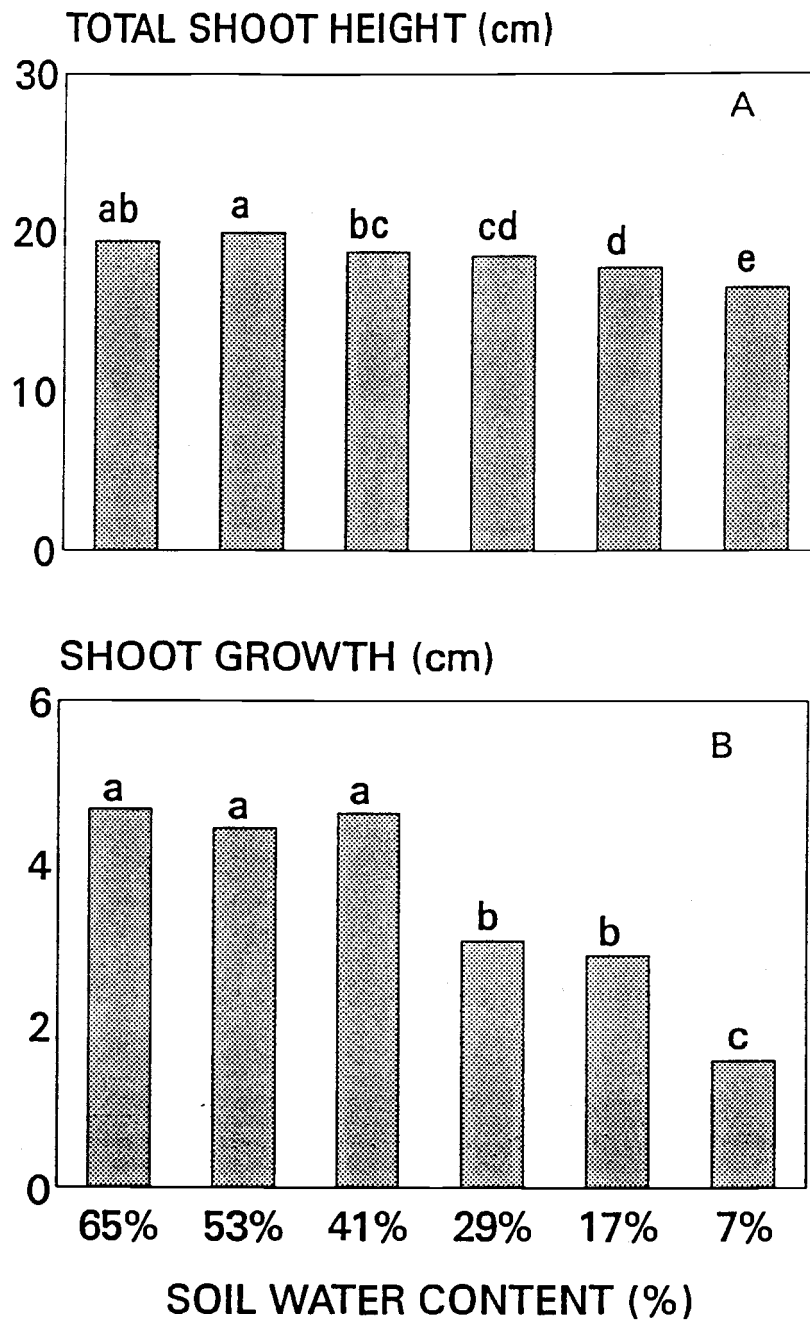
SOIL WATER CONTENT (%)

Figure 26. Effect of soil water content on seedling's final morphology: (A) total shoot height; (B) shoot growth. Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

TOTAL CALIPER (mm)

CALIPER GROWTH (mm)
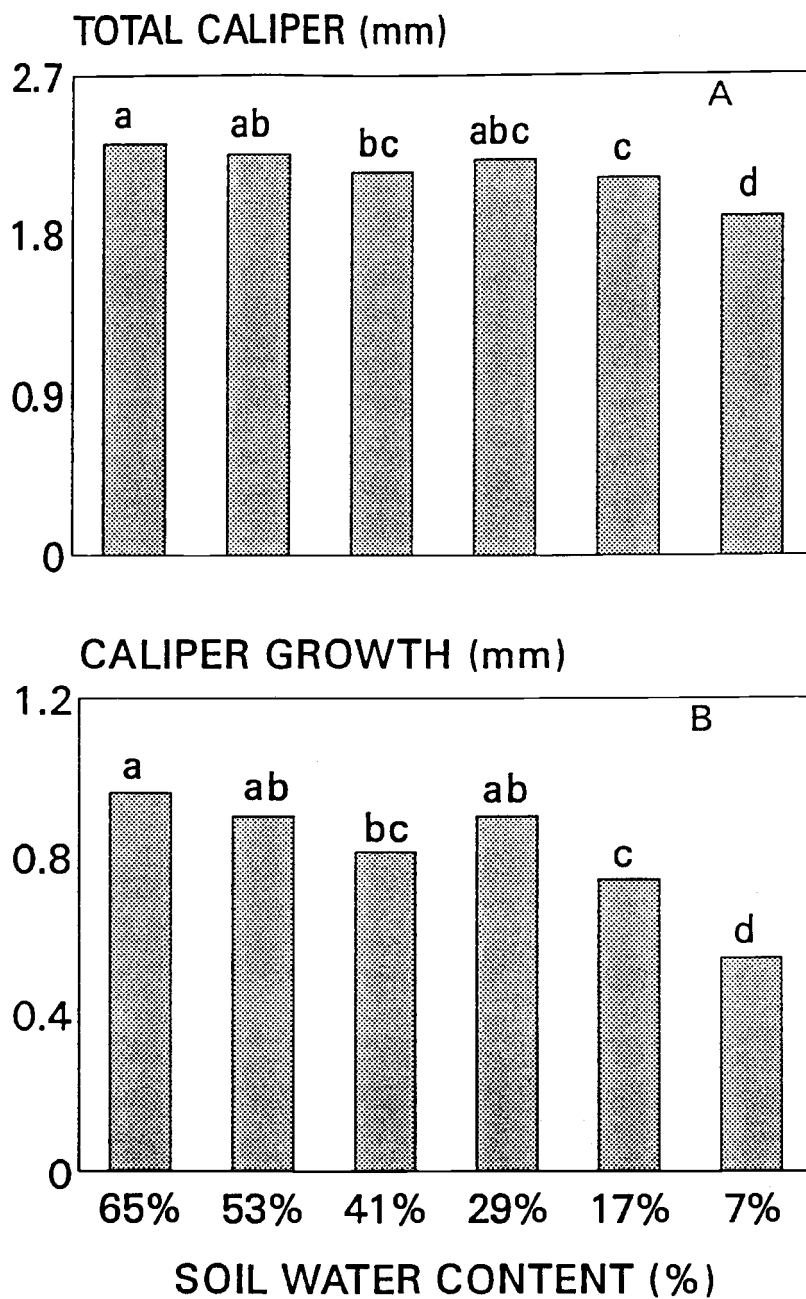
SOIL WATER CONTENT (%)

Figure 27. Effect of soil water content on seedling's final morphology: (A) total caliper; (B) caliper growth. Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

TERMINAL BUD LENGTH (mm)

TERMINAL BUD DIAMETER (mm)

NEEDLE PRIMORDIA (#)
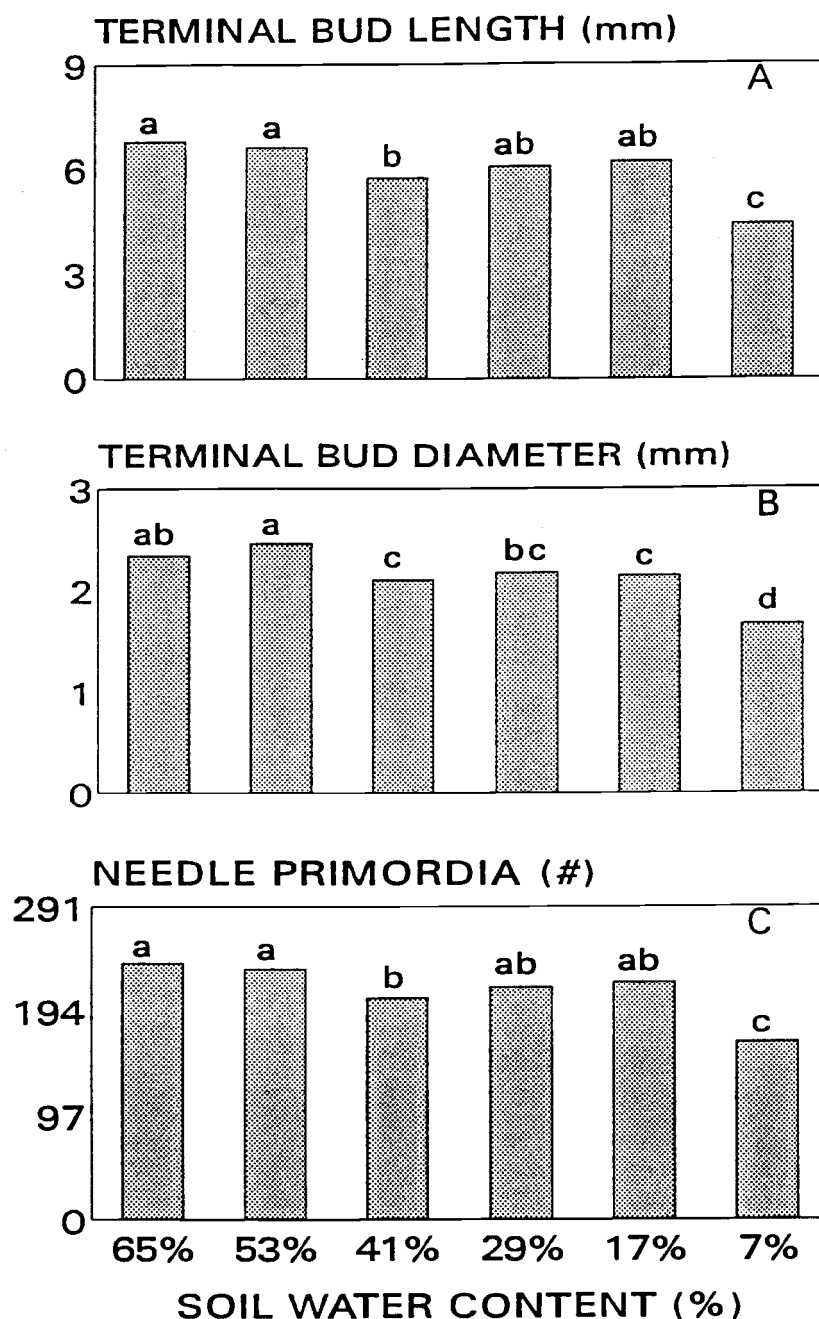
SOIL WATER CONTENT (%)

Figure 28. Effect of soil water content on final terminal bud dimensions: (A) length; (B) diameter; (C) number of needle primordia per mm bud length = 31 (bud height (mm) + 28.3) (from Thompson, 1984). Bars with the same letters are not significantly different at $\alpha = 0.01$ level.

higher moisture stress, had fewer number of needle primordia (Figure 28C). This may have quite an effect on the subsequent year's growth.

4.3.3. FRESH AND DRY MATTER ALLOCATION

As previously mentioned in the beginning of the results section, there was a significant interaction between soil water content and measurement time for shoot fresh weight and root fresh and dry weight (Appendix VA. 39 and 41-42). There were marked differences amongst water stress treatments at the same level of measurement time (Figure 22B and 23A and B). Similarly total root fresh and dry weights also drastically decreased (Appendix VD. 50-51) with decreasing soil water content at 81 days of measurement. An approximately 69% and 27% reduction took place, respectively, ($P \leq 0.0001$ for both) in root fresh and dry weights of seedlings grown from wettest to driest soils (Figure 29A). A similar trend was found in total stem and needle fresh and dry weights of seedlings. Total stem fresh and dry weight significantly decreased ($P \leq 0.0001$ for both) with decreasing soil water content. An approximately 25% and 21% decrease was found in total stem fresh and dry weight from the wettest to driest soil (Figure 29B). likewise, total needle fresh and dry weight decreased by about 25% and 21% (Appendix VD. 52-53) from the highest to lowest soil water content (figure 30A). Since seedlings were very small, they did not have many branches. Thus, fresh and dry weight data of branches was not sufficient enough to analyze, therefore, it was excluded from the analysis.

TOTAL ROOT WEIGHT (g)

TOTAL STEM WEIGHT (g)
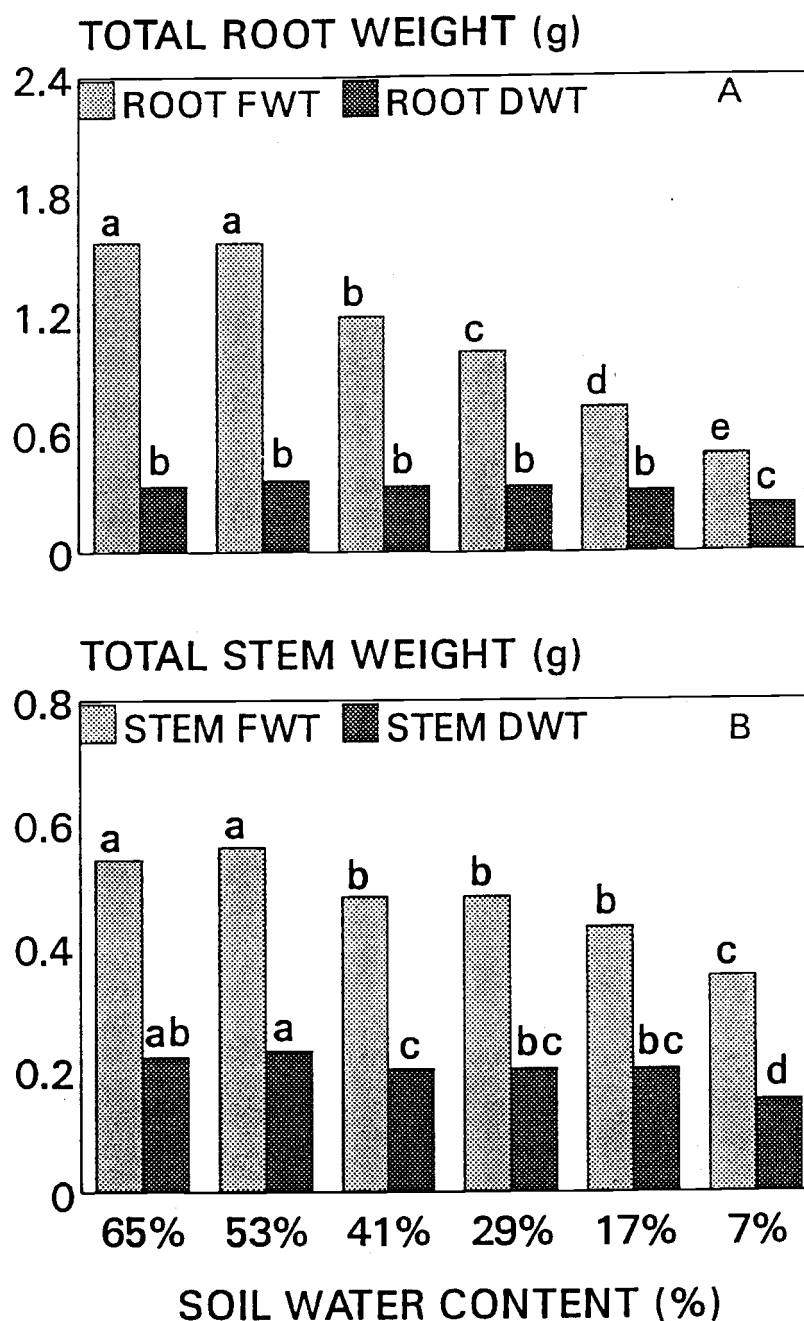
SOIL WATER CONTENT (%)

Figure 29. Effect of soil water content on seedling's final fresh and dry matter allocation: (A) total root fresh and dry weight (means are back-transformed from log); (B) total stem fresh and dry weight. Bars with the same shading and letters are not significantly different at $\alpha = 0.01$ level.
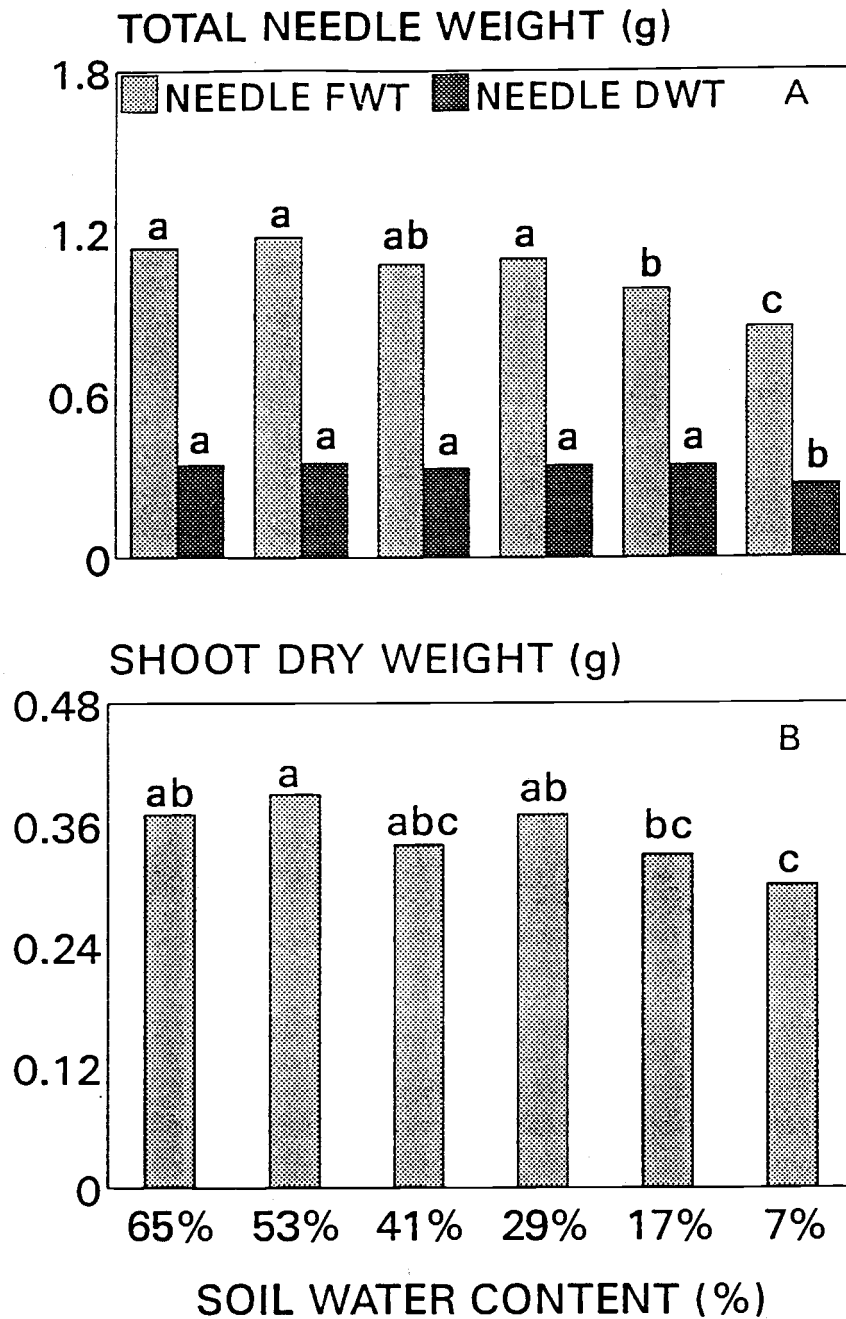
Figure 30. Effect of soil water content on seedling's final fresh and dry matter allocation: (A) total needle fresh and dry weight; (B) shoot dry weight (there was no soil water content by measurement time interaction for shoot dry weight, therefore, the effects for moisture content were averaged over time). Means are back-transformed from log. Bars with the same shading and letters are not significantly different at $\alpha = 0.05$.

As already explained, there was no significant interaction between soil water content and measurement time for shoot dry weight, therefore data were averaged for treatment means. Moisture stress treatments had a marginally significant effect on shoot dry weight ($P = 0.049$). However, shoot dry weight tended to decrease with decreasing soil water content (Figure 30B).

4.4. MORTALITY

All 24 trays of seedlings (a total of 4,800) were monitored for any mortality throughout the study. No mortality was observed in seedlings subjected to 65, 53, 41, 29 and 17% soil water content. However, some mortality was recorded in seedlings in each of the 4 blocks at 7% soil water content. This worked out to be a total of 109 seedlings (13.6%) out of 800 seedlings in 4 blocks (4 blocks * 1 treatment * 200 seedlings per treatment). Since, mortality occurred in only one treatment and treatment effect was obvious, data was not subjected to statistical analysis. However, data are presented in tabulated form (Table 14).

TABLE 14. Percentage of mortality in each of the four blocks at 7% soil water content. Data was not statistically analyzed. Numbers in parentheses show number of seedlings died out of 200 in an experimental unit (one tray) in each block.

block	treatment	percentage of mortality (out of 200 in each block)
B1	7%	24% (48)
B2	7%	21% (42)
B3	7%	4% (8)
B4	7%	5.5% (11)

Treatment total:
(based on 800 seedlings
for 4 blocks)   13.6% (109)

5. DISCUSSION

5.1. PHENOLOGY

Moisture stress treatments had a profound effect on bud activity. A higher percentage of seedlings initiating and setting buds with minimum time period was achieved with decreasing soil water content, thus rejecting the hypotheses that decreasing soil water content does not result in increased and earlier terminal bud initiation and budset. Too much and too little water (65% and 7% soil water content) resulted in delayed bud initiation and budset and a reduced percentage of seedlings which set bud. The lowest soil water content stressed these seedlings so severely that they took longer to set bud. These results are quite consistent with those of many other studies. Becker, et al., (1987) have reported that 95% of total red pine seedlings initiated buds while only 33% set bud at the lowest soil water content. They further explained that no bud formation took place in extremely dry conditions. These results support the findings of current study, since none of seedlings subjected to the lowest soil water content could reach the most advanced bud developmental stage (stage 5). The results of current study are also comparable to those presented by White (1987) who found earlier budset in 1 year old Douglas-fir seedlings at mild water stress treatments. Similarly, Lavender and Cleary (1974) found that frequent watering to relieve moisture stress due to late summer drought can result in delayed dormancy initiation to complete the sequence of various physiological processes necessary for plant growth.

It was also reported that seedlings grown under dry regimes set buds earlier (Zaerr et al., 1981, and Tung and Deyoe 1991) but were too small to meet minimum size standards for plantable seedlings, whereas those treated with wet regime were not sufficiently dormant (Zaerr, et al., 1981). Macey and Arnott (1986) found that both periodic moisture stress and nutrient withdrawal were effective in inducing bud formation and reducing shoot growth while no evidence of bud formation was found in unstressed seedlings. Results presented by O'Reilly et al., (1989a) support findings of the current study that extreme moisture stress decreases the rate of bud development.

It was also found in current study that moderate water stress treatments (53% to 17% soil water content) resulted in higher percentage of seedlings initiating and setting buds and reaching different stages of bud development. It is supported by the findings reported by Blake et al., (1979) that 2+0 Douglas-fir seedlings subjected to 3 different water stress treatments (0-4, 4-6, and 6-8 bars pre-dawn PMS) showed that moderate water stress (4-8 bars) enhanced onset of dormancy. Larson and Whitemore (1970) observed several weeks delayed bud break in red oak seedlings subjected to lower water potential. Similarly Rose et al. (1992) have also reported that all 3 stocktypes of Douglas-fir seedlings (mini-plug™ transplants, 1+1 bare root transplants and 2+0 bare root seedlings) subjected to maximum soil moisture stress took significantly longer to break bud. Ritchie (1984a) explained that longer it takes for buds to break, the higher the level of dormancy is, thus confirming results of the current study that severe

moisture stress resulted in significantly delayed terminal bud initiation and budset.

These findings show that moderate soil water content results in earlier dormancy induction in seedlings but too much or too little water causes delayed budset as was observed in current study.

5.2. PHYSIOLOGY

5.2.1. NUTRIENT STATUS

Water stress treatments had a significant influence on nutrient status of seedlings. Nutrient concentration and content in needles, shoots and roots decreased significantly with decreasing soil water content, thus the hypothesis, that decreasing soil water content does not decrease nutrient concentration and content, is rejected. However, nitrogen concentration in both needles and roots was found higher at 7% soil water content (the driest treatment). The concentration of mineral nutrients is independent of seedling size, while on the other hand, content reflects seedling size because a larger seedling will contain more nutrient contents (Landis, 1985). Thus higher percentage of N in this study does not indicate vigorous growth and larger size of the seedlings, rather, this may be due to decreased growth, translocation and nutrient use under extremely dry conditions. These results are similar to the findings presented by many other researchers. Schomaker (1969) has reported in a study with white pine seedlings that nutrient contents decreased from 34.8 mg to 22.9 mg from frequent to less frequent irrigation regimes. Similar findings were reported by Timmer and Miller

(1991) in a study to examine the effects of nutrients and moisture regimes on 16 week old container grown red pine seedlings.

There could be other reasons for decreased concentration and content of nutrients at lower soil water content, (e.g.), a) the movement of certain nutrients (particularly of phosphorous) is largely dependent on water movement in soil (Mengel and Kirkby, 1982) thus it can be reasonably assumed that rate of absorption of nutrients can be regulated by altering irrigation practices, b) insufficient irrigation can result in decreased absorption of nutrients by reducing root surface area (Duryea and McClain, 1984), c) high levels of nitrogen restricts mycorrhizal development which, in turn, results in poor phosphorous absorption (Richards and Wilson, 1963). This leads to the conclusion that nutrient contents of seedlings would be reduced with decreasing soil water content which confirms results of the current study.

Furthermore, the influence of nutrients depends not only on their chemical composition but also on form. The form of one nutrient can affect uptake and utilization of other nutrients (Fisher and Mexal, 1984). If the principal form of nitrogen in growing medium solution is ammonium (NH_4^+) then certain cations (K^+, Ca^{2+} and Mg^{2+}) are taken up in less quantities (Landis, 1989a). These studies suggest that nutrients are not absorbed and utilized independently of each other. Any change in concentration of one element is usually accompanied by changes in concentration of others. Thus a dilution effect can occur when an increase in concentration of one element causes increased growth of seedlings

resulting in decreased absorption of other elements. Similarly an antagonism effect occurs between nutrients which can reduce absorption of other elements, for example, an excess level of ammonium nitrogen can cause reduced uptake of potassium (Armson, 1977 in Landis, 1985). Sometimes a deficiency or imbalance of certain salts, (e.g.), calcium, can reduce availability of other nutrients such as iron or phosphorous (Landis and Steinfeld, 1990), whereas, itself absorption of calcium depends upon transpirational intensity of seedlings, which can be reduced and inadequate where rate of transpiration is low (Mengel and Kirkby, 1982).

In the current study, only 4-5 month old containerized Douglas-fir seedlings were used. Furthermore, these tiny seedlings were subjected to a wide range of PMS ranging from 5.61 to 22.34 bars pre-dawn and 11.34 to 23.95 bars mid-day PMS. Thus, keeping all these findings reported by various researchers in view, it is speculated that severe PMS might have reduced absorption capacity of seedlings by adversely affecting their root system, thus resulting in reduced uptake of water and nutrients. Conversely, moderate moisture stress resulted in increased growth of seedlings and total nutrient contents. Many studies (e.g.), Bachelard, (1986), Mazzoleni and Dickmann, (1988), O'Reilly, (1989b), Myers and Landsberg, (1989), and Timmer and Miller, (1991), confirming results of the current study, have shown that severe moisture stress causes reduced growth of seedlings and biomass production, which should imply reduced nutrient contents.

5.2.2. CARBOHYDRATE (STARCH) RESERVES

Carbohydrate (starch) reserves were significantly affected by water stress treatments. Both needle and root starch concentration decreased at lower soil water content. It is speculated that photosynthetic apparatus of little tiny seedlings, subjected to severe PMS, might have been affected, thus resulting in reduced production of food reserves, thus, the hypothesis formulated in the beginning is rejected. The results of this study are comparable with the findings of some other studies. Carl Jr, et al., (1978) have reported in a study that low water levels (higher PMS) resulted in less than half as much sugar and starch in stems and roots of 3 year old sugar maple seedlings as did in those grown at higher moisture levels. McNabb, (1985) has pointed out in a study that slash pine (Pinus elliottii var. ellittii (Engelm) seedlings subjected to severe moisture stress were found to have higher sugar but reduced starch concentration compared to the seedlings receiving more water. Similarly (Landis, 1989b) has reported that high moisture stress causes reduction of, both, leaf conductance and rate of photosynthesis of seedlings, thus resulting in reduced production of carbohydrate reserves and currently available photosynthates. Consequently, this results in decreased accumulation of starch reserves in seedlings (Hermann, 1990).

It was observed in current study that mild water stress did not affect needle starch concentration as much as severe water stress did. These results also agree with some other studies. For example, starch increases sharply in seedlings experiencing mild water stress but as stress increases and becomes more severe,

photosynthesis is reduced thus reducing starch reserves (Vartanian, 1981). Similar

results were reported by Kuhns and Gjerstad (1987) in a study to examine the

effects of water stress on photosynthetic allocation in loblolly pine (Pinus taeda)

seedlings.

Furthermore, higher concentration of starch was found in needles than in

roots in the current study, thus resulting in increased needle:root starch

concentration ratio. This indicates a decreased allocation of starch to roots. This

can be explained by the fact that foliage is considered as a manufacturing industry

for food production in seedlings. This process of food production can be

accelerated at optimum environmental conditions. But when seedings are exposed

to abnormal conditions, their growth can be impaired resulting in decreased

production of photosynthates. These results are supported by findings of some

other studies conducted by Kramer and Kozlowski, (1960), Kuhns and Gjerstad,

(1987) and Cannell et al., (1990).

Nevertheless, the results presented in current study do contradict those

reported by Kennedy et al., (1987). They found that higher moisture stress (< 1.5

MPa= 15 bars) resulted in increased total nonstructural carbohydrates (TNC) in

Douglas-fir and lodgepole pine seedlings. Many explanations can be given for this

controversy in results of these two studies. In the current study only 4-5 month old

Douglas-fir seedlings were subjected to as severe as 22.34 and 23.95 bars (2.23

and 2.40 MPa, respectively) pre-dawn and mid-day PMS, respectively. Obviously

seedlings in current study experienced enormously high PMS which was sufficient

enough to halt their growth by reducing uptake of moisture and nutrients from growing media and CO_2 from air. These seedlings remained under severe moisture stress for a quite long time (about 2 week) before they were re-watered. The effects of abnormal PMS are long lasting and damage root system of seedlings to absorb water and nutrients from soil (Warkentin, 1984). Moreover, stomata and leaf anatomy might have been damaged resulting in breakdown of metabolic system and reduced production of food reserves as explained by many researchers (e.g.), Kramer, (1983), Zaerr, (1983), Ritchie (1984b), Glerum, (1985), Joly (1985), Pezeshki and Chambers (1986), and Lopushinsky, (1990).

All these studies show that severe soil moisture stress disrupts a seedling's whole photosynthetic machinery which is a primary source of food production whereas moderate stress increases production of carbohydrate reserves as was found in current study.

5.2.3. PLANT MOISTURE STRESS (PMS)

Seedlings grown in the lowest soil water content experienced the most severe pre-dawn and mid-day PMS which affected adversely each and every aspect of seedlings. Similar findings were reported by many other researchers (e.g.), Sands, (1984) with Pinus radiata, Mazzoleni and Dickmann, (1988) with 2 hybrid populus clones, and Timmer and Miller (1991) with red pine seedlings and Rose et al., (1992) with three stocktypes of Douglas-fir, explaining that reduced water availability resulted in decreased soil water potential (higher PMS). In the current

study, seedlings subjected to the lowest soil water content averaged 22.34 and 23.95 bars pre-dawn and mid-day PMS respectively relative to all other treatments which ranged from 5.24 to 6.75 and 10.78 to 15.03 bars pre-dawn and mid-day PMS respectively. These results are quite comparable with those presented by Becker, et al., (1987). They found in a study that red pine seedlings in severe water stress treatment averaged -22 bars plant water potential (PWP) relative to those in other treatments which ranged from -8 to -11 bars. Therefore, in light of these results the hypothesis, that decreasing water stress does not affect PMS, is rejected.

5.3. MORPHOLOGY

5.3.1. INITIAL, MIDDLE, AND FINAL MORPHOLOGY

Various morphological parameters (e.g.), shoot height, caliper, fresh and dry weight of shoot and root measured at day 0, 43 and 81 (initial, middle and final harvests respectively) and many others measured at day 81 in the current study were significantly reduced in seedlings subjected to high PMS. Therefore, I reject these hypotheses that decreasing soil water content does not result in reduced growth of morphological parameters. These results are quite consistent with recent findings presented by many other researchers. For example, Shoot growth of red oak (Quercus rubra L.) (Larson and Whitmore, 1970), shoot dry weight, shoot height and stem diameter of western larch (Vance and Running, 1985), shoot height of three Eucalyptus species (Bachelard, 1986), caliper and needle

elongation of red pine (Becker, et al., 1987), shoot height, leaves, root development and leaf area of two hybrid populus clones (Mazzoleni and Dickmann, 1988), final stem diameter of western hemlock (O'Reilly et al., (1989b), various morphological parameters of two Eucalyptus species (Myers and Landsberg, 1989), shoot development of red pine (Timmer and Miller, 1991), many morphological parameters of 2+0 Douglas-fir seedlings (Haase, 1991) and various morphological parameters of three Douglas-fir stcktypes (Rose et al., 1992) were significantly reduced at lower soil water content.

Lopushinsky (1990) reported that a pre-dawn PMS of 2.0 MPa (20 bars), is not likely to result in mortality of seedlings, however, it will result in stomatal closure during day time thus greatly reducing photosynthesis and severely suppressing and stopping plant growth. Similarly, Hsiao, (1973) has reported that as soil moisture stress increases, growth of seedlings is reduced long before there is any reduction in photosynthesis. McDonald and Running (1979) in McDonald (1984) have reported that generally when mid-day plant water potential decreases to -12 to -15 bars, moisture stress begins to impair growth of seedlings. Comparing with these results, seedlings, in the current study, experienced pre-dawn as well as mid-day PMS almost double than that reported in former study which resulted in decreased growth in all parameters.

No significant differences were found in shoot height and shoot fresh weight measured at day 43 and 81 in the current study. This can be explained by the fact that most seedlings at that time (43 to 81 days) were in stage of terminal budset

which resulted in near cessation of their average height growth. Figure 3B explains this situation more clearly that seedlings took a minimum period of 55 days to set bud which falls in between middle and final measurements. Although, budset caused cessation in shoot height and fresh weight, seedlings continued putting on caliper increment and root weights throughout the time which resulted in significant differences among different measurement times. These results also agree with findings of some other studies. McDonald, (1984) has explained that trees commonly cease their height growth temporarily in summer at the onset of dormancy but may resume growth before deeper dormancy (winter dormancy) occurs. But on the other hand, stem diameter continues to grow at a decreasing rate due to expansion of cells produced by vascular cambium until well after height growth has stopped.

Similarly drastic effects of high water stress on other aspects of seedlings are also reported. Leaf area of loblolly pine (Pinus taeda L.) seedlings subjected to decreasing soil water content was reported to be greatly reduced than those of well watered seedlings (Teskey et al., 1987). It is also documented that water stress reduces cell enlargement more than cell division and differentiation, thus resulting in seedling with heavily cutinized leaves, lignified stem and reduced height (Tanaka and Timmis, 1974).

5.3.2. FRESH AND DRY MATTER ALLOCATION

Biomass of seedlings was significantly reduced at lower soil water content in the current study. Explanation for this effect has already been given above, however, these results are consistent with those of many researchers. Squire, et al., (1987) have reported that dry weight of foliage, stems and roots of Monterery pine were drastically reduced with increasing moisture stress. Grossnickle et al., (1990) found a decreased root dry weight in western hemlock seedlings subjected to decreasing soil water content. Similarly, biomass production of Linum usitatissimum (flax) (Newman, 1966), 5 month old Douglas-fir (Timmis and Tanaka, 1967), 1 year old loblolly pine (Seiler and Johnson, 1985), red pine (Becker, et al., 1987), 16 week old red pine (Timmer and Armstrong, 1989), red spruce (Seiler and Cazell, 1990), 2+0 Douglas-fir (Haase, 1991), red pine (Timmer and Miller, 1991) and three Douglas-fir stocktypes (Rose, et al., 1992) was appreciably reduced at lower soil water content. Thus, the hypothesis formulatedin the beginning, is rejected in light of the results of the current study.

6. CONCLUSIONS AND RECOMMENDATIONS

Water stress treatments applied in this study were found to have a highly significant impact on all aspects of 4-5 month old container-grown Douglas-fir seedlings, including terminal bud activity (initiating and setting buds and bud development), bud dimensions (length and diameter), nutrient and starch reserves and many other morphological parameters. The percentage of seedlings initiating and setting terminal buds increased significantly with decreasing soil water content. Moderate water stress resulted in earlier bud initiation and budset while too much and too little water (65% and 7% soil water content) caused delayed bud initiation and budset. The rate of physical development of terminal buds from one developmental stage to other also slowed in response to severe moisture stress.

Generally, moderate water stress (53 to 17% soil water content), imposed on seedlings throughout the period of study, did not have adverse effects. But when seedlings were stressed beyond 17% soil water content, marked differences were observed in every aspect of their life. Seedlings grown in the lowest soil water content (7%) experienced the most severe stress. It resulted in complete breakdown of metabolic system and cessation of growth of a few seedlings, resulting in their death. Similarly, nutrient and starch reserves were also negatively affected in seedlings exposed to severe moisture stress. All the nutrients (N, P, K, Ca, and Mg) measured in this study were drastically reduced at the

lowest soil water content (7%). These nutrients play a key role in different physiological activities of seedlings like chlorophyll, nucleic and amino acids, protein synthesis, energy transfer, cell wall formation and many enzymatic functions. Therefore, any imbalance or deficiency in these elements can result in serious morphological as well as physiological disorders in plants like disruption and breakdown of whole photosynthetic machinery, stunted growth, necrosis, and poor meristem elongation. However, these risks can be avoided by not exposing seedlings to severe moisture stress.

Generally, blocking was effective in increasing precision and minimizing experimental error. Therefore, it is recommended that blocking should be done while conducting similar kind of studies in the greenhouse.

The results of this study are in agreement with many other studies and can be easily implemented by container grown nursery managers. Although, seedlings can be stressed to get early dormancy induced in seedlings, the key point to be considered is, it should not be done at expense of their reduced growth and depleted nutrients and starch reserves. Seedlings should be avoided from both severe moisture stress (7% soil water content) as well as overwatering (65% soil water content). So that, on one hand, precious and scarce resources are not wasted on account of extravagant use of water and on the other hand, growth of seedlings is not jeopardized by insufficient watering.

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8. APPENDICES

APPENDIX I. ANALYSIS OF VARIANCE (ANOVA) TABLES FOR SELECTED PHENOLOGICAL PARAMETERS.

1. ANOVA TABLE FOR % OF SEEDLINGS BREAKING BUDS FROM STAGE 1

SOURCE	DF	SS	MS	P
Block	3	0.039	0.013	0.1496
Treatment	5	0.098	0.019	0.0418
Error	15	0.096	0.006	
Total	23	0.234		

2. ANOVA TABLE FOR DAYS TO BUD INITIATION (STAGE 1)

SOURCE	DF	SS	MS	P
Block	3	262.242	87.414	0.5893
Treatment	5	4809.582	961.916	0.0012
Error	15	78714.302	178.490	
Total	23	85727.385		

3. ANOVA TABLE FOR TERMINAL BUDSET (STAGE 3)

SOURCE	DF	SS	MS	P
Block	3	0.017	0.006	0.5131
Treatment	5	0.172	0.035	0.0073
Error	15	0.106	0.007	
Total	23	0.297		

4. ANOVA TABLE FOR DAYS TO TERMINAL BUDSET (STAGE 3)

SOURCE	DF	SS	MS	P
Block	3	4213.927	1404.642	0.0113
Treatment	5	6598.188	1319.638	0.0072
Error	391	71721.654	183.431	
Total	414	87452.973		

5. ANOVA TABLE FOR % OF SEEDLINGS REACHING STAGE 4

SOURCE	DF	SS	MS	P
Block	3	0.233	0.078	0.0508
Treatment	5	0.990	0.198	0.0006
Error	15	0.358	0.024	
Total	23	1.581		

APPENDIX II. ANALYSIS OF VARIANCE (ANOVA) TABLES FOR NUTRIENT ANALYSES.

IIA) TOTAL NEEDLE NUTRIENT CONCENTRATIONS AND CONTENTS

6. ANOVA TABLE FOR TOTAL NEEDLE N CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	0.258	0.086	0.0001
Treatment	5	0.109	0.022	0.0093
Error	15	0.070	0.005	
Total	23	0.437		

7. ANOVA TABLE FOR TOTAL NEEDLE N CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	116.815	38.938	0.4274
Treatment	5	622.93	124.587	0.0388
Error	15	594.547	39.637	
Total	23	1334.296		

8. ANOVA TABLE FOR TOTAL NEEDLE P CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	0.077	0.026	0.0002
Treatment	5	0.035	0.007	0.0274
Error	15	0.030	0.002	
Total	23	0.142		

9. ANOVA TABLE FOR TOTAL NEEDLE P CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	32.998	10.999	0.2269
Treatment	5	773.406	154.681	0.0001
Error	15	101.913	6.794	
Total	23	908.317		

10. ANOVA TABLE FOR TOTAL NEEDLE K CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	2656.582	885.527	0.0148
Treatment	5	5278.185	1055.637	0.0036
Error	15	2732.559	182.171	
Total	23	10667.327		

11. ANOVA TABLE FOR TOTAL NEEDLE Ca CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	0.002	0.001	0.0889
Treatment	5	0.016	0.003	0.0001
Error	15	0.003	0.0002	
Total	23	0.021		

12. ANOVA TABLE FOR TOTAL NEEDLE Ca CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	12.627	4.209	0.0022
Treatment	5	167.688	33.538	0.0001
Error	15	8.058	0.537	
Total	23	188.373		

13. ANOVA TABLE FOR TOTAL NEEDLE Mg CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	0.002	0.001	0.0437
Treatment	5	0.015	0.003	0.0001
Error	15	0.002	0.0002	
Total	23	0.019		

14. ANOVA TABLE FOR TOTAL NEEDLE Mg CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	15.975	5.325	0.0112
Treatment	5	167.539	33.508	0.0001
Error	15	15.191	1.013	
Total	23	198.705		

IIB) TOTAL ROOT NUTRIENT CONCENTRATIONS AND CONTENTS

15. ANOVA TABLE FOR TOTAL ROOT N CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	0.020	0.007	0.0309
Treatment	5	0.039	0.008	0.0106
Error	15	0.026	0.002	
Total	23	0.085		

16. ANOVA TABLE FOR TOTAL ROOT N CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	312.710	104.236	0.0006
Treatment	5	921.380	184.276	0.0001
Error	15	151.912	10.127	
Total	23	1386.002		

17. ANOVA TABLE FOR TOTAL ROOT P CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	0.007	0.002	0.0114
Treatment	5	0.037	0.007	0.0001
Error	15	0.006	0.0004	
Total	23	0.050		

18. ANOVA TABLE FOR TOTAL ROOT P CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	29.401	9.800	0.0245
Treatment	5	536.545	107.309	0.0001
Error	15	35.174	2.345	
Total	23	601.120		

19. ANOVA TABLE FOR TOTAL ROOT K CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	0.026	0.009	0.0928
Treatment	5	0.037	0.007	0.1061
Error	15	0.050	0.003	
Total	23	0.112		

20. ANOVA TABLE FOR TOTAL ROOT K CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	67.590	22.530	0.2235
Treatment	5	1762.672	352.534	0.0001
Error	15	206.772	13.785	
Total	23	2037.035		

21. ANOVA TABLE FOR TOTAL ROOT Ca CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	0.003	0.001	0.6931
Treatment	5	0.054	0.011	0.0059
Error	15	0.032	0.002	
Total	23	0.089		

22. ANOVA TABLE FOR TOTAL ROOT Ca CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	91.241	30.414	0.0909
Treatment	5	644.197	128.839	0.0001
Error	15	175.700	11.713	
Total	23	911.139		

23. ANOVA TABLE FOR TOTAL ROOT Mg CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	0.012	0.004	0.7251
Treatment	5	0.639	0.128	0.0001
Error	15	0.140	0.009	
Total	23	0.791		

24. ANOVA TABLE FOR TOTAL ROOT Mg CONTENT (mg)

SOURCE	DF	SS	MS	P
Block	3	45.521	15.174	0.8206
Treatment	5	4340.765	868.153	0.0001
Error	15	743.673	49.578	
Total	23	5129.959		

IIC) FINAL NEEDLE NUTRIENT RATIOS TO N

25. ANOVA TABLE FOR PHOSPHOROUS RATIO

SOURCE	DF	SS	MS	P
Block	3	6.10	12.03	0.3202
Treatment	5	390.61	78.12	0.0006
Error	15	142.06	9.47	
Total	23	568.77		

26. ANOVA TABLE FOR POTASSIUM RATIO

SOURCE	DF	SS	MS	P
Block	3	4600.89	1533.6	0.0298
Treatment	5	3940.53	788.11	0.1343
Error	15	5860.95	390.73	
Total	23	14402.38		

27. ANOVA TABLE FOR CALCIUM RATIO

SOURCE	DF	SS	MS	P
Block	3	18.87	6.29	0.0491
Treatment	5	137.04	27.41	0.0001
Error	15	28.51	1.90	
Total	23	184.43		

28. ANOVA TABLE FOR MAGNESIUM RATIO

SOURCE	DF	SS	MS	P
Block	3	22.77	7.59	0.0643
Treatment	5	121.27	24.25	0.0003
Error	15	38.08	2.54	
Total	23	182.12		

IID) FINAL ROOT NUTRIENT RATIOS TO N

29. ANOVA TABLE FOR PHOSPHOROUS RATIO

SOURCE	DF	SS	MS	P
Block	3	38.38	12.79	0.3943
Treatment	5	707.30	141.46	0.0001
Error	15	180.61	93.21	
Total	23	926.29		

30. ANOVA TABLE FOR POTASSIUM RATIO

SOURCE	DF	SS	MS	P
Block	3	537.92	179.31	0.1816
Treatment	5	852.58	170.52	0.1821
Error	15	1454.43	96.96	
Total	23	2844.92		

31. ANOVA TABLE FOR CALCIUM RATIO

SOURCE	DF	SS	MS	P
Block	3	27.75	9.25	0.8651
Treatment	5	807.72	161.54	0.0133
Error	15	571.36	38.09	
Total	23	1406.83		

32. ANOVA TABLE FOR MAGNESIUM RATIO

SOURCE	DF	SS	MS	P
Block	3	433.25	144.42	0.4332
Treatment	5	10097.47	2019.49	0.0001
Error	15	2235.62	149.04	
Total	23	12766.34		

APPENDIX III. ANALYSIS OF VARIANCE (ANOVA) TABLES FOR STARCH ANALYSIS.

33. ANOVA TABLE FOR TOTAL NEEDLE STARCH CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	244.276	81.425	0.0001
Treatment	5	114.548	22.910	0.0104
Error	15	76.107	5.074	
Total	23	434.930		

34. ANOVA TABLE FOR TOTAL ROOT STARCH CONCENTRATION (%)

SOURCE	DF	SS	MS	P
Block	3	2.119	0.706	0.0807
Treatment	5	4.452	0.890	0.0286
Error	15	3.880	0.259	
Total	23	10.451		

35. ANOVA TABLE FOR NEEDLE:ROOT STARCH RATIO

SOURCE	DF	SS	MS	P
Block	3	67.7	22.59	0.0017
Treatment	5	38.09	7.62	0.0558
Error	15	40.81	2.72	
Total	23	146.69		

APPENDIX IV. ANALYSIS OF VARIANCE (ANOVA) TABLES FOR PLANT MOISTURE STRESS (PMS).

36. ANOVA TABLE FOR PRE-DAWN PMS (LOG-TRANSFORMED)

SOURCE	DF	SS	MS	P
Block	3	0.521	0.174	0.1737
Treatment	5	29.350	5.870	0.0001
Error	15	1.374	0.092	
Sub-sampling error	96	1.796	0.019	
Total	119	33.042		

37. ANOVA TABLE FOR MID-DAY PMS (LOG-TRANSFORMED)

SOURCE	DF	SS	MS	P
Block	3	0.089	0.030	0.7770
Treatment	5	8.590	1.718	0.0001
Error	15	1.202	0.080	
Sub-sampling error	96	2.132	0.022	
Total	119	12.013		

APPENDIX V. ANALYSIS OF VARIANCE (ANOVA) TABLES FOR SELECTED MORPHOLOGICAL PARAMETERS.

VA) PARAMETERS MEASURED AT INITIAL, MIDDLE AND FINAL HARVESTS. DATA LOG-TRANSFORMED

38. ANOVA TABLE FOR SHOOT HEIGHT

SOURCE	DF	SS	MS	P
Block	3	0.895	0.298	0.0079
Treatment	5	2.419	0.484	0.0003
Error (a)	15	0.776	0.052	
Time	2	13.571	6.785	0.0001
Treatment*Time	10	1.264	0.126	0.0001
Error (b)	36	0.671	0.019	
Sub-sampling error	1368	15.374	0.011	
Total	1439	34.970		

39. ANOVA TABLE FOR SHOOT FRESH WEIGHT

SOURCE	DF	SS	MS	P
Block	3	4.400	1.467	0.0020
Treatment	5	10.823	2.165	0.0001
Error (a)	15	2.736	0.182	
Time	2	87.625	43.812	0.0001
Treatment*Time	10	5.756	0.576	0.0001
Error (b)	36	1.336	0.037	
Sub-sampling error	1368	41.341	0.030	
Total	1439	154.018		

40. ANOVA TABLE FOR CALIPER

SOURCE	DF	SS	MS	P
Block	3	0.624	0.208	0.0032
Treatment	5	2.012	0.402	0.0001
Error (a)	15	0.434	0.029	
Time	2	51.769	25.884	0.0001
Treatment*Time	10	1.415	0.141	0.0001
Error (b)	36	0.767	0.021	
Sub-sampling error	1368	13.029	0.010	
Total	1439	70.049		

41. ANOVA TABLE FOR ROOT FRESH WEIGHT (E_a WAS < E_b, THEREFORE, E_a WAS DROPPED FROM THE MODEL)

SOURCE	DF	SS	MS	P
Block	3	15.645	5.215	0.0001
Treatment	5	95.301	19.060	0.0001
Error (a)	15			
Time	2	101.083	50.542	0.0001
Treatment*Time	10	61.684	6.168	0.0001.
Error (b)	51	15.816	0.310	
Sub-sampling error	1368	56.790	0.042	
Total	1439	346.319		

42. ANOVA TABLE FOR ROOT DRY WEIGHT

SOURCE	DF	SS	MS	P
Block	3	4.521	1.507	0.0002
Treatment	5	7.906	1.581	0.0001
Error (a)	15	1.760	0.117	
Time	2	130.795	65.398	0.0001
Treatment*Time	10	6.264	0.626	0.0001
Error (b)	36	1.847	0.051	
Sub-sampling error	1368	62.070	0.045	
Total	1439	215.163		

43. ANOVA TABLE FOR SHOOT DRY WEIGHT

SOURCE	DF	SS	MS	P
Block	3	6.834	2.278	0.0490
Treatment	5	10.554	2.111	0.0419
Error (a)	15	10.318	0.688	
Time	2	205.405	102.703	0.0001
Treatment*Time	10	6.536	0.654	0.3591
Error (b)	36	20.580	0.572	
Sub-sampling error	1368	43.423	0.032	
Total	1439	303.650		

VB). MORPHOLOGICAL PARAMETERS MEASURED AT FINAL HARVEST.

44. ANOVA TABLE FOR TOTAL SHOOT HEIGHT

SOURCE	DF	SS	MS	P
Block	3	54.357	18.119	0.0871
Treatment	5	582.933	116.587	0.0001
Error	15	102.785	6.852	
Sub-sampling error	456	2078.050		
Total	479	2818.125		

45. ANOVA TABLE FOR SHOOT GROWTH (FINAL-INITIAL SHOOT HEIGHT)

SOURCE	DF	SS	MS	P
Block	3	61.190	20.397	0.1211
Treatment	5	624.586	124.917	0.0001
Error	15	134.164	8.944	
Sub-sampling error	456	2949.831	6.469	
Total	479	3769.771		

46. ANOVA TABLE FOR TOTAL CALIPER

SOURCE	DF	SS	MS	P
Block	3	0.511	0.170	0.2068
Treatment	5	8.321	1.664	0.0001
Error	15	1.490	0.099	
Sub-sampling error	456	23.721	0.052	
Total	479	34.042		

47. ANOVA TABLE FOR CALIPER GROWTH (FINAL - INITIAL CALIPER)

SOURCE	DF	SS	MS	P
Block	3	0.109	0.036	0.8117
Treatment	5	9.635	1.927	0.0001
Error	15	1.706	0.114	
Sub-sampling error	456	30.207	0.066	
Total	479	41.657		

VC) TERMINAL BUD DIMENSIONS AT FINAL HARVEST

48. ANOVA TABLE FOR TERMINAL BUD LENGTH

SOURCE	DF	SS	MS	P
Block	3	9.575	3.192	0.1121
Treatment	5	72.567	14.513	0.0002
Error	15	20.250	1.350	
Sub-sampling error	96	136.900	1.426	
Total	119	239.292		

49. ANOVA TABLE FOR TERMINAL BUD DIAMETER

SOURCE	DF	SS	MS	P
Block	3	0.230	0.077	0.4399
Treatment	5	7.539	1.508	0.0001
Error	15	1.20.	0.0805	
Sub-sampling error	96	8.369	0.087	
Total	119	17.342		

VD) FRESH AND DRY MATTER ALLOCATION AT FINAL HARVEST

50. ANOVA TABLE FOR TOTAL ROOT FRESH WEIGHT (LOG-TRANSFORMED)

SOURCE	DF	SS	MS	P
Block	3	1.115	0.372	0.0623
Treatment	5	81.771	16.354	0.0001
Error	15	1.841	0.123	
Sub-sampling error	456	16.697	0.037	
Total	479	101.425		

51. ANOVA TABLE FOR TOTAL ROOT DRY WEIGHT (LOG-TRANSFORMED)

SOURCE	DF	SS	MS	P
Block	3	1.996	0.665	0.0001
Treatment	5	8.377	1.675	0.0001
Error	15	0.709	0.047	
Sub-sampling error	456	21.506	0.047	
Total	479	32.589		