ESTABLISHMENT AND EARLY GROWTH OF BLACK SPRUCE (*Picea mariana* [Mill.] B.S.P.) IN RELATION TO SELECTED NURSERY LIFTING AND STORAGE PRACTICES

by

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Co-Adviser: Dr. K. M. McClain	Date
Co-Adviser: Prof. R. J. Day	Date

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ABSTRACT

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KEYWORDS: bareroot nursery practice, black spruce, field performance, *Picea mariana*, root growth capacity, seedling establishment, storage practices, stomatal conductance, transpiration, water relations

Problems associated with the establishment and early growth of overwinter frozen stored black spruce (*Picea mariana* [Mill.] B.S.P.) seedlings led to research on the effects of selected nursery lifting and storage practices on post-planting performance. The broad objective was to evaluate important physiological and morphological response attributes of fall lifted, overwinter frozen stored, spring lifted, cool stored, and freshly lifted $1^1/_2 + 1^1/_2$black spruce transplants during concurrent potting and field trials established in May and June, 1987. The potting trials were conducted in a controlled environment chamber under two soil water regimes (well-watered vs. water stressed). The outplanting trials were conducted on a cultivated nursery soil and the scarified soil of a regional outplanting site. The nursery trial included undisturbed (i.e. not planted, thinned *in situ*), control seedlings as an additional treatment.

The research conducted under controlled environment conditions indicated that the selected lifting-storage treatments affect early plant water relations through interactions with both root growth capacity and stomatal function. Most importantly, the fall lifted seedlings exhibited prolific root growth but showed poor stomatal control over transpirational losses. In contrast, the spring lifted seedlings showed poorer root growth but maintained better stomatal control over transpirational losses. Shoot-tissue water relations determined using the pressure-volume technique varied between lifting-storage treatments, water regimes, and potting times and often showed a lack of agreement between the selected parameters. Pre-potting osmotic potentials at full turgor and the turgor loss point increased between potting times for all seedlings. In general, post-planting osmotic potentials were lower for the water stressed than well-watered seedlings and increased with renewed bud and shoot activity. Physiological response differed between the fall and spring lifted seedlings under field conditions and generally compared with the results of the potting trials. After one growing season, the undisturbed seedlings were clearly larger than any of the outplants, particularly the spring lifted, stored seedlings. Regardless of variations in physiological and morphological response, all seedlings showed acceptable growth and survival after one growing season.

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R. G. B.

ESTABLISHMENT AND EARLY GROWTH OF BLACK SPRUCE (*Picea mariana* [Mill.] B.S.P.) IN RELATION TO SELECTED NURSERY LIFTING AND STORAGE PRACTICES

INTRODUCTION

Forest regeneration by planting continues to be the mainstay of the regeneration program in Ontario. This is emphasized by the combined provincial production of bare root and container stock which increased twofold from 80 million trees produced in 1983 to 163 million trees produced in 1988 (O.M.N.R. 1988). In the foreseeable future, planting will likely become even more prominent than other less dependable reforestation methods because it can most effectively minimize future thinning practices and concentrate genetically superior stock produced through tree improvement programs on high quality sites (i.e. 'prime sites' [Greenwood 1987]). Indeed, planting has recently been recommended as the best method of increasing the yield and the quality of a desired species within a specified time (Galloway and Squires 1988). Unfortunately, survival and early growth continue to be variable for newly planted seedlings (Armson 1975, Hambly 1980, Burdett 1983, Lavender 1988). This, coupled with the increasing costs associated with plantation establishment are currently of considerable concern in Ontario (von Althen 1985).

Poor plantation performance is a problem that has been well documented for almost 70 years (McClain 1986). Although the importance of seedling physiology was recognized by Wakeley (1949) over 40 years ago, research addressing plantation failures has historically searched for morphological attributes of seedling quality that might correlate well with outplanting performance because the latter are more readily defined and measured (Day 1982). Presumably, the determination of such attributes would guide future nursery practice. More recently, physiological attributes of seedling quality have received considerable attention (Sutton 1979, Chavase 1980, Ritchie 1984a, Duryea 1985, Sutton 1988).

Today, there is increased recognition that a single indicator of seedling quality will not likely be found (Ritchie 1984a). Rather, seedling quality is believed to reflect the integration of all physiological and morphological characteristics that collectively comprise the entire seedling complex. This entire complex must be in tune to respond to the full potential of the planting site (Burdett 1983). The numerous biological, physical, and environmental factors that influence seedling development between the time cones are collected and seedlings are planted affect this complex and likely obviate a singularly useful predictor of seedling quality (Navratil 1973, McClain 1986, DeYoe 1988).

This realization has recently focused attention on the effects of nursery cultural and handling practices on seedling physiology and consequent outplanting performance (Duryea and Landis 1984). These practices must be investigated because: (1) the production of nursery stock represents the greatest monetary and technological investments in the reforestation cycle (Gordon 1984), (2) stresses imposed by each phase of nursery practice are cumulative and decrease the seedling's ability to respond to the full potential of the planting site (Navratil 1973, Edgren 1984, DeYoe 1988), (3) survival and growth liabilities imposed at the early stages will be reflected by reduced stand growth and longer rotations over the entire area serviced by the nursery (McClain 1986), and (4) the potential losses increase as nursery stock production begins to bear the costs of tree improvement programs (Armson 1988).

Frozen and cool storage are now two common nursery practices in Ontario. Although first tested provincially over forty years ago (Leslie 1945), interest in both storage methods has intensified in recent years, largely out of impetus to supply newly expanded planting programs with unflushed seedlings (Sutton 1984). Cold storage offers several additional advantages (Mullin 1966, Brown 1971, Hocking and Nyland 1971, Venn 1980, Colombo and Racey 1988) such as satisfying the chilling requirement and reducing the heavy spring workload. Frozen storage involves the overwintering of fall lifted seedlings at sub-freezing temperatures. The seedlings are sometimes warmed to a few degrees above freezing for a short period prior to shipping. Cool storage involves lifting seedlings in the spring and holding them within a narrow range just above freezing until shipment to the planting site. Both storage methods are known to affect seedling physiology and outplanting performance (Hocking and Nyland 1971, Sutton 1979, Venn 1980, Burdett and Simpson 1984) but these effects are not well defined (McCracken 1978, Ericsson *et al.* 1983, Duryea and McClain 1984).

With a single notable exception (Blake 1983), studies comparing the effects of varied storage methods on plant water relations during early establishment are lacking for Ontario's boreal conifers. These effects must be investigated because all plant growth processes are variably affected by cellular water status (Hsiao 1973). Furthermore, the maintenance of a favourable water balance during establishment is critical to ensure survival and subsequent rapid growth (McClain 1986, Glerum 1988, Grossnickle 1988a). The need to document these effects increases as growth rhythms become increasingly disrupted by lengthened storage periods and wider departures from the conventional method of spring planting with freshly lifted stock (Sutton 1977, 1979).

Physiologically, water is important as: (1) the prime constituent of cell sap, (2) a solvent in which gases, minerals, and other solutes, move between cells, tissues, and organs, (3) a reactant in which many important biochemical and metabolic processes, including photosynthesis, occur, and (4) to maintain turgidity (Kramer 1983).

Forest scientists have typically characterized seedling water status (i.e. the condition of water in a seedling relative to its requirement) by measuring plant water potential (i.e. the difference between the chemical potential of pure, free water [assumed to equal zero] and water in the seedling, when both are measured under identical conditions of temperature, elevation, and atmospheric pressure) because it is simple to determine and likely the best single indicator (Slatyer 1967, Kramer 1983, Spomer 1985). However, the total water potential of a seedling represents the sum of several component potentials, the most important in seedling water relations being the osmotic (effect of solutes) and pressure (effect of cell turgor) potentials. Sometimes, matric potential, a third component accounting for adsorption, capillary, and colloidal forces is also considered to be important (Kramer 1983, Salisbury and Ross 1985).

It is now generally believed that plant function is better related to the status of these component potentials than to total water potential (Hsiao 1973, Hsiao *et al.* 1976, Hsiao and Bradford 1983). Indeed, turgor pressure, or pressure potential has been the subject of considerable research. Its importance was emphasized by Lockhart (1965) when he proposed that plant growth ceased below a threshold turgor pressure level. Turgor pressure is essential for growth because it is necessary for cell enlargement (Ting 1982). This is of paramount importance to establishing outplants which, to assure survival, must re-establish intimate contact with the soil (Sands 1984) and increase soil water absorption by initiating new roots and elongating existing roots (Ritchie and Dunlap 1980). As well, new shoots must be extended above the competing vegetation to increase the photosynthetic capacity of the seedling and enable it to support the expanding root/shoot system (Blake 1986). Finally, turgor pressure is necessary to open the stomata and allow atmospheric carbon dioxide to enter the plant and become converted, through a series of photochemical reactions, into the intermediate and end products of photosynthesis (Ting 1982).

The research presented in this thesis tests the hypothesis that the date of lifting and the temperature and duration of storage affects seedling physiology and thereby influences the physiological and morphological response following outplanting. Information on physiological response during early establishment may improve understanding of these effects and lead to improvements in lifting and storage practices.

Black spruce (*Picea mariana* [Mill.] B.S.P.) transplants ($1^1/_2 + 1^1/_2$) were selected as the experimental material for the following reasons. This species is commercially important in Ontario and recent statistics indicate that this trend will continue. Indeed, black spruce seedling production increased by 362 percent from 18 million trees produced in 1983 to 68 million trees produced in 1988 (O.M.N.R. 1987, 1988). During 1986-87, this stock type was the only black spruce bare root stock type produced at the Ontario Ministry of Natural Resources Thunder Bay Forest Nursery and production forecasts indicate that this will continue (O.M.N.R. 1986a). Furthermore, the tendency in northern Ontario is towards an increased production of transplant stock (Reffle 1988).

The broad objective of this research was to evaluate morphological and physiological response attributes of seedlings variously conditioned prior to planting. To satisfy this objective, the experimental seedlings were subjected to commonly practiced lifting and storage methods and then evaluated for physiological and/or morphological response during concurrent potting and outplanting trials. Past experiments designed to measure treatment response under natural conditions only have often failed because the ever changing factors of the natural environment often induce variations that hide the responses to the experimental treatments (Downs 1975). This has led to the realization that environmental control is useful, and often necessary, particularly when investigating plant physiological processes (Downs and Hellmers 1976, Jarvis 1976, Blake 1986). The growth chamber and outplanting trials were established at approximately the same time (within equipment and labour constraints) using similar stock lots taken from a single nursery bed. It was hoped that the potting trials would provide the classic response and that this information would be useful in interpreting the response of the treatments under the more variable field conditions. Trials were initiated in early and late spring and were monitored at varying levels of intensity to meet trial specific objectives.

Chapter one of this thesis, subtitled 1. Physiological Response Under Controlled Environment Conditions, reports on the potting trials conducted in a controlled environment chamber at Lakehead University. This research was undertaken to evaluate important physiological response attributes of seedlings selected from each lifting-storage method under controlled environmental conditions and two soil water regimes.

Chapter two of this thesis, subtitled 2. Physiological and Morphological Response Following Outplanting, reports on experimental field trials conducted at the Thunder Bay Forest Nursery and on a recently scarified outplanting site near Raith, Ontario. The nursery trial was conducted to evaluate important physiological and morphological response attributes of seedlings selected from each lifting-storage method in a semi-controlled environment and to include undisturbed (i.e. not planted, thinned *in situ*) stock as an experimental treatment. The outplanting trial conducted at Raith evaluated the morphological response of seedlings selected from each lifting-storage method on a typical northwestern Ontario outplanting site.

Chapter three of this thesis, subtitled 3. Summary, Conclusions, and Implications for Forest Management, provides a synthesis of results and their implications for more effective reforestation programs.

CHAPTER 1

ESTABLISHMENT AND EARLY GROWTH OF BLACK SPRUCE (*Picea mariana* [Mill.] B.S.P.) IN RELATION TO SELECTED NURSERY LIFTING AND STORAGE PRACTICES. 1. PHYSIOLOGICAL RESPONSE UNDER CONTROLLED ENVIRONMENT CONDITIONS.

ABSTRACT

Butson, R. G. 1989. Establishment and early growth of black spruce (*Picea mariana* [Mill.] B.S.P.) in relation to selected nursery lifting and storage practices. 1. Physiological response under controlled environment conditions. M. Sc. F. Thesis. Lakehead Univ., Sch. For., Thunder Bay, Ont.

KEYWORDS: bareroot nursery practice, black spruce, *Picea mariana*, root growth capacity, seedling establishment, storage practices, stomatal conductance, transpiration, water relations

Problems associated with the establishment and early growth of outplanted black spruce (*Picea mariana* [Mill.] B.S.P.) seedlings led to research on the effects of selected nursery lifting and storage practices on early physiological response. The broad objective was to evaluate important physiological response attributes of fall lifted, overwinter frozen stored, spring lifted, cool stored and freshly lifted $1^1/_2 + 1^1/_2$ black spruce transplants following potting in a controlled environment chamber in mid-May and mid-June, 1987. Each potting trial consisted of three simultaneous experiments. In Experiment 1, stomatal conductance and transpiration rates were measured for well-watered (every second day) and water stressed (soil drying) seedlings. In Experiment 2, osmotic potentials at full turgor and the turgor loss point and the relative water content at the turgor loss point were estimated using the pressure-volume technique prior to potting, and after 13 days for both well-watered and water stressed seedlings. In Experiment 3, the root growth capacity was evaluated after 14 days for well-watered seedlings only.

Shoot-tissue water relations varied among lifting-storage treatments, water regimes, and potting times and often showed a lack of agreement between the selected parameters. Pre-potting osmotic potentials increased between potting times for the stored seedlings indicating that drought tolerance was reduced following the extended storage periods. In general, post-planting osmotic potentials were lower for the water stressed than well-watered seedlings and increased with renewed bud and shoot activity suggesting that all seedlings were especially prone to desiccation at this time. Stomatal and root growth response recorded for the fall and spring lifted seedlings indicated that nursery lifting-storage practices effected each group a different survival mechanism. Most importantly, the fall lifted seedlings exhibited prolific root growth but poorly regulated transpirational losses during establishment. In contrast, the spring lifted seedlings showed poorer root growth but maintained better stomatal control over transpirational losses. While this response difference may have increased the photosynthetic capacity and favoured growth for the fall lifted seedlings in the short term, it would place them under greater risk to desiccation following outplanting during droughty periods or when water absorption is limited by cold soil temperatures or flooding.

INTRODUCTION

The field performance of a newly planted seedling is determined by its potential to respond to the edaphic, atmospheric, and biotic constraints of the planting site (Sutton 1982a). To ensure growth and survival, it must replenish its limited water reserves as quickly as possible (Kozlowski and Davies 1975, Burdett 1987). The attainment of a favourable water balance is primarily dependent on the outplants inherent ability to control its initial rate of water loss and to access additional water by regenerating and extending new, unsuberized root tips (Burdett *et al.* 1983, Ritchie 1985). A seedling that is unable establish intimate root-soil contact (Sands 1984) by expanding its limited root system is subject to water stress because additional soil water outside the immediate vicinity of the existing root system must be exploited to meet the high evaporative demands that frequently characterize atmospheric conditions at the time of planting (McClain 1986). Furthermore, the existing, generally suberized root system is relatively inefficient at water absorption (Chung and Kramer 1975, Sands *et al.* 1982).

During periods of high evaporative demand and/or low soil water availability, a seedling's water reserves invariably decline. A healthy seedling is able to protect itself against short term water deficits by closing stomata and reducing transpirational losses before its stored water becomes critically low (Jarvis 1980, Mansfield and Davies 1985). A seedling's water relations usually improve at night when the evaporative demand falls to a minimum and absorption replaces transpirational losses (Slatyer 1967). In the face of continuing drought, a seedling's chances of survival depend on its ability to expand its root system to access additional soil water. If the rate of water consumption continues to exceed the rate of absorption, water stress can develop, prompting a sequence of physiological and metabolic disorders that can result in turgor loss, stomatal closure, photosynthesis reduction, growth cessation and finally death (Hsiao 1973). A seedling subjected to excessive water stress will at best become poorly established and grow slowly for several years (Day 1976).

Seedling water status is often quantified in terms of water potential (i.e. the difference between the chemical potential of pure, free water [assumed to equal zero] and water in the seedling, when both are measured under identical conditions of temperature, elevation, and atmospheric pressure) (Slatyer 1967, Kramer 1983). As well as quantifying the physiochemical availability of water for plant processes, plant water potential gradients largely determine the direction of water movement within the plant. The total water potential of a seedling is the sum of several measurable component potentials. Those most frequently discussed by modern investigators are pressure, osmotic, and matric potentials (Kramer and Kozlowski 1979, Kozlowski 1982).

In seedling water relations, the matric potential generally has a negligible effect on total water potential and is usually ignored (Kramer 1983). However, the pressure and osmotic potentials are key components in the maintenance of a favourable water balance during moisture deficits and in determining drought resistance (Brown 1977, Joly 1985). The pressure potential is a positive physical force exerted inwards on the cell contents by the distended cell wall (turgor pressure). Its magnitude is determined by volume increases that occur with protoplasmal water uptake and by cell wall elasticity. The osmotic potential represents the depressive effect of osmotic solutes (e.g. inorganic cations, amino and organic acids, and sugars) occurring within the cell solution. As the cell solution becomes more concentrated, the osmotic potential becomes increasingly negative (Brown 1977, Hsiao and Bradford 1983).

The importance of maintaining satisfactory seedling water relations can be explained in terms of pressure potential. Nearly all physiological processes are mediated by cell turgor such that a sustained reduction below a threshold turgor pressure can be lethal. The presence of solutes in the cell solution (osmotic potential) play an important role in the adaptation of plants to drought conditions. As water stress intensifies, total plant water potential decreases and the cell solution becomes more concentrated (osmotic potential decreases) through one or more of the following processes: (1) an increase in cell wall elasticity, (2) an increase in solute concentrations as cells are dehydrated, and (3) an active accumulation of solutes (Hsiao *et al.* 1976, Turner 1979). Osmotic potential decreases enable a seedling to maintain positive turgor and hence, turgor mediated processes essential for growth as total water potential declines in response to increased levels of water stress (Hsiao *et al.* 1976, Turner 1979). The relationship between relative water content, water potential, osmotic potential, and pressure potential of plant tissues can be quantified using the pressure-volume technique as developed by Scholander *et al.* (1964, 1965) and Tyree and Hammel (1972). This technique is useful when investigating the influence of nursery cultural practices on seedling physiology because it provides meaningful insights into a seedling's turgor maintenance mechanisms (Hennessey and Dougherty 1984).

The reality of plantation establishment is that seedlings commonly experience a decline in plant water potential within a short period after planting (McClain 1986). This condition is further exacerbated by the numerous stresses imposed on the stock during handling, storage, shipping, and planting (Chavasse 1980, McClain 1986). Each stress event exposes the seedling to an excess or deficiency of any factor needed for growth (Timmis 1980). These unfavorable conditions need not be life threatening to trigger a response in the affected seedling (Larcher 1980).

The stress events that occur during each substandard phase are believed to be cumulative; damage occurring in one phase of the nursery operation is added to any damage that occurred prior to that phase, or has yet to occur in a following phase (Navratil 1973, DeYoe 1988). Thus, even mild stress, if persistent, will eventually injure the seedling by reducing its ability to recuperate from further stress events (Timmis 1980). It follows that stock must be flawlessly handled during each phase of nursery and planting practice

to minimize the incidence of stress and thereby, maximize seedling fitness and outplanting performance potential (Edgren 1980).

Cold storage of planting stock is one phase of nursery practice commonly used in Ontario and known to influence plantation success by affecting seedling physiology (Hocking and Nyland 1971, Sutton 1979, Venn 1980, Burdett and Simpson 1984). Cold storage involves the holding of fall lifted seedlings at sub-freezing temperatures over the winter months or the holding of spring lifted seedlings within a narrow range just above freezing until planting. Although coniferous seedlings have been successfully stored overwinter at above freezing temperatures (Mullin and Bunting 1970, 1972) and after lifting in early spring at below freezing temperatures (Mullin 1976, Mullin and Forcier 1976, Mullin and Reffle 1980, Sutton 1982b), neither of these methods is practiced operationally in Ontario. The former places seedlings at an increased risk to physiological (particularly the consumption of carbohydrate reserves) and pathological deterioration (Hocking and Nyland 1971, Navratil 1973, Venn 1980) while the latter is detrimental to seedlings lifted following dormancy release (Mullin 1976, Mullin and Forcier 1976, 1979, Mullin and Reffle 1980), a condition that occurs prior to any visible evidence of renewed growth (Ryker 1976).

Several studies have revealed that the physiological quality of seedlings changes during cold storage. Most importantly, carbohydrate concentration (Hellmers 1962, Winjum 1963, Ronco 1973, McCracken 1979, van den Driessche 1979, Mattsson 1982, Ritchie 1982, Ritchie *et al.* 1985), seedling dry weight (Aldhous 1964, Navratil 1976, Navratil *et al.* 1976, McCracken 1979, DeWald and Feret 1988), root growth capacity (Sutton 1980, Ritchie 1982, Carlson 1985, Ritchie *et al.* 1985), stomatal response (Blake 1983, Grossnickle and Blake 1985, Grossnickle 1987, 1988b), and photosynthetic activity (McCracken 1978, Mattsson and Troeng 1986) have been influenced by storage treatment.

With one notable exception (Blake 1983), studies have not been conducted to compare the effects of varied storage methods on plant water relations during early establishment for Ontario's boreal conifers. Blake found that frozen storage at -3±1°C conditioned the stomata of 2+0 white spruce (*Picea glauca* [Moench] Voss) seedlings to reduce water loss after potting under simulated drought conditions (imposed by the osmoticum polyethylene glycol 4000). This occurred without markedly reducing the stomatal aperture and thus, the photosynthetic capacity under well-watered conditions. The physiological mechanisms underlying the greater stomatal responsiveness of the frozen stored seedlings could not be fully explained, although it was suggested that it might be due to greater endogenous abscisic acid (ABA) concentrations (either total ABA or the ratio of free form of ABA relative to bound ABA) that presumably followed frozen storage. This suggestion was based on previous research which indicated that: (1) freezing plants induces a high degree of moisture stress (Cleary and Tinus 1980), a condition that would be intensified during overwinter frozen storage, (2) free ABA levels increased with stressful cold temperatures in tomato plants (Daie and Campbell 1981) and during bud dormancy of *Vitis vinifera* L.

(Düring and Bachmann 1975), and (3) drought stress increases ABA concentrations (Wright 1978). This altered stomatal response, in addition to an observed delay in flushing and lower leaf water potentials in the post-planting period, prompted Blake to propose that frozen stored stock was better adapted to survive outplanting than freshly lifted stock. These effects must be further investigated because of the importance of maintaining favourable water relations after outplanting and because growth rhythms are becoming increasingly disrupted as non-conventional lifting and storage practices gain widespread use (Sutton 1977, 1979).

The research presented in this chapter tests the hypothesis that the date of lifting and the temperature and duration of storage affects seedling physiology and thereby influences the physiological response during early establishment. This hypothesis was tested by evaluating water vapour exchange, specific shoot-tissue water relations components, and root growth capacity of both fall and spring lifted $1^1/_2 + 1^1/_2$ black spruce (*Picea mariana* [Mill.] B.S.P.) transplants. Seedling physiology is difficult to study under field conditions because interacting environmental factors frequently mask treatment effects (Downs 1975, Jarvis 1976, Blake 1986). Therefore, research was conducted in a controlled environment chamber at Lakehead University to achieve uniform soil and atmospheric (light, absolute humidity deficit, etc.) factors known to affect the water relations of an outplant and to eliminate vegetative competition. Furthermore, the controlled environment facilitated the measurement of seedling response while two soil water regimes were maintained to create conditions of stress and non-stress. Prior to potting in the mid-May and mid-June, the seedlings were subjected to the following lifting-storage treatments: (1) fall lifted (October 29, 1986), overwinter stored at $-2 \pm 1^\circ$ C and conditioned at $+2 \pm 1^\circ$ C for 7 or 48 days, (2) spring lifted (May 6, 1987), stored at $+2 \pm 1^\circ$ C until removed, and (3) spring lifted, stored at $+2 \pm 1^\circ$ C for 1 day (i.e. freshly lifted). The objectives of this research were as follows:

1. To determine seedling response in terms of gaseous exchange (i.e. rates of stomatal conductance and transpiration) for both well-watered and water stressed seedlings during a 21 day establishment period.

2. To determine the osmotic potential at full turgor, the osmotic potential at the turgor loss point, and the relative water content at the turgor loss point of both well-watered and water stressed seedlings immediately prior to potting, and immediately after the current growth of stressed seedlings had visibly lost turgor (i.e. become flaccid).

3. To determine the root growth capacity of well-watered seedlings after 14 days in a test environment.

METHODS AND MATERIALS

On May 21 and June 24, 1987, potting trials were established in a controlled environment chamber at Lakehead University. Each trial consisted of three simultaneous experiments. Each experiment was designed to evaluate a different physiological response for fall and spring lifted $1^1/_2 + 1^1/_2$ black spruce transplants which were conditioned prior to potting as described in Table 1.1. In Experiment 1, the stomatal conductance (g_s) and transpiration (E_t) rates were measured for the variously conditioned seedlings under two soil water regimes (well-watered vs. water stressed). In Experiment 2, the osmotic potential at full turgor ($\Psi_{\pi(sat)}$), the osmotic potential at the turgor loss point ($\Psi_{\pi(TLP)}$), and the relative water content at the turgor loss point ($RWC_{(TLP)}$) were evaluated prior to potting and after 13 days for both well-watered and water stressed seedlings. In Experiment 3, the root growth capacity (RGC) was evaluated after 14 days for well-watered seedlings only since, by definition, RGC is evaluated under optimum conditions (Ritchie and Dunlap 1980) when used to assess physiological quality.

EXPERIMENTAL MATERIAL

Black spruce transplants ($1^1/_2 + 1^1/_2$) (seed source 34-25-0-00)[1] were obtained from the Ontario Ministry of Natural Resources (OMNR) Thunder Bay Forest Nursery (TBFN). All stock was taken from a single nursery bed (See Table 1.1 for treatment descriptions and codes). With the exception of treatment SL-1-P2, all seedlings were loosened by a shaker lifting blade (Egedal) and pulled by hand. SL-1-P2 seedlings were loosened with planting shovels to minimize damage to current growth that had developed since earlier lifting. The average morphological characteristics were determined immediately following lifting using Day *et al.* 's (1985) mean and standard deviation method (Table 1.2). Due to time limitations, average morphology was not determined for the freshly lifted seedlings (SL-1-P1, SL-1-P2). Rather, the values reported in Table 1.2 were determined 7 to 9 days earlier for freshly lifted stock outplanted during approximately concurrent field trials (Chapter 2). Therefore, the average morphological characteristics reported in Table 1.2 may deviate slightly from those of the freshly lifted seedlings for both potting trials.

The standard errors of the average morphological characteristics and significant differences

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[1] seed source information code: 34 = site region code (3W), 25 = geographic location code (Thunder Bay District), 0 = agency code (OMNR), 00 = collection type code (general collection) (O.M.N.R. 1986b).

Table 1.1. The treatments evaluated in the controlled environment chamber at Lakehead University in 1987. Black spruce transplants ($1^1/_2 + 1^1/_2$) from the Thunder Bay Forest Nursery were tested (seed source 34-25-0-00).

Treatment Code[1]	Treatment Description[2]	Lifting Date	Duration and Temperature of Storage	Potting Date
Potting Time 1 (May 21)				
FL-48-P1	Fall lifted, frozen stored for 155 days, conditioned in cold storage for 48 days,	October 29, 1986	155 days at - 2 ± 1 °C 48 days at +2 ± 1 °C	May 21, 1987
FL-7-P1	Fall lifted, frozen stored for 196 day, conditioned in cold storage for 7 days	October 29, 1986	196 days at - 2 ± 1 °C 7 days at +2 ± 1 °C	May 21, 1987
SL-14-P1	Spring lifted, cold stored for 14 days	May 6, 1987	14 days at +2 ± 1 °C	May 21, 1987
SL-1-P1	Spring lifted, cold stored for 1 day	May 20, 1987	1 day at +2 ± 1 °C	May 21, 1987
Potting Time 2 (June 24)				
FL-48-P2	Fall lifted, frozen stored for 189 days, conditioned in cold storage for 48 days	October 29, 1986	189 days at - 2 ± 1 °C 48 days at +2 ± 1 °C	June 24, 1987
FL-7-P2	Fall lifted, frozen stored for 230 day, conditioned in cold storage for 7 days	October 29, 1986	230 days at - 2 ± 1 °C 7 days at +2 ± 1 °C	June 24, 1987
SL-48-P2	Spring lifted, cold stored for 48 days	May 6, 1987	48 days at +2 ± 1 °C	June 24, 1987
SL-1-P2	Spring lifted, cold stored for 1 day	June 23, 1987	1 day at +2 ± 1 °C	June 24, 1987

[1] Treatment Code: FL = fall lifted; SL = spring lifted; 48, 14, 7, 1 = number of days stored at +2 ± 1 °C; P1 = Potting Time 1 (May 21, 1987); P2 = Potting Time 2 (June 24, 1987).

[2] Half the potted seedlings were watered to the drip point every second day (well-watered). Pots drained freely between waterings. The other half were watered in the same way for three days and then subjected to a decreasing soil water potential by withholding water (water stressed).

Table 1.2. Morphological measurements ($\bar{x}$, S.E. [in brackets], n = 100 seedlings) by treatment for $1^1/_2 + 1^1/_2$ black spruce transplants potted in a controlled environment chamber at Lakehead University during 1987. These characteristics were determined upon lifting from randomly selected samples using the mean and standard deviation method (Day *et al.* 1985). Unless otherwise noted, all determinations are derived from methods described by Day *et al.* Means within a column without a common letter are significantly different ($\alpha = 0.05$).

Treatment Code[1]	Treatment Description[2]	Root Collar Diameter (mm)	1986 Height[3] (cm)	1987 Leader Extension[4] (cm)	Top Dry Weight (g)	Root Dry Weight (g)	Root Area Index (cm^2)	Root Volume (cm^3)
Potting Time 1 (May 21)								
FL-48-P1	Fall lifted, frozen stored for 155 days, conditioned in cold storage for 48 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a, (0.33)
FL-7-P1	Fall lifted, frozen stored for 196 days, conditioned in cold storage for 7 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
SL-14-P1	Spring lifted, cold stored for 14 days	4.662a (0.138)	24.7a (0.55)	n/a	5.150a (0.3042)	1.608ab (0.1151)	56.3bc (2.97)	5.8a (0.40)
SL-1-P1	Spring lifted, cold stored for 1 day	5.28b (0.134)	28.3b (0.64)	n/a	6.523b (0.3161)	1.822b (0.0904)	63.6c (3.53)	6.1a (0.30)
Potting Time 2 (June 24)								
FL-48-P2	Fall lifted, frozen stored for 189 days, conditioned in cold storage for 48 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
FL-7-P2	Fall lifted, frozen stored for 230 days, conditioned in cold storage for 7 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
SL-48-P2	Spring lifted, cold stored for 48 days	4.662a (0.138)	24.7a (0.55)	n/a	5.150a (0.3042)	1.608ab (0.1151)	56.3bc (2.97)	5.8a (0.40)
SL-1-P2	Spring lifted, cold stored for 1 day	5.50b (0.138)	23.8a (0.54)	11.3 (0.37)	8.335c (0.4548)	1.429a (0.0732)	46.9a (2.22)	4.8b (0.26)

[1] Treatment Code: FL = fall lifted; SL = spring lifted; 48, 14, 7, 1 = number of days stored at +2 ± 1 °C; P1 = Potting Time 1 (May 21, 1987); P2 = Potting Time 2 (June 24, 1987).

[2] Half the potted seedlings were watered to the drip point every second day (well-watered). Pots drained freely between waterings. The other half were watered in the same way for three days and then subjected to a decreasing soil water potential by withholding water (water stressed).

[3] Defined as the distance from the root collar to the base of the terminal bud on the tallest leader.

[4] Defined as the distance from the base of the previous years growth node to the tip of the growing dominant terminal or lateral.

between these average values were determined using Student-Newman-Keuls' (SNK) multiple range test (Steel and Torrie 1980) and are presented for each lifting-storage treatment in Table 1.2. These statistics indicate that the fall lifted treatments and the spring lifted, stored treatments (SL-14-P1, SL-48-P2) were very uniform in size; no significant differences were found in any of the morphological characteristics measured. Treatment SL-1-P2 had the largest tops (note that these seedlings averaged 35.1 cm in height when lifted) and treatment SL-1-P1 had the largest roots. The reduced root size of SL-1-P2 seedlings was likely a consequence of lifting with shovels.

Trees that met the OMNR TBFN minimum acceptable standards for $1^1/_2 + 1^1/_2$ black spruce transplants of 2.6 mm in root collar diameter and 15 cm in height (Phillion 1986, pers. comm.) were bundled into groups of ten and root pruned to 23 cm in accordance with standard nursery practice. These standards are considerably lower than the root collar diameter culling limit (≤3.5 mm), and slightly greater than the height culling limit (≤14 cm) recommended by Reese and Sadreika (1979). Spring lifted stock had to be further culled because of needle desiccation and bud mortality. This damage, particularly evident on the 1986 terminal whorls, resulted from inadequate snow cover during the 1986-87 winter months. Seedlings were then packed in sealed polyethylene bags in waxed kraft boxes in lots of 400.

Trees of similar morphological description (i.e. within 10 % of the mean root collar diameter and mean height determined for each lifting-storage treatment [Day *et al.* 1985]) were chosen for study. It was reasoned that the use of mean trees would control the rate of drying, particularly for the non-watered treatments (Kramer 1979), and thereby render the results of the three simultaneous experiments more comparable (i.e. it was hoped that the responses measured for Experiments 1, 2, and 3 could be discussed collectively, as if the information were taken from the same seedlings).

TREATMENTS

Each of the potting trials investigated the physiological response of the selected seedlings subjected to the the following date of lifting - temperature and duration of storage treatments:

1. Fall lifted and overwinter frozen stored at - 2 ± 1 ° C, conditioned at +2 ± 1 ° C for 7 or 48 days.
2. Spring lifted and stored at +2 ± 1 ° C for 14 and 48 days.
3. Spring lifted and stored at +2 ± 1 ° C for 1 day (i.e. freshly lifted).

The specific lifting dates, temperatures, storage durations, and potting dates are presented along with treatment codes and treatment descriptions in Table 1.1. Fall lifted seedlings (FL-48-P1, FL-7-P1, FL-48-P2, FL-7-P2; see Table 1.1 for code descriptions) were stored in OMNR freezers at Thunder Bay until April when they were removed for further storage at Lakehead University. Spring lifted seedlings

(SL-14-P1, SL-1-P1, SL-48-P2, SL-1-P2; see Table 1.1 for code descriptions) were stored at Lakehead University.

The lifting-storage treatments were chosen for the following reasons. The fall lifted treatments are standard for overwinter frozen stored stock at the TBFN except for the 7 or 48 day conditioning period at +2 ± 1 ° C prior to planting. This period was included to investigate its affect on post-planting physiology. It was believed to be beneficial because it provided a transition period over which the seedlings, in a frozen state for the past 5 to 7 months, could thaw, become physiologically active while still in storage, and thereby be better prepared to grow rapidly and survive after outplanting. Indeed, Venn (1980) reported that direct outplanting of frozen stored Norway spruce (*Picea abies* [L.] Karst.) seedlings is detrimental to seedling establishment. The spring lifted, stored treatments (SL-14-P1, SL-48-P2) are standard for the TBFN. The 14 and 48 day delay between lifting and potting was designed to simulate short and moderately long periods of spring storage, respectively. Sutton (1980) reported low survival for spring lifted 3+0 black spruce seedlings that had been held in cool storage for 8 weeks or longer and Colombo and Racey (1988) advised that spring lifted bare root stock be stored for no longer than 3 weeks. The freshly lifted treatments (SL-1-P1, SL-1-P2), when properly handled, have been used successfully in past experimental field trials (McClain 1979, 1981). The delay between lifting and planting was designed to simulate that imposed by grading, packaging, storage, and transport, in all other treatments.

To assess the selected shoot-tissue water relations components under non-limiting and diminishing soil water potential (Ψ_{soil}), half the potted seedlings were watered to the drip point with tap water every second day (well-watered). The other half were watered in the same way for the first three days of each experimental period and then subjected to an increasing soil water deficit by withholding water (water stressed). Pots drained freely between waterings. This method of imposing water stress is the most natural and also the most difficult to control (Krizek 1985) because rates of dehydration may vary with plant size, species, and cultivar, the water holding capacity of the rooting medium, and the size of the pot (Kramer 1979). This effect was reduced by carefully measuring equal quantities (i.e. air dry weight) of homogenized rooting medium into identical pots.

The rate of drying was determined gravimetrically at the same time daily and expressed as a percentage of soil water holding capacity. The obvious limitation of this method is that it is not sensitive to changes in seedling fresh weight. However, more accurate equipment was unavailable. Furthermore, calculations based on average seedling fresh and dry weights determined that errors inherent in the gravitational method could not have affected soil water determinations by more than of 2 or 3 %. This error would reduce the calculated percentages. It would be minimal at the start of the experimental period and become progressively larger towards the end as the water stressed seedlings became desiccated.

GROWING ENVIRONMENT

Seedlings selected for plant water relations measurements (Experiments 1 and 2) were potted individually in plastic pots (13 cm in diameter, 12 cm in depth, and 0.8 L in capacity), in 1100 g of air dry soil taken from Compartment 113 at the TBFN, sifted through a 2 mm sieve to ensure a uniform soil texture, and thoroughly mixed in a cement mixer to assure a homogeneous soil type for each potting trial. Following mixing, the soil texture was characterized as a loamy sand (86 % sand, 11.2 % silt, 2.8% clay) using the Bouyoucos hydrometer method (Wilde *et al.* 1979). A soil water retention curve, developed according to the procedures outlined in the operating manual for the ceramic plate extractor (Soil Moisture Equipment Corp., Santa Barbara, Calif.), is presented in Appendix IV, Figure IV.1.

Seedlings selected for RGC measurements (Experiment 3) were potted, 5 seedlings per 20.5 cm diameter plastic bulb pan of 3.5 L capacity, in a peat vermiculite (2:1, by volume) mixture. All pots were watered with tap water every second day until saturated. Pots drained freely between waterings.

Experimental seedlings were potted on May 21 (Potting Time 1) and June 24 (Potting Time 2) and held under night conditions until the lights were turned on the following day (Day 1 for each trial). All experimentals were conducted in a single walk-in growth chamber programmed for an 18 hour day with 13 hours at 50 000 lx illuminance from a mixture of cool white fluorescent and incandescent lighting at seedling height. Dawn was simulated over a 225 minute period by switching on successive light banks at 45 minute intervals until 50 000 lx illuminance was reached. Night temperature was 17.5° C and was increased gradually over the 225 minute dawn to a daytime maximum of 25° C. Relative humidity was programmed to decrease over the same period from approximately 70 % during the night to approximately 60 % during the day.

MEASUREMENT OF SEEDLING WATER RELATION COMPONENTS

Experiment 1 - Stomatal Conductance and Transpiration

Experimental Design

The experiment was a randomized complete block design with four blocks, each comprised of eight treatment combinations (four lifting-storage treatments and two watering treatments) (see Table 1.1 for treatment descriptions). A single seedling per treatment combination per block was potted. Thus, 32 seedlings were potted in total.

Sampling Procedure

The g_s ($cm \cdot sec^{-1}$) and E_t ($mg \cdot cm^{-2} \cdot sec^{-1}$) rates of each individually potted seedling were measured using the model CS-102 whole seedling transient type porometer (Micromet Systems Inc., Vancouver, B. C.), the design and calibration of which are described by Livingston *et al.* (1984). The entire measurement process required approximately 90 seconds per seedling. Each seedling was measured once every 45 minutes over a 7.5 hour sampling day beginning at first light on 17 of the 21 days that each trial ran. Equipment constraints did not allow seedlings to be sampled every day. Therefore, approximately 6000 individual seedling measurements of g_s and E_t were taken during each study.

To minimize the error related to changing g_s and E_t during the day (particularly the sharp rise at dawn), each experiment was consistently sampled in a block by block, left to right pattern. In this manner, each treatment combination was measured for g_s and E_t at least once every 11.25 minutes. To further minimize variability in g_s and E_t over the sample period, the measurements from the four seedlings representing each treatment combination (one potted seedling per block) were averaged after being corrected for projected needle surface area (Appendix I). Therefore, approximately 1500 measurements of average g_s and E_t were recorded during each potting trial.

Measurements were discontinued on Day 18 for the water stressed seedlings of Potting Time 1 due to their poor physical condition at this time. Although the water stressed seedlings were also in poor physical condition about 17 days into the second trial, they were measured for the full 21 day period to document the very low g_s and E_t rates that occur under conditions of severe water stress. At the completion of each experiment, xylem pressure potential (Ψ_{xylem}) measurements were taken on excised terminal branches from each of the water stressed seedlings using the pressure chamber technique detailed by Ritchie and Hinckley (1975).

Experiment 2 - Shoot-Tissue Water Relations

Experimental Design

The experiment was a completely randomized design with eight treatment combinations (four lifting-storage treatments and two watering treatments) (see Table 1.1 for treatment descriptions). Two seedlings per treatment combination were individually potted to determine $\Psi_{\pi(sat)}$ (MPa), $\Psi_{\pi(TLP)}$ (MPa), and $RWC_{(TLP)}$ (%). Thus, 16 seedlings were potted in total.

Sampling Procedure

Prior to potting the above experimental design, the selected shoot-tissue water relations parameters (i.e. $\Psi_{\pi(sat)}$, $\Psi_{\pi(TLP)}$, $RWC_{(TLP)}$) were determined from two seedlings per lifting-storage

treatment by constructing pressure-volume (P-V) curves in accordance with the method detailed by Cheung *et al.* (1975) and modified by Joly (1984). This method provides a reasonable approximation of average shoot-tissue water relation parameters for the needles and whole shoots (Tyree and Hammel 1972). These curves quantified the plant water potential (Ψ_{plant}) of the lifting-storage treatments prior to potting.

The current growth of water stressed treatment SL-1-P1 had visibly lost turgor (i.e. the current shoots were drooping) by Day 13 of the first trial and the experiment was discontinued. To be consistent, the second trial was also discontinued on Day 13. Upon completion of each experiment, each potted seedling was sealed in a plastic bag with a small tray of water and placed in a refrigerator until its P-V curve could be determined. P-V determinations were time consuming and required from 4-5 hours per treatment to compile. It was, therefore, necessary to store the potted trees in the refrigerator for up to four days. It is unlikely that refrigeration time affected the results in a significant way since, prior to P-V determinations, the plant material is rehydrated and physiological activity reduced.

All P-V determinations were conducted at the Ontario Forest Research Institute's Northern Forest Research Unit in Thunder Bay. The technique developed at the Institute incorporates an Apple® IIe microcomputer interfaced with an electronic balance. During P-V determinations, all data were electronically stored and later transferred to a Tecktronics computer programmed to plot Höfler diagrams, inverse pressure vs. cumulative weight of sap expressed, and inverse pressure vs. relative water content.

MEASUREMENT OF ROOT GROWTH CAPACITY

Experiment 3 - Root Growth Capacity

Experimental Design

The experiment was a completely randomized design with four lifting-storage treatments (see Table 1.1 for treatment descriptions). Twenty-five seedlings were potted (5 seedlings per bulb pan) per treatment. Thus, 100 seedlings were potted in total.

Sampling Procedure

Fourteen days after potting, the seedlings were excavated and the roots carefully washed in running water to remove the rooting medium. RGC was evaluated using the coding system developed by Burdett (1979) for lodgepole pine (*Pinus contorta* Dougl.) and modified for black spruce to include two additional classes (Appendix II). Burdett's method is based on the assumption that the first new roots to develop increase the seedling's drought resistance to a greater degree than the last new roots (Burdett 1987).

DATA EVALUATION AND ANALYSIS

Experiment 1 - Stomatal Conductance and Transpiration

Two seedlings from the well-watered treatments and one from the water stressed treatments were excluded from the analysis of Potting Time 1 because of errors made while determining new foliage development. One well-watered seedling was excluded from the analysis of each potting trial because they died during the experiment.

First light (measured during the first 45 minute sample period following illumination) and daytime (measured during the sixth 45 minute sample period following illumination) g_s and E_t, and the differences between these values (Δg_s and ΔE_t) were plotted over time to visually assess treatment similarities, differences, and trends over the course of each potting trial and to compare patterns of behaviour between trials. These sample periods were chosen to simulate low (first light) and moderately high (daytime) periods of atmospheric stress since differences in g_s and E_t response are most apparent under such conditions (Matin *et al.* 1989). Well-watered and water stressed treatments were plotted separately and corresponding plots were scaled equally.

Experiment 1 was analysed by calculating standard errors for mean g_s and E_t values and conducting a conventional two-way analysis of variance (ANOVA) for each first light and daytime sample period. This approach has recently been taken to determine statistically significant differences between means within sample times by a number of other researchers investigating physiological (Blake 1983, Buxton *et al.* 1985, Roberts and Dumbroff 1986, Blake and Sutton 1987, Grossnickle 1988c) and growth (Blake 1983, Grossnickle and Blake 1985, Mattsson and Troeng 1986, Blake and Sutton 1987, Grossnickle 1987) response variables. When the ANOVA procedure indicated at least one significant difference (α=0.05) between treatment means, the SNK multiple range test was used to provide more detailed information about the differences (Steel and Torrie 1980). The SNK test was chosen because it is conservative, has good power ($1-\beta$) and maintains a constant α level for all pairs of means being investigated (Anderson and McLean 1974). ANOVA's and SNK tests were performed using the SAS® GLM procedure on a Trojan-286 personal computer at the Northern Forest Research Unit in Thunder Bay.

Experiment 2 - Shoot-Tissue Water Relations

The shoot-tissue water relations parameters determined for seedlings in storage (i.e. prior to potting) were analysed by calculating standard errors and determining statistically significant differences (α=0.05) between lifting-storage treatment means using SNK multiple range tests.

The shoot-tissue water relations parameters determined for seedlings at the end of each experimental period were analysed by calculating standard errors and conducting a conventional one-way ANOVA for each trial. When a significant difference (α=0.05) was found to exist between treatment means, the SNK multiple range test was used to provide more detailed information about the differences.

Finally, the differences between the osmotic potentials at full turgor and the turgor loss point ($\Delta\Psi_\pi$) were determined for seedlings just out of storage and at the end of the experimental period.

Experiment 3 - Root Growth Capacity

The results of Experiment 3 were not analysed statistically because the nature of the response variables did not lend themselves to strict statistical test procedures. The data were therefore analysed graphically.

RESULTS

POTTING TIME 1 (MAY 21)

Water Relations Response

Stomatal Conductance and Transpiration

Gaseous exchange patterns indicate that the fall lifted treatments (FL-48-P1, FL-7-P1) and the spring lifted treatments (SL-14-P1, SL-1-P1) formed two distinct groups regardless of soil water condition. There are very similar g_S and E_t behaviour patterns within each group and considerable differences amongst the groups. Response patterns are very similar for g_S and E_t (first light and daytime) regardless of soil water condition, although isolated differences occurred; an increase or decrease in g_S is generally associated with a similar increase or decrease in E_t (Figures 1.1 to 1.4). Day to day fluctuations were particularly apparent for the well-watered seedlings. The general trend under both soil water regimes was for all lifting-storage treatments to approach similar first light and daytime g_S and E_t rates towards the end of the experimental period.

Under well-watered conditions, first light g_S ranged between treatments by a maximum of 0.406 $cm \cdot sec^{-1}$ (Figure 1.1a) on Day 11 to a minimum of 0.068 $cm \cdot sec^{-1}$ (averaged from Figures 1.1a and b) on Day 3. The range in first light E_t increased from 0.091 $mg \cdot cm^{-2} \cdot sec^{-1}$ on Day 1 (averaged from Figures 1.2a and b) to 0.130 $mg \cdot cm^{-2} \cdot sec^{-1}$ between Days 11 to 17 inclusive, and then decreased to 0.046 $mg \cdot cm^{-2} \cdot sec^{-1}$ on Day 21 (Figure 1.2a). The spring lifted treatments, particularly SL-1-P1, had the greatest first light g_S and E_t rates immediately following potting (Figure 1.1a and b, Figure 1.2a and b). However, by Day 3, the freshly lifted seedlings had the lowest overall rates and only a marginal difference separated the fall and spring lifted, stored seedlings. Thereafter (Days 4-21), first light rates were greatest for the well-watered fall lifted seedlings (Figures 1.1a and 1.2a). These differences were significant between Days 10 and 16 inclusive, and again on Day 19 (Appendix III, Table III.1). FL-48-P1 seedlings had greater rates than FL-7-P1 seedlings until Day 10 after which FL-7-P1 seedlings had greater rates. The only recorded incidence of a singularly different (α=0.05) treatment occurred on Day 17 when FL-7-P1 seedlings had the greatest first light g_S and E_t rates (Appendix III, Table III.1). The spring lifted treatments maintained minimal first light g_S and E_t rates after Day 6 averaging 0.122 $cm \cdot sec^{-1}$ and 0.045 $mg \cdot cm^{-2} \cdot sec^{-1}$, respectively. SL-1-P1 seedlings had slightly lower rates than SL-14-P1 seedlings

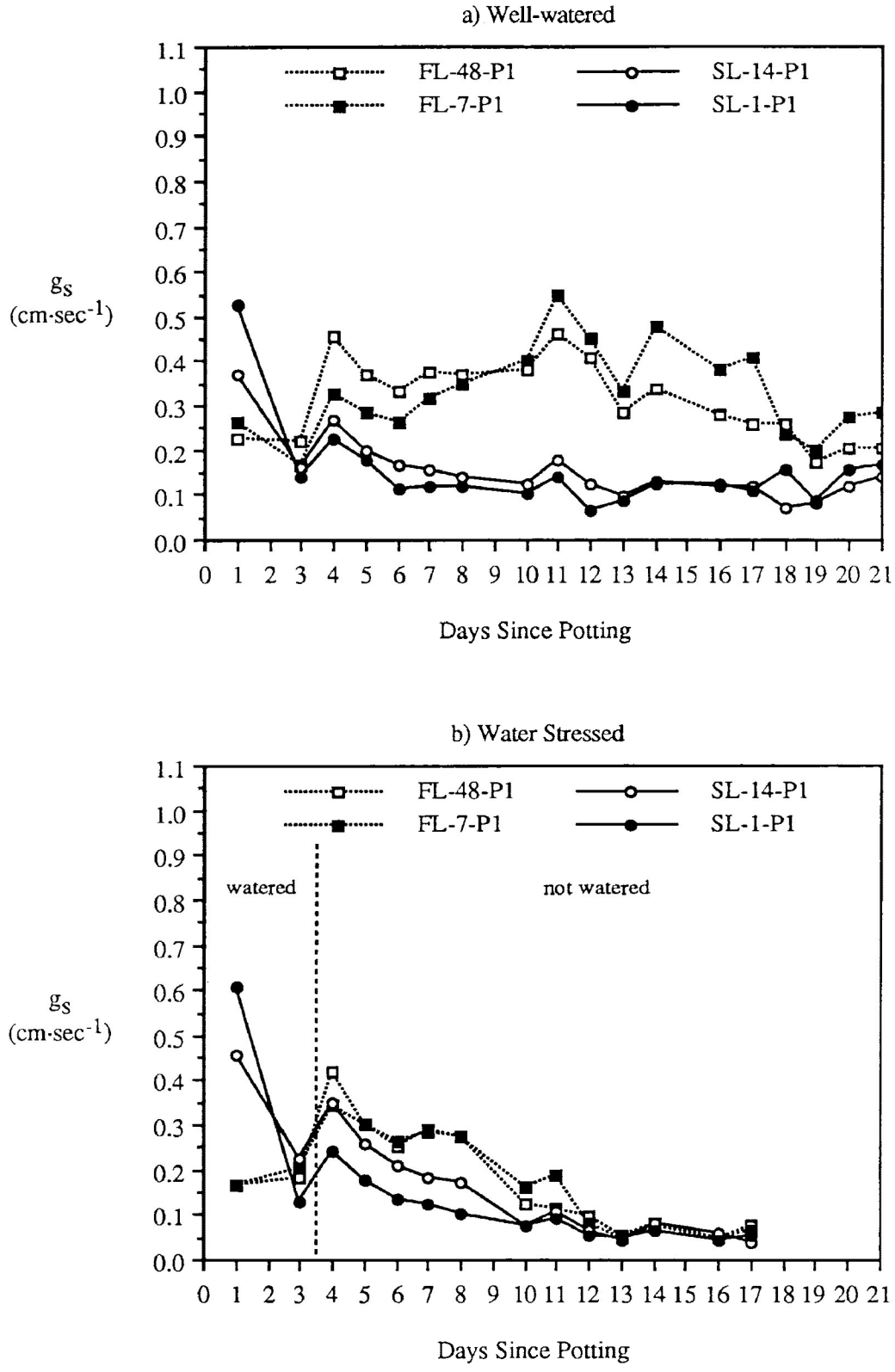

Figure 1.1. First light stomatal conductance (g_S) for the lifting-storage treatments monitored during Potting Time 1 (May 21): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). See Table 1.1 for treatment code descriptions and Appendix III, Table III.1 for treatment means, standard errors, sample sizes, and SNK multiple range test results.

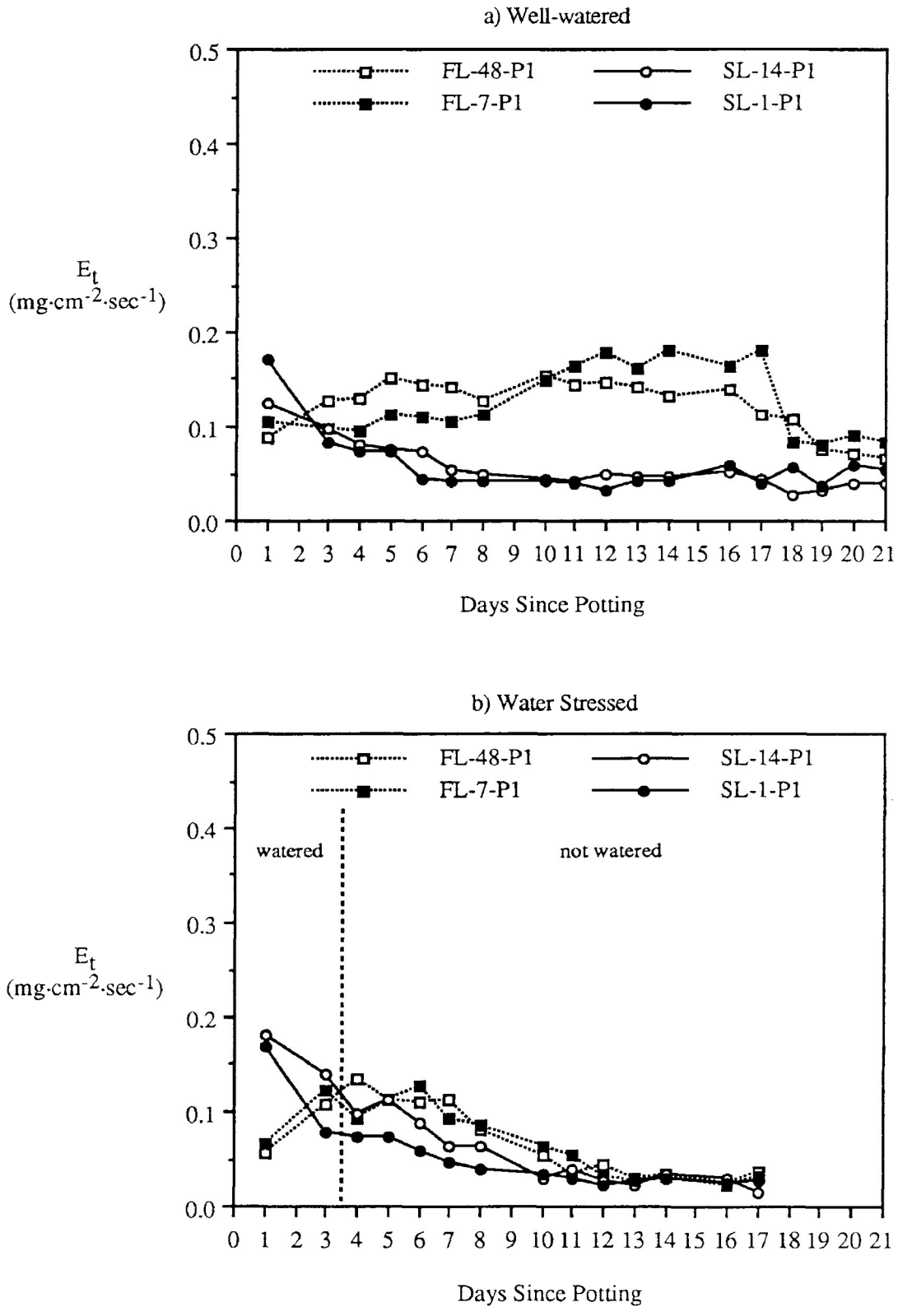

Figure 1.2. First light transpiration (E_t) for the lifting-storage treatments monitored during Potting Time 1 (May 21): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). See Table 1.1 for treatment code descriptions and Appendix III, Table III.1 for treatment means, standard errors, sample sizes, and SNK multiple range test results.

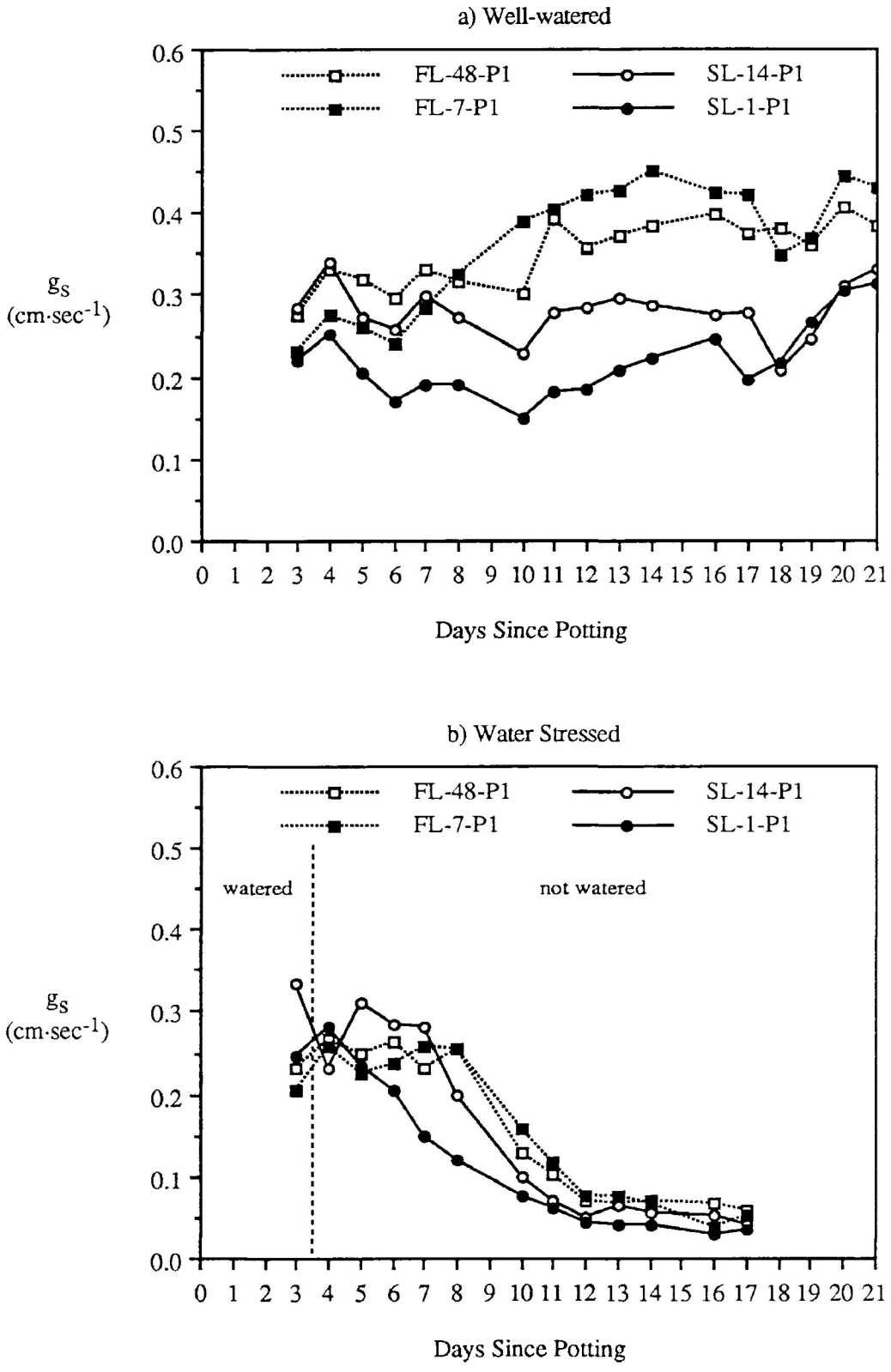

Figure 1.3. Daytime stomatal conductance (g_S) for the lifting-storage treatments monitored during Potting Time 1 (May 21): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). See Table 1.1 for treatment code descriptions and Appendix III, Table III.1 for treatment means, standard errors, sample sizes, and SNK multiple range test results.

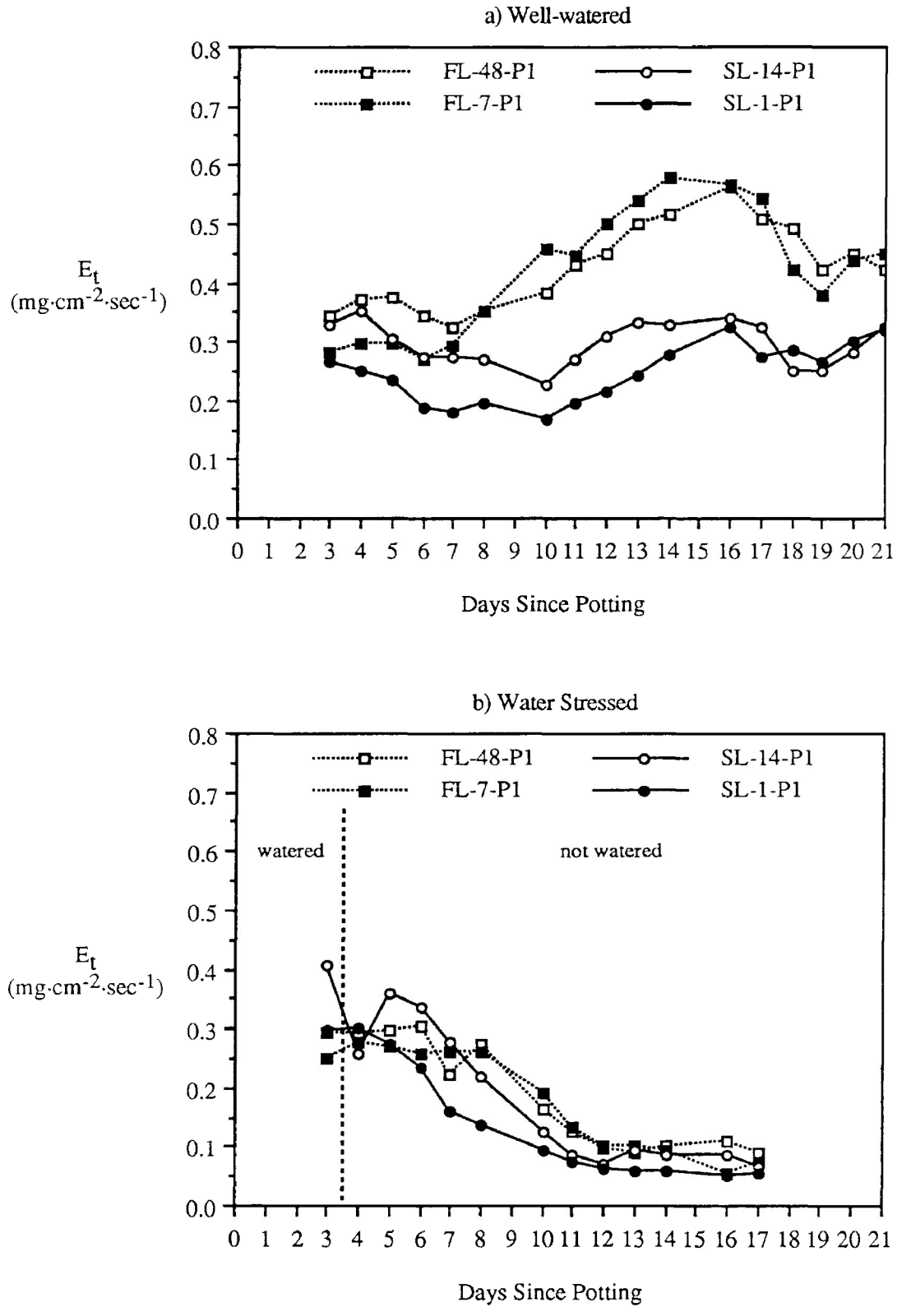

Figure 1.4. Daytime transpiration (E_t) for the lifting-storage treatments monitored during Potting Time 1 (May 21): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). See Table 1.1 for treatment code descriptions and Appendix III, Table III.1 for treatment means, standard errors, sample sizes, and SNK multiple range test results.

until Days 13 to 17 inclusive, over which period both treatments showed a similar response (Figures 1.1a and 1.2a). Thereafter, first light rates were slightly greater for the freshly lifted seedlings.

In comparison with the well-watered seedlings, first light g_s and E_t rates recorded for the water stressed seedlings generally exhibited: (1) a greater difference between the spring lifted treatments, (2) a narrower difference between the fall lifted treatments, and (3) a narrower difference between the fall and spring lifted treatments when grouped together (Figures 1.1b and 1.2b). Moreover, the water stressed seedlings approached a narrower range in first light g_s (0.041 $cm \cdot sec^{-1}$) and E_t (0.021 $mg \cdot cm^{-2} \cdot sec^{-1}$) than the well-watered seedlings on the last measurement day. First light g_s and E_t differed between water stressed treatments by a maximum of 0.179 $cm \cdot sec^{-1}$ on Day 4 and 0.068 $mg \cdot cm^{-2} \cdot sec^{-1}$ on Days 6 to 7, respectively. All treatments showed an increased first light g_s similar to that observed for the well-watered treatments on Day 4. SL-1-P1 seedlings had the lowest first light g_s and E_t rates until about Day 10 after which both spring lifted treatments had similar rates averaging 0.062 $cm \cdot sec^{-1}$ and 0.027 $mg \cdot cm^{-2} \cdot sec^{-1}$, respectively. The fall lifted treatments had the greatest rates until Day 11. At this time, the average soil water content varied between 10 % and 15 % by weight of the total soil water holding capacity (i.e. $\Psi_{soil} < -1.5$ MPa) (Appendix IV, Figure IV.1, Appendix V, Figure V.1a). Thereafter, first light g_s and E_t rates were similar for all treatments. No significant differences occurred between first light g_s and E_t rates for any of the water stressed treatments (Appendix III, Table III.1).

The results for daytime g_s (Figure 1.3) and E_t (Figure 1.4) are generally consistent with those reported for first light g_s and E_t indicating that the previously noted treatment differences and similarities also occurred during relatively stressful atmospheric conditions. The most apparent difference that occurred between sample times under well-watered conditions was the overall increase in daytime rates vs. the overall decrease in first light rates. In some instances there is a clearer difference among daytime than first light values. For example, first light g_s and E_t differed by a maximum of 0.014 $cm \cdot sec^{-1}$ and 0.006 $mg \cdot cm^{-2} \cdot sec^{-1}$, respectively for well-watered spring lifted seedlings between Days 14 and 17 (Figures 1.1a and 1.2a), while daytime g_s and E_t differed by a maximum of 0.064 $cm \cdot sec^{-1}$ and 0.053 $mg \cdot cm^{-2} \cdot sec^{-1}$, respectively (Figures 1.3a and 1.4a). However, the greater daytime differences were not significant at α=0.05 (Appendix III, Table III.1). The daytime rates also suggest that gaseous exchange differed between the water stressed seedlings after Day 10. Specifically, the fall lifted treatments exhibited the greatest rates.

Under well-watered conditions, Δg_s became increasingly positive for the spring lifted treatments (Figure 1.5a) as the experimental period progressed reflecting both decreased first light (Figure 1.1a) and increased daytime rates (Figure 1.3a). In contrast, Δg_s was generally negative for the fall lifted seedlings until Day 13 and there was no clear trend of increasing values until after this time. By Day 19, Δg_s was similar for all treatments and averaged about 0.176 $cm \cdot sec^{-1}$. ΔE_t was positive for all well-watered treatments over the entire experimental period and the greatest differences were generally recorded for the

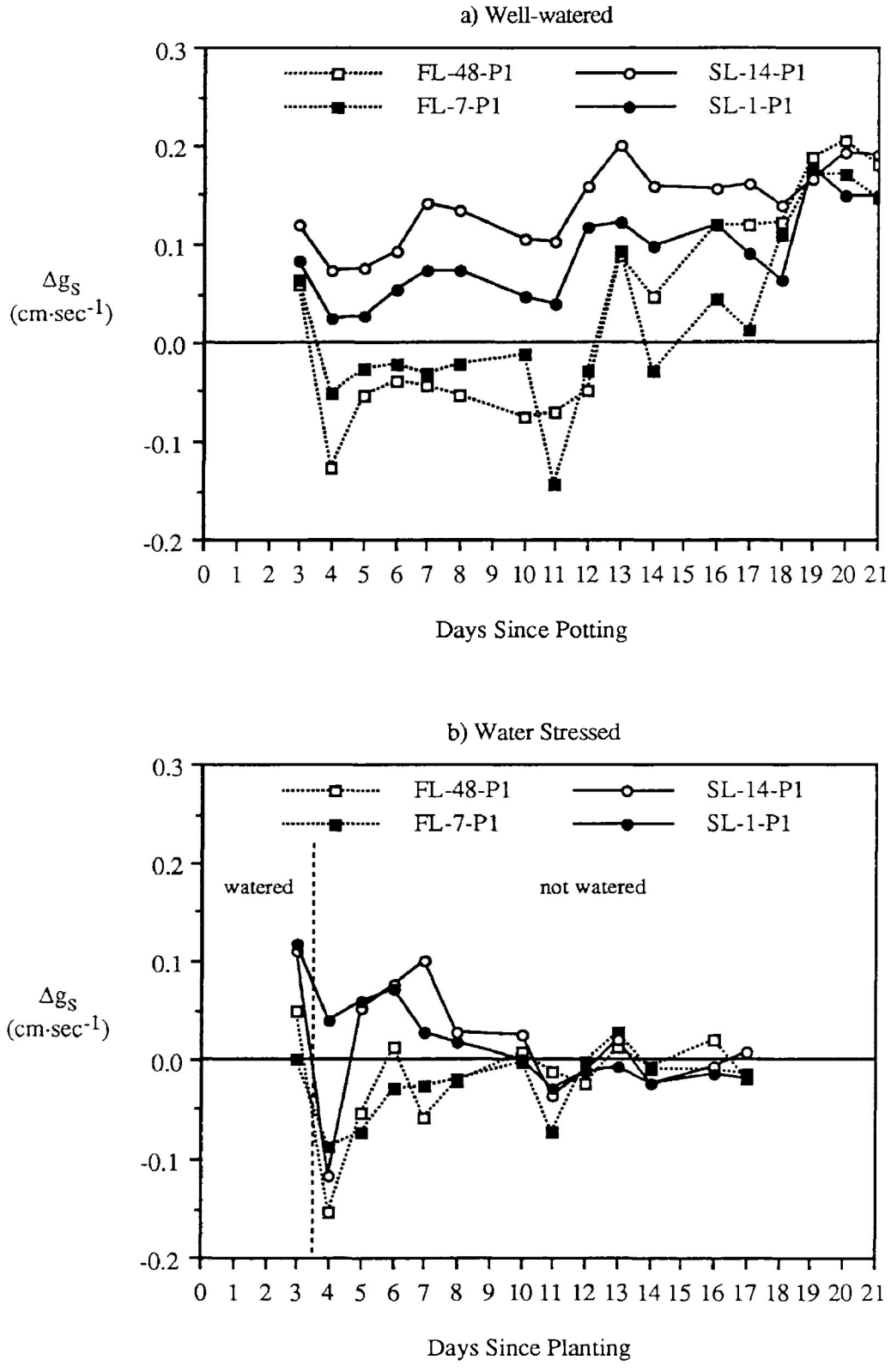

Figure 1.5. The difference between first light and daytime stomatal conductance (Δg_S) for the lifting-storage treatments monitored during Potting Time 1 (May 21): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). A positive value indicates a greater daytime rate. See Table 1.1 for treatment code descriptions and Appendix III, Table III.1 for treatment means, standard errors, sample sizes.

fall lifted seedlings (Figure 1.6a). The increased ΔE_t values over time were largely due to increased daytime rates for all treatments (Figure 1.4a). The ΔE_t values appear to be converging by the end of the experimental period but this is less apparent than for the Δg_s values.

The water stressed spring lifted treatments generally exhibited a positive Δg_s until Day 10 while the fall lifted seedlings generally showed a negative Δg_s over the same period (Figure 1.5b). The smaller differences over time are a consequence of both decreasing first light (Figure 1.1b) and daytime rates (Figure 1.3b). Thereafter, Δg_s fluctuated around zero for all treatments indicating that daytime and first light rates were similar. ΔE_t was initially greater for the spring lifted treatments, particularly SL-14-P1 (Figure 1.6b). However, the fall lifted treatments had slightly larger differences than treatment SL-14-P1 and clearly larger differences than treatment SL-1-P1 between Days 8 and 11 inclusive. Thereafter, ΔE_t was approximately stable for all treatments; SL-1-P1 showed the smallest differences of about 0.030 mg·cm^{-2}·sec^{-1} while the other treatments were similar averaging 0.058 mg·cm^{-2}·sec^{-1}.

When measurements were discontinued for the water stresses treatments on Day 17, Ψ_{xylem} was less than -4.0 MPa for all seedlings and all seedlings were in very poor physical condition (becoming defoliated and turning brown). Soil water depletion curves indicated that all pots dried at approximately the same rate (Appendix V, Figure V.1a) over the entire experimental period. Approximately 50 % of the soil water present at saturation had been lost by Day 7 (i.e.Ψ_{soil} > -0.03 MPa) (Appendix IV, Figure IV.1, Appendix V, Figure V.1a).

Shoot-Tissue Water Relations

The selected shoot-tissue water relations parameters were less similar for the fall lifted than the spring lifted seedlings prior to potting (Table 1.3). FL-7-P1 seedlings had the lowest (most negative) $\Psi_{\pi(sat)}$ of -1.71 MPa and $\Psi_{\pi(TLP)}$ of -2.28 MPa. FL-48-P1 seedlings had the highest (least negative) $\Psi_{\pi(sat)}$ of -1.49 MPa and $\Psi_{\pi(TLP)}$ of -1.96 MPa. The spring lifted treatments had nearly identical $\Psi_{\pi(sat)}$ averaging -1.61 MPa and very similar $\Psi_{\pi(TLP)}$ averaging -2.24 MPa, the latter differing by only 0.05 MPa. The $RWC_{(TLP)}$ was highest for treatment FL-7-P1 at 88.1 % and lowest for treatment SL-1-P1 at 85.0 %. The osmotic potentials differed by a maximum of 0.66 MPa for the SL-14-P1 seedlings.

Thirteen days after potting, the water stressed seedlings had visibly lost turgor (i.e. the current shoots were drooping) and the experiment was terminated. At this time, the soil water content averaged between 3 % and 8 % by weight (i.e. Ψ_{soil} < -1.5 MPa) (Appendix IV, Figure IV.1, Appendix V, Figure V.1a). Post-potting osmotic potentials and $RWC_{(TLP)}$ were commonly greater, and $\Delta\Psi_\pi$ commonly lower for the well-watered seedlings. $\Psi_{\pi(sat)}$ was highest, and nearly identical for the well-water fall lifted treatments. However, this equality was not reflected by any of the other measured

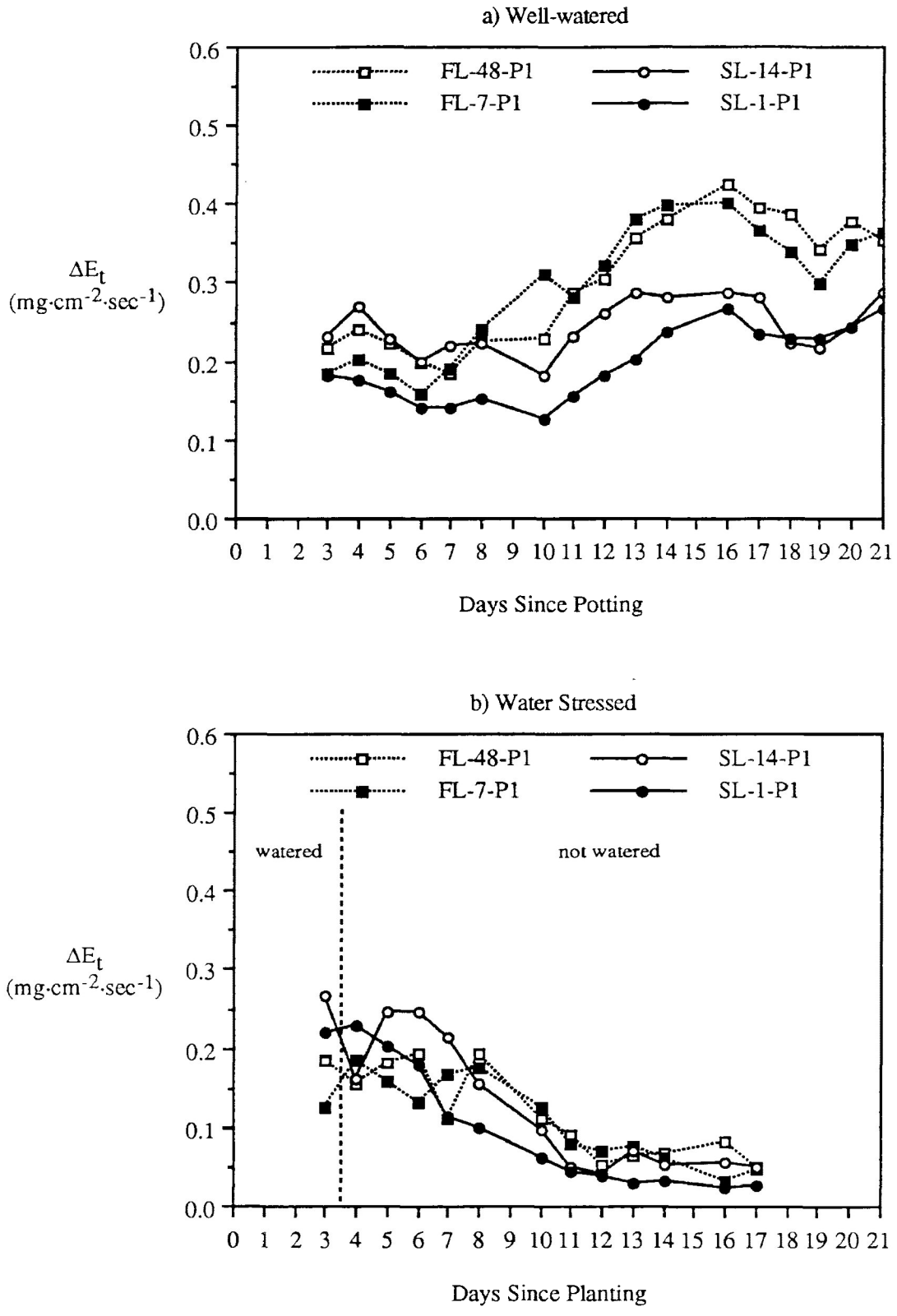

Figure 1.6. The difference between first light and daytime transpiration (ΔE_t) for the lifting-storage treatments monitored during Potting Time 1 (May 21): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). See Table 1.1 for treatment code descriptions and Appendix III, Table III.1 for treatment means, standard errors, sample sizes.

Table 1.3. Comparison of pre- and post-potting shoot-tissue water potential components ($\bar{x}$ ± S.E., n = 2 seedlings) for $1^1/_2 + 1^1/_2$ black spruce transplants evaluated during Potting Time 1 (May 21). Half the potted seedlings were watered to the drip point every second day (well-watered = WW). The other half were watered in the same way for 3 days and then allowed to dry (water stressed = WS). Means within a column and sample time without a common letter are significantly different ($\alpha = 0.05$).

Treatment Code[1]	Osmotic Potential - saturated (MPa) -	Osmotic Potential - turgor loss point (MPa) -	Osmotic Potential - Difference (MPa) -	Relative Water Content - turgor loss point (%) -
stored				
FL-48-P1	-1.49 ± 0.02	-1.96 ± 0.11	0.47 ± 0.08	86.1 ± 2.6
FL-7-P1	-1.71 ± 0.04	-2.28 ± 0.01	0.57 ± 0.03	88.1 ± 1.0
SL-14-P1	-1.60 ± 0.14	-2.26 ± 0.11	0.66 ± 0.03	86.2 ± 0.0
SL-1-P1	-1.62 ± 0.01	-2.21 ± 0.01	0.59 ± 0.00	85.0 ± 2.6
potted				
FL-48-P1-WW	-1.14 ± 0.01	-1.46 ± 0.01a	0.32 ± 0.02	85.6 ± 0.5
FL-7-P1-WW	-1.13 ± 0.06	-1.66 ± 0.01ab	0.53 ± 0.07	89.5 ± 1.3
SL-14-P1-WW	-1.27 ± 0.06	-1.57 ± 0.09a	0.30 ± 0.03	86.9 ± 1.4
SL-1-P1-WW	-1.51 ± 0.03	-1.88 ± 0.03abc	0.37 ± 0.00	85.9 ± 1.9
FL-48-P1-WS	-1.51 ± 0.16	-2.11 ± 0.02c	0.60 ± 0.17	87.5 ± 0.8
FL-7-P1-WS	-1.68 ± 0.07	-2.44 ± 0.18d	0.76 ± 0.11	84.0 ± 1.7
SL-14-P1-WS	-1.21 ± 0.28	-1.76 ± 0.13abc	0.55 ± 0.15	85.9 ± 0.9
SL-1-P1-WS	-1.68 ± 0.01	-2.03 ± 0.01bc	0.35 ± 0.01	84.6 ± 0.8

[1] See Table 1.1 for treatment code descriptions.

parameters. Well-watered SL-1-P1 seedlings had considerably lower osmotic potentials than the well-watered SL-14-P1 seedlings. The greatest $\Delta\Psi_\pi$ was recorded for FL-7-P1 seedlings under both soil water conditions. The water stressed fall lifted seedlings had the lowest $\Psi_{\pi(TLP)}$. This value was significantly lower at -2.44 MPa for treatment FL-7-P1 and represents the only recorded instance of a singularly different (α=0.05) treatment. Water stressed FL-7-P1 and SL-1-P1 seedlings had the lowest $\Psi_{\pi(sat)}$ which were equivalent at -1.68 MPa and similar a $RWC_{(TLP)}$.

Root Growth Capacity Response

Classification of RGC suggested that root activity was strongly influenced by lifting-storage treatment (Figure 1.7a). The treatments are ranked in descending order by their mean modified Burdett code in Table 1.4. FL-48-P1 had the best new root growth at the end of the 14 day RGC test period. Treatment SL-14-P1 was the only treatment that did exceptionally poorly, eight of the 25 potted seedlings produced no new white roots. Three of these seedlings died during the experimental period. All other seedlings produced at least some new white root tips.

POTTING TIME 2 (JUNE 24)

Water Relations Response

Stomatal Conductance and Transpiration

Gaseous exchange patterns indicate that the fall lifted treatments (FL-48-P2, FL-7-P2) and the spring lifted treatments (SL-48-P2, SL-1-P2) formed two distinct groups regardless of soil water condition but their association is not as distinct as in Potting Time 1. Response patterns are very similar for g_s and E_t (first light and daytime) regardless of soil water condition although isolated differences occurred; an increase or decrease in g_s is generally associated with a similar increase or decrease in E_t (Figures 1.8 to 1.11). Day to day fluctuations in gaseous exchange were particularly apparent for the well-watered seedlings. The general trend under both soil water regimes was for all lifting-storage treatments to approach similar first light and daytime g_s and E_t rates towards the end of the study.

Under well-watered conditions, first light g_s ranged by a maximum of 0.406 $cm \cdot sec^{-1}$ on Day 9 and a minimum of about 0.038 $cm \cdot sec^{-1}$ between Days 19 and 21 inclusive (Figure 1.8a). First light E_t ranged by a maximum of about 0.184 $mg \cdot cm^{-2} \cdot sec^{-1}$ on Days 9 and 11 and a minimum of about 0.025 $mg \cdot cm^{-2} \cdot sec^{-1}$ between Days 19 to 21 inclusive (Figure 1.9a). All treatments exhibited the greatest first light g_s and E_t rates immediately following potting at which time g_s (averaged from Figures 1.8a and b) was greatest for treatment FL-48-P2 (0.966 $cm \cdot sec^{-1}$) and E_t (averaged from Figures 1.9a and b) was greatest for treatment SL-48-P2 (0.407 $mg \cdot cm^{-2} \cdot sec^{-1}$). First light g_s and E_t rates declined substantially

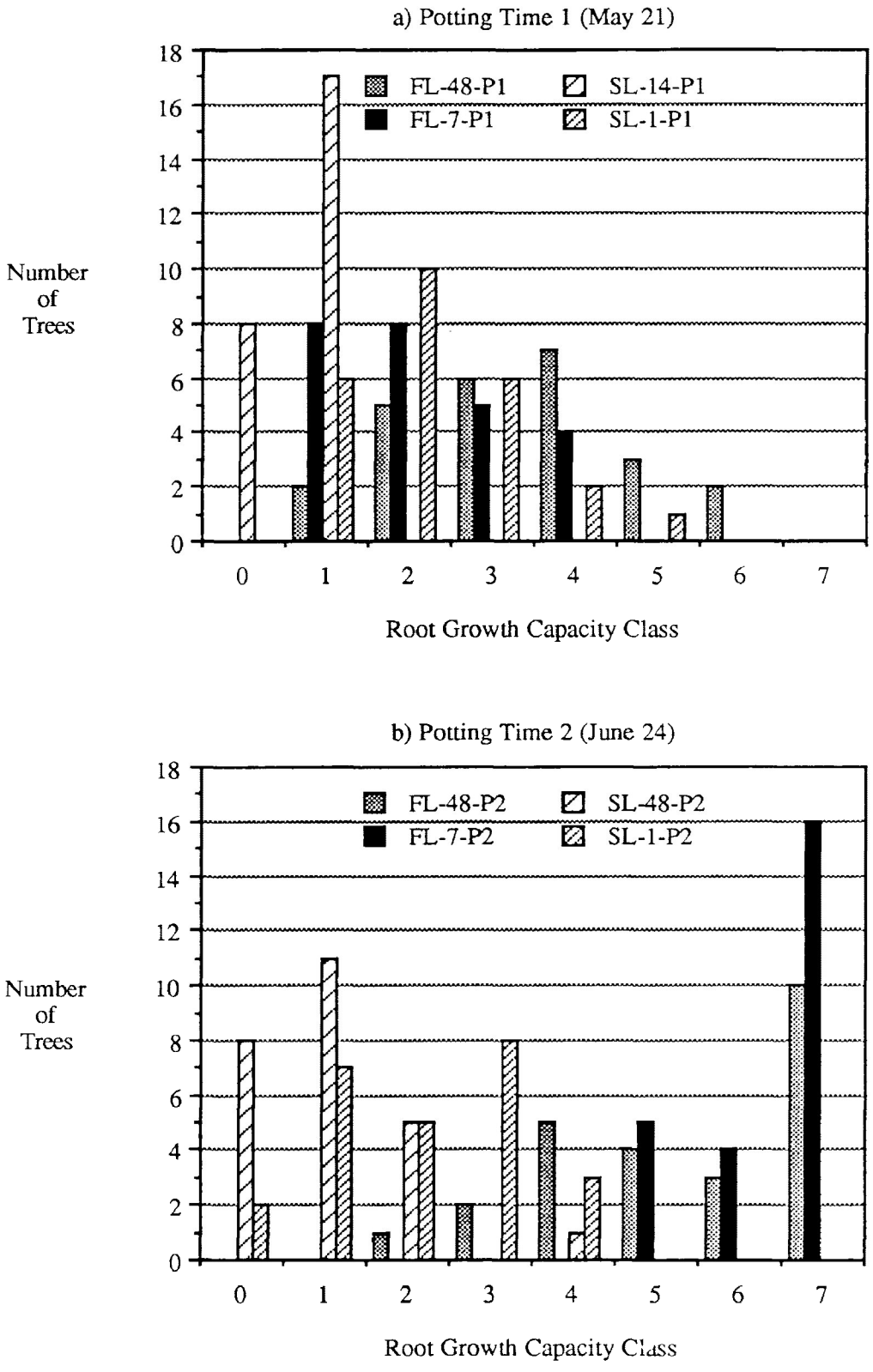

Figure 1.7. The frequency of occurrence by the Burdett (1979) root growth capacity classes modified to include two additional classes (Appendix II) for: a) Potting Time 1 (May 21), and b) Potting Time 2 (June 24). A larger class value indicates increased root growth. See Table 1.1 for treatment code descriptions.

Table 1.4. The lifting-storage treatments ranked in descending order of average root growth capacity response determined using the Burdett (1979) classification code modified to include two additional classes (Appendix II).

Treatment Code[1]	Treatment Description	Modified Burdett Code
Potting Time 1 (May 21)		
FL-48-P1	Fall lifted, overwinter frozen stored, conditioned at +2 ± 1°C for 48 days	3.40
SL-1-P1	Spring lifted, stored at +2 ± 1°C for 1 day	2.28
FL-7-P1	Fall lifted, overwinter frozen stored, conditioned at +2 ± 1°C for 7 days	2.20
SL-14-P1	Spring lifted, stored at +2 ± 1°C for 14 days	0.68
Potting Time 2 (June 24)		
FL-7-P2	Fall lifted, overwinter frozen stored, conditioned at +2 ± 1°C for 7 days	6.44
FL-48-P2	Fall lifted, overwinter frozen stored, conditioned at +2 ±1°C for 48 days	5.44
SL-1-P2	Spring lifted, stored at +2 ± 1°C for 1 day	2.12
SL-48-P2	Spring lifted, stored at +2 ± 1°C for 48 days	1.00

[1] See Table 1.1 for treatment code descriptions, lifting and potting dates, and temperatures and durations of storage.

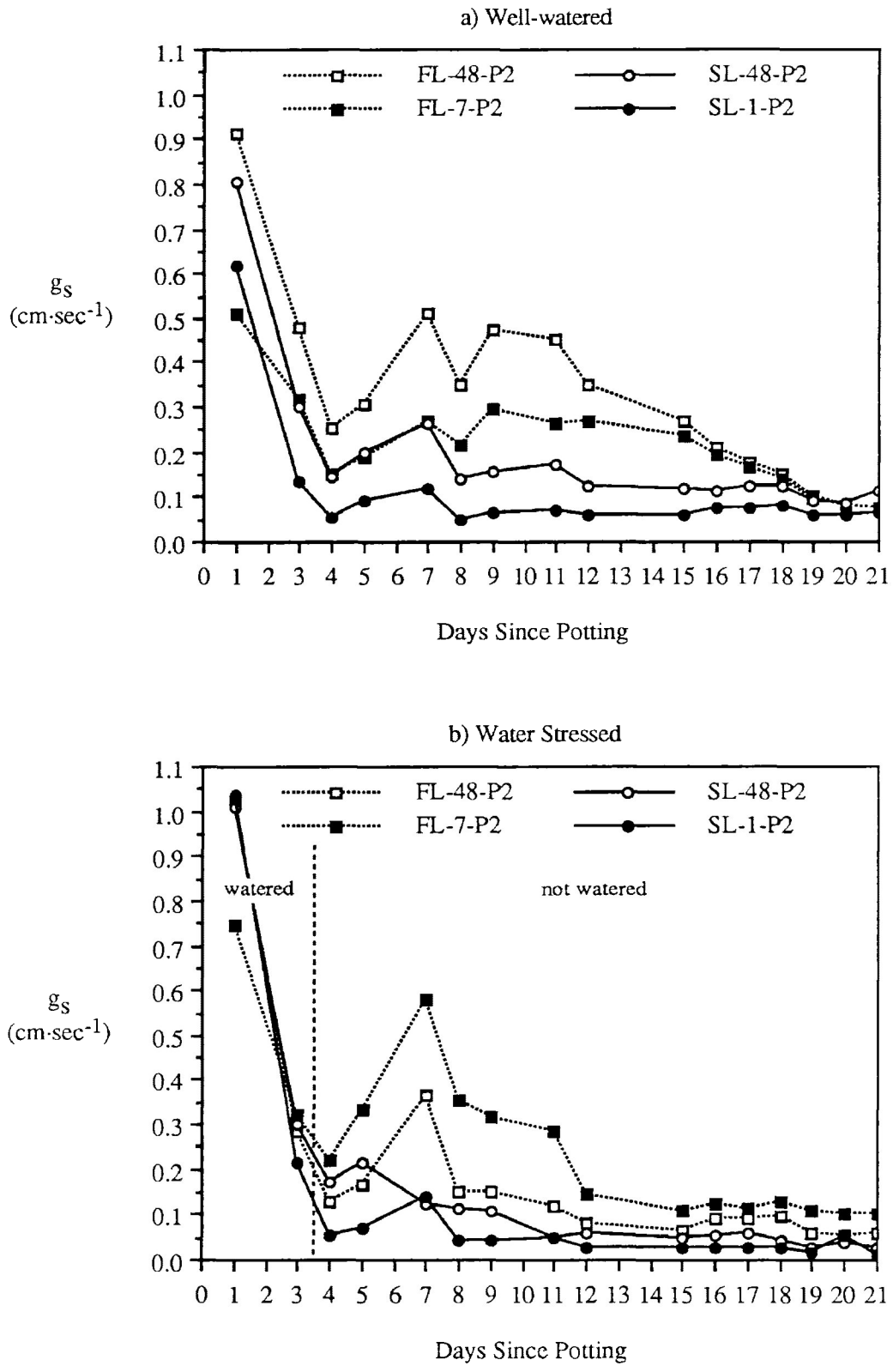

Figure 1.8. First light stomatal conductance (g_s) for the lifting-storage treatments monitored during Potting Time 2 (June 24): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). See Table 1.1 for treatment code descriptions and Appendix III, Table III.2 for treatment means, standard errors, sample sizes, and SNK multiple range test results.

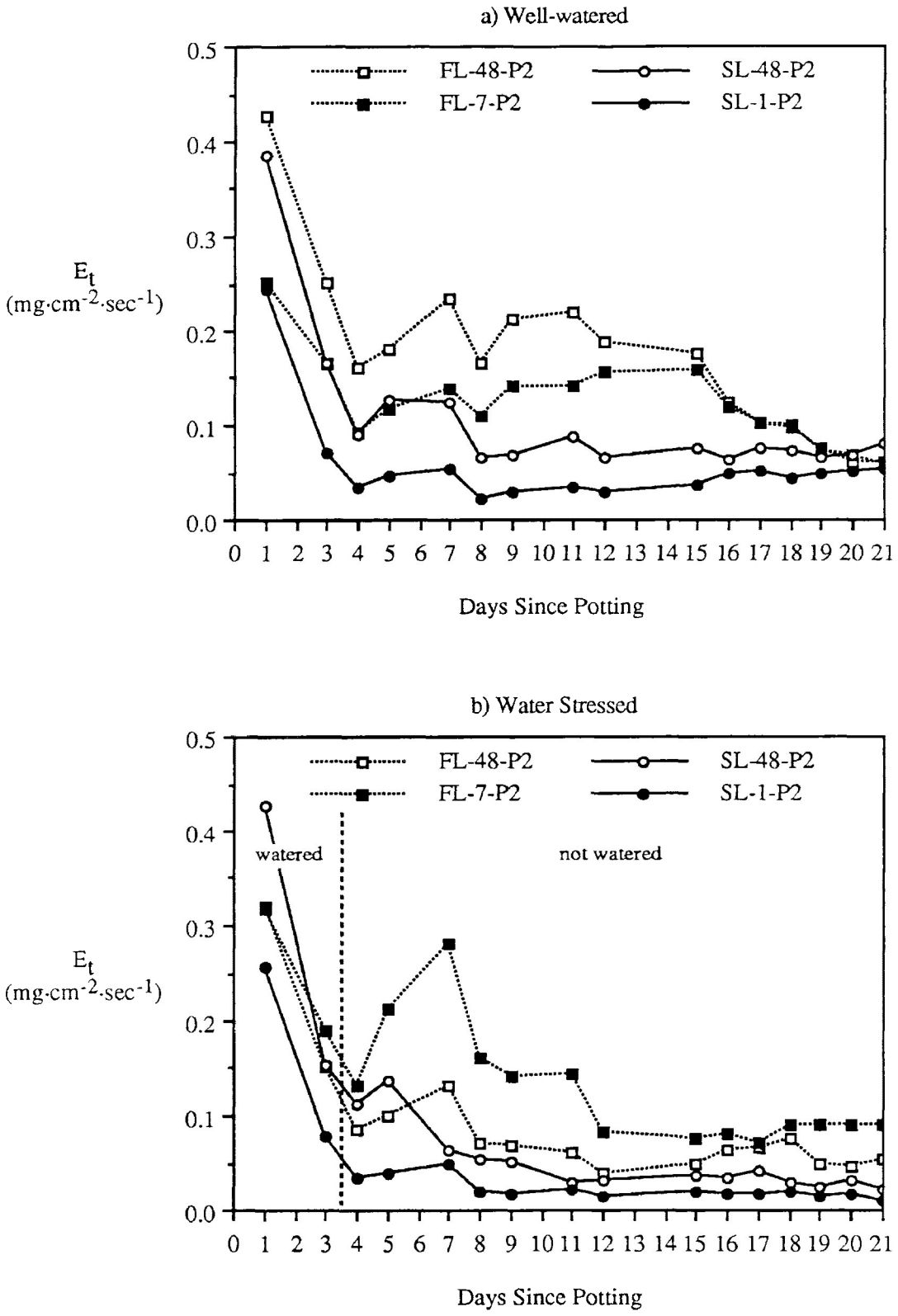

Figure 1.9. First light transpiration (E_t) for the lifting-storage treatments monitored during Potting Time 2 (June 24): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). See Table 1.1 for treatment code descriptions and Appendix III, Table III.2 for treatment means, standard errors, sample sizes, and SNK multiple range test results.

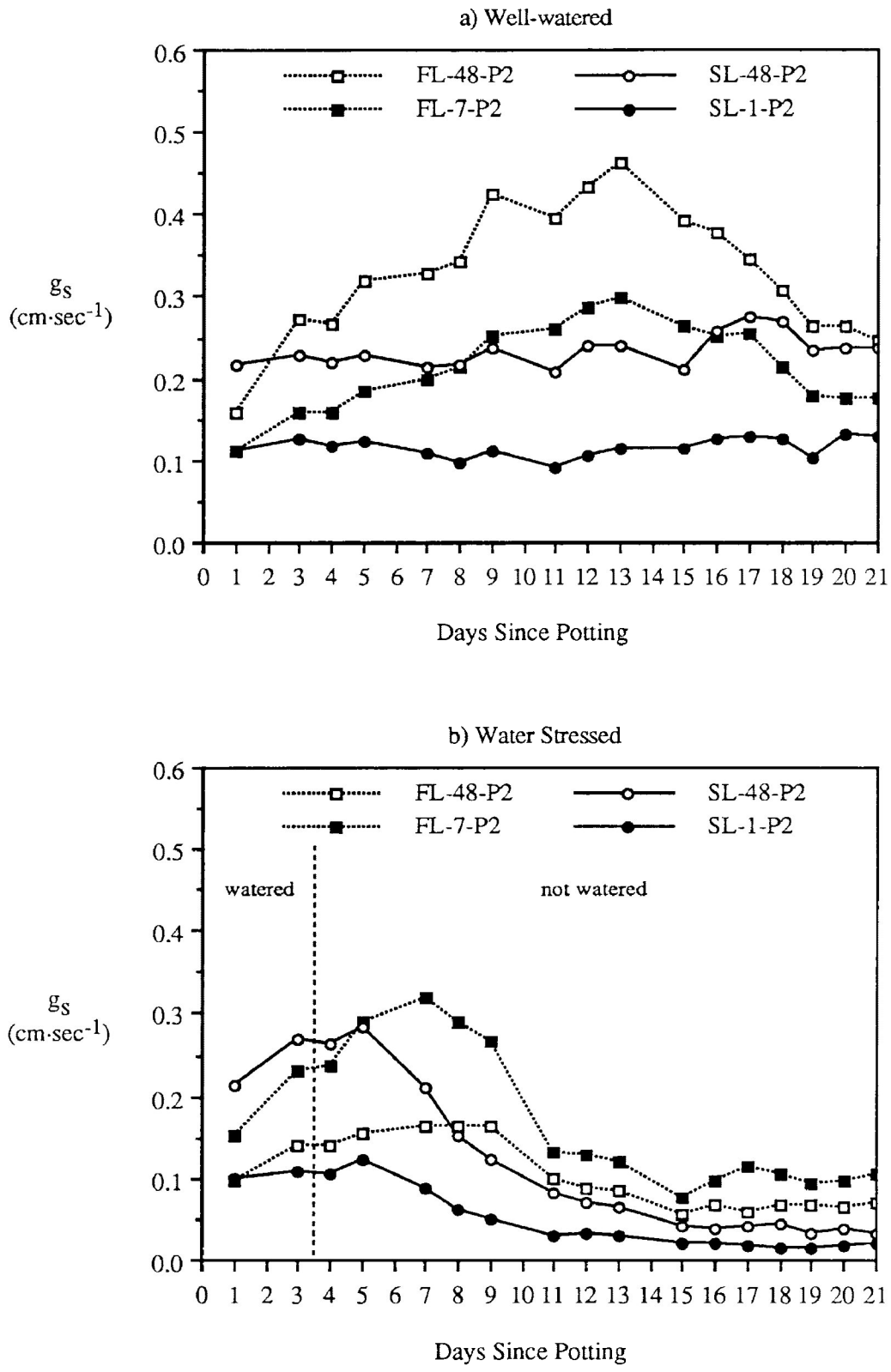

Figure 1.10. Daytime stomatal conductance (g_S) for the lifting-storage treatments monitored during Potting Time 2 (June 24): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). See Table 1.1 for treatment code descriptions and Appendix III, Table III.2 for treatment means, standard errors, sample sizes, and SNK multiple range test results.

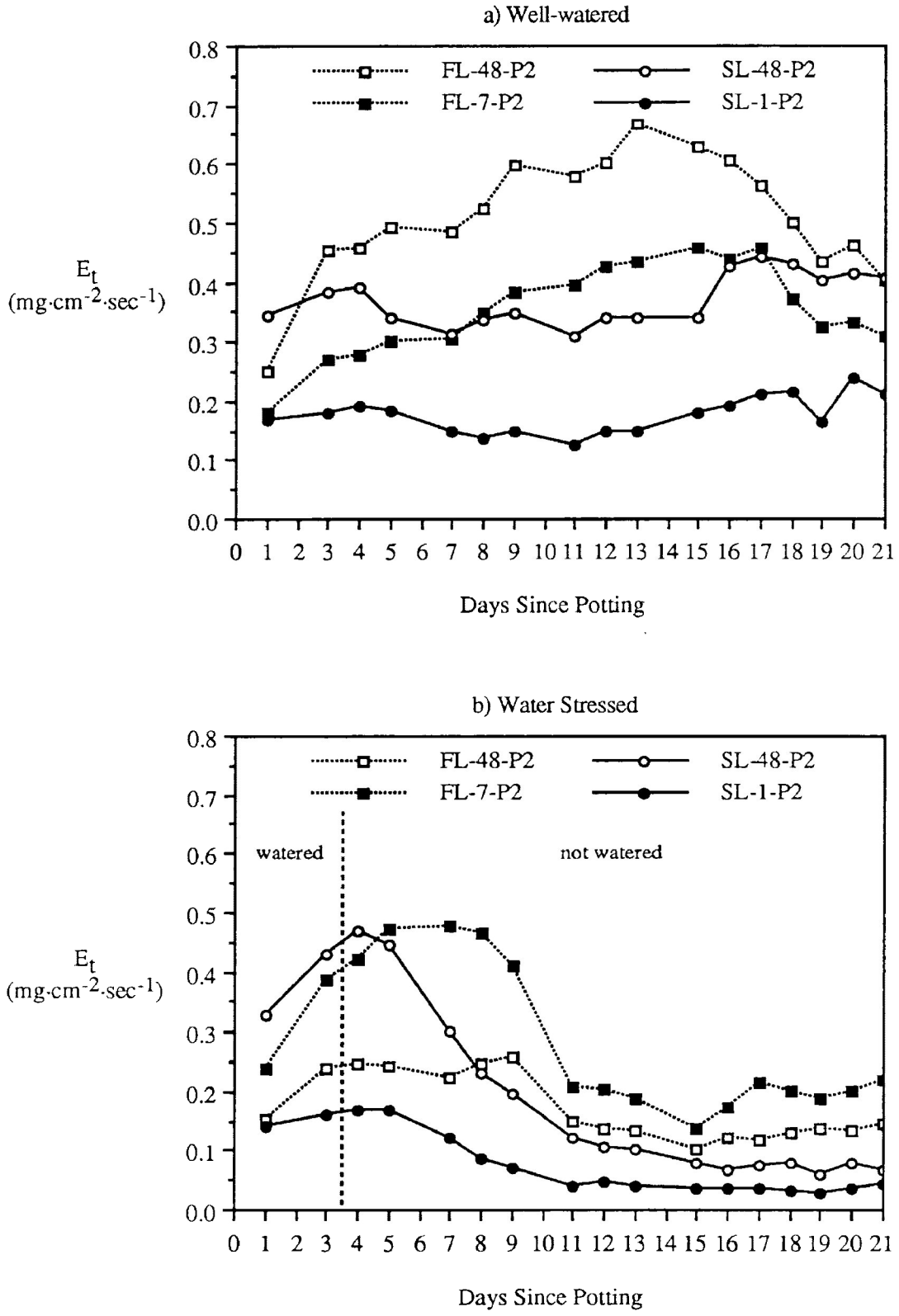

Figure 1.11. Daytime transpiration (E_t) for the lifting-storage treatments monitored during Potting Time 2 (June 24): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). See Table 1.1 for treatment code descriptions and Appendix III, Table III.2 for treatment means, standard errors, sample sizes, and SNK multiple range test results.

for all treatments by Day 4 and then increased the following day. These increases were comparatively transient for the spring lifted seedlings. Thereafter, the fall lifted treatments had the greatest rates until Day 20 when differences between all treatments were minimal. The fall lifted treatments had significantly greater rates of first light g_s on Days 12 to 16 inclusive, and first light E_t on Days 12 and 15. FL-48-P2 seedlings had greater rates of first light g_s and E_t than FL-7-P2 seedlings until Day 16 (this difference was significant on Day 9) after which gaseous exchange was similar for both treatments. SL-1-P2 seedlings had lower first light rates than SL-48-P2 seedlings over the entire study.

In comparison with the well-watered seedlings, first light g_s and E_t rates recorded for the water stressed seedlings generally exhibited: (1) a narrower difference between the spring lifted treatments, (2) a greater difference between the fall lifted treatments, and (3) a narrower difference between the fall and spring lifted treatments when grouped together. In contrast with Potting Time 1, the water stressed treatments demonstrated a greater difference in first light g_s (0.091 $cm \cdot sec^{-1}$) and E_t (0.081 $mg \cdot cm^{-2} \cdot sec^{-1}$) than the well-watered treatments on the last measurement day (Figures 1.8 and 1.9). Under conditions of declining Ψ_{soil}, first light g_s and E_t differed between treatments by a maximum of 0.453 $cm \cdot sec^{-1}$ and 0.231 $mg \cdot cm^{-2} \cdot sec^{-1}$, respectively on Day 7. All seedlings showed increased first light g_s and E_t rates similar to those observed for the well-watered seedlings on Day 4. First light rates declined for all treatments after Day 7. At this time, approximately 65 % of the soil water had been lost (i.e.$\Psi_{soil} > -0.05$ MPa) (Appendix IV, Figure IV.1, Appendix V, Figure V.1b). FL-7-P2 seedlings had the greatest first light g_s and E_t rates throughout the study and significantly greater rates than any other water stressed treatment on Days 8 and 9. SL-1-P2 seedlings had the lowest rates over the entire study. Minimum first light g_s and E_t rates averaging about 0.056 $cm \cdot sec^{-1}$ and 0.028 $mg \cdot cm^{-2} \cdot sec^{-1}$, respectively were reached for the spring lifted and FL-48-P2 seedlings about 9 days after water was withheld (Day 12). At this time, soil water content averaged about 12 % of total water holding capacity (i.e.$\Psi_{soil} < -1.5$ MPa). First light g_s and E_t rates decreased slightly for the FL-7-P2 seedlings after this time.

The results for daytime g_s (Figure 1.10) and E_t (Figure 1.11) are generally consistent with those reported for first light g_s and E_t indicating that the previously noted treatment differences and similarities also occurred during relatively stressful atmospheric conditions. The most apparent difference occurred between sample times for the well-watered seedlings; daytime vs. first light rates were greater at the end than the beginning of the experimental period. In some instances there is a clearer difference between daytime than first light rates. For example, first light g_s and E_t rates were very similar for the well-watered fall lifted seedlings between Days 15 and 21 inclusive, while daytime rates were clearly greater for treatment FL-48-P2. Furthermore, this difference was significant on Days 15 and 16. Daytime gaseous exchange rates also differed more widely between the well-watered spring lifted treatments and indicated significantly greater rates for SL-48-P2 seedlings between Days 12 and 20 inclusive. Lastly, daytime

rates showed different treatment hierarchies than first light rates, particularly between well-watered treatments FL-7-P2 and SL-48-P2 at the beginning and end of the experimental period.

Under well-watered conditions, negative Δg_s values were recorded for all treatments on Days 1 and 3 (Figure 1.12a and b). Δg_s was approximately equal for the spring lifted treatments on Day 4 when it averaged 0.069 $cm \cdot sec^{-1}$ and generally positive values were recorded thereafter. This response was largely due to the rapid decline in first light rates (Figure 1.8a) since daytime rates (Figure 1.10a) were relatively stable for both treatments over the entire experimental period. In contrast, Δg_s was generally negative for the fall lifted seedlings until Day 12, and positive thereafter as first light rates decreased to a greater degree than daytime rates. All treatments approached a common Δg_s value of about 0.116 $cm \cdot sec^{-1}$ by the end of the experimental period. ΔE_t was negative for all treatments on the first measurement day and positive thereafter; ΔE_t was generally greatest for FL-48-P2, least for SL-1-P2, and intermediate for FL-7-P2 and SL-48-P2 seedlings (Figure 1.13a). The ΔE_t values appear to be converging by the end of the experimental period but this was less apparent than for the Δg_s values.

The water stressed spring lifted treatments generally exhibited positive Δg_s values between Days 4 and 11 inclusive, while the fall lifted treatments generally showed a negative Δg_s over the same period (Figure 1.12b). The smaller differences over time are a consequence of both decreasing first light (Figure 1.8b) and daytime rates (Figure 1.10b). Thereafter, Δg_s was ordinarily slightly negative for all treatments. ΔE_t was greatest for treatment SL-48-P2 the first four days after water was withheld (Days 4 to 7 inclusive) (Figure 1.13b). Thereafter, the greatest ΔE_t values were commonly recorded for the fall lifted treatments, particularly FL-7-P2. The lowest ΔE_t values consistently occurred for the freshly lifted seedlings. ΔE_t was fairly stable for all treatments between Days 11 and 21 inclusive, over which treatment FL-7-P1 averaged the the greatest values (0.105 $mg \cdot cm^{-2} \cdot sec^{-1}$) and treatment SL-1-P2 averaged the lowest (0.017 $mg \cdot cm^{-2} \cdot sec^{-1}$).

When the experiment was terminated on Day 21, Ψ_{xylem} was less than -4.0 MPa for all water stressed seedlings and all water stressed seedlings were in very poor physical condition (defoliating and turning brown). In particular, current foliage was necrotic and desiccated. Soil water depletion curves indicated that all pots dried at approximately the same rate (Appendix V, Figure V.1b) over the entire experimental period. Between 50% and 60 % of the soil water had been lost by Day 7 (i.e. $\Psi_{soil} > -0.04$ MPa) (Appendix IV, Figure IV.1, Appendix V, Figure V.1b).

Shoot-Tissue Water Relations

Pre-potting osmotic potentials were higher (less negative) for all treatments prior Potting Time 2 (Table 1.5) than Potting Time 1 (Table 1.3). The lowest (most negative) potentials and the greatest $\Delta\Psi_\pi$ occurred for treatment FL-7-P2. The $\Psi_{\pi(TLP)}$ was significantly lower (-2.27 MPa), and the $\Delta\Psi_\pi$

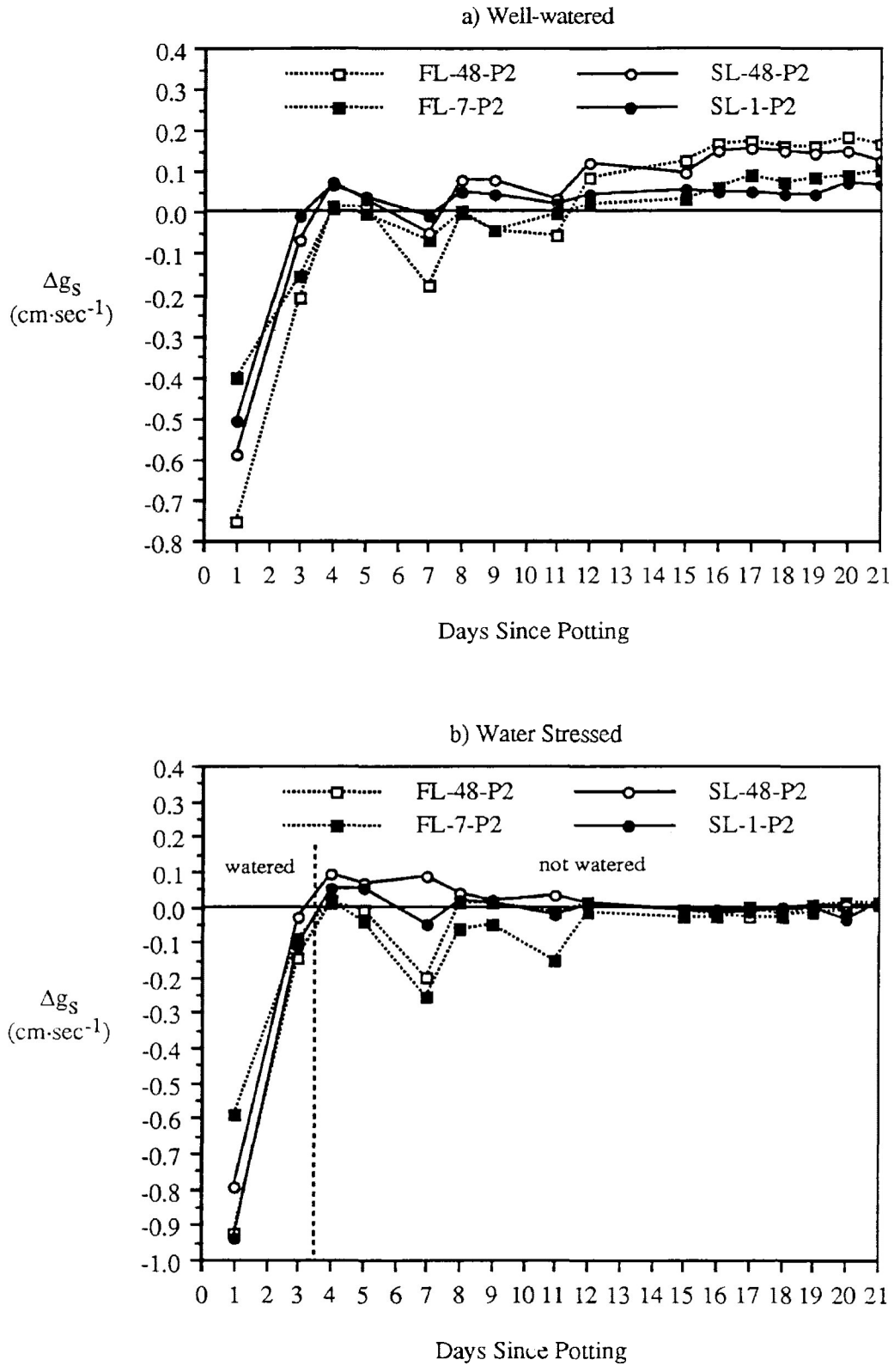

Figure 1.12. The difference between first light and daytime stomatal conductance (Δg_S) for the lifting-storage treatments monitored during Potting Time 2 (June 24): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). A positive value indicates a greater daytime rate. See Table 1.1 for treatment code descriptions and Appendix III, Table III.2 for treatment means, standard errors, sample sizes.

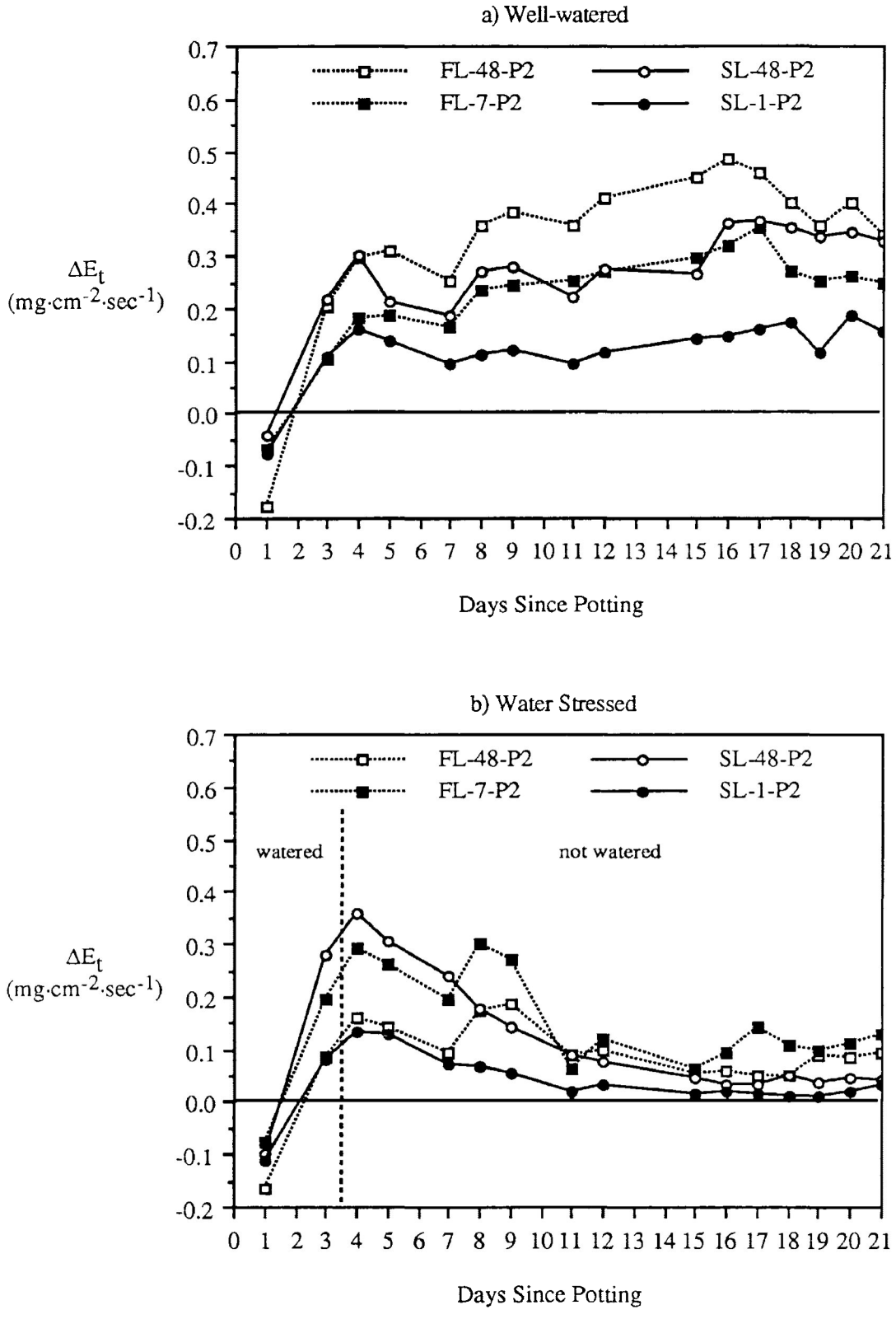

Figure 1.13. The difference between first light and daytime transpiration (ΔE_t) for the lifting-storage treatments monitored during the Potting Time 2 (June 24): a) well-watered seedlings (every second day), and b) water stressed seedlings (soil drying). A positive value indicates a greater daytime rate. See Table 1.1 for treatment code descriptions and Appendix III, Table III.2 for treatment means, standard errors, sample sizes.

Table 1.5. Comparison of pre- and post-potting shoot-tissue water potential components ($\bar{x} \pm$ S.E., n = 2 seedlings) for $1^1/_2 + 1^1/_2$ black spruce transplants evaluated during Potting Time 2 (June 24). Half the potted seedlings were watered to the drip point every second day (well-watered = WW). The other half were watered in the same way for 3 days and then allowed to dry (water stressed = WS). Means within a column and sample time without a common letter are significantly different ($\alpha = 0.05$).

Treatment Code[1]	Osmotic Potential - saturated (MPa) -	Osmotic Potential - turgor loss point (MPa) -	Osmotic Potential - Difference (MPa) -	Relative Water Content - turgor loss point (%) -
stored				
FL-48-P2	-1.44 ± 0.06b	-1.90 ± 0.04b	0.46 ± 0.03b	86.9 ± 0.0
FL-7-P2	-1.65 ± 0.01b	-2.27 ± 0.01c	0.62 ± 0.01c	85.7 ± 0.4
SL-48-P2	-1.44 ± 0.06b	-1.92 ± 0.10b	0.48 ± 0.04b	86.1 ± 0.6
SL-1-P2	-1.15 ± 0.00a	-1.41 ± 0.05a	0.26 ± 0.02a	85.0 ± 0.2
potted				
FL-48-P2-WW	-1.39 ± 0.07	-1.90 ± 0.12	0.51 ± 0.05b	86.7 ± 0.0
FL-7-P2-WW	-1.33 ± 0.04	-1.86 ± 0.10	0.53 ± 0.06b	87.4 ± 1.6
SL-48-P2-WW	-1.37 ± 0.01	-1.76 ± 0.11	0.39 ± 0.10b	86.7 ± 0.7
SL-1-P2-WW	-1.38 ± 0.09	-1.87 ± 0.11	0.49 ± 0.02b	85.3 ± 0.9
FL-48-P2-WS	-1.38 ± 0.02	-1.90 ± 0.11	0.52 ± 0.10b	87.8 ± 0.1
FL-7-P2-WS	-1.23 ± 0.09	-2.05 ± 0.11	0.83 ± 0.02a	85.5 ± 0.2
SL-48-P2-WS	-1.52 ± 0.01	-1.91 ± 0.03	0.39 ± 0.02b	87.3 ± 0.0
SL-1-P2-WS	-1.58 ± 0.11	-2.08 ± 0.12	0.50 ± 0.02b	84.3 ± 2.0

[1] See Table 1.1 for treatment code descriptions.

significantly larger (0.62 MPa) than for any other treatment. Significantly higher osmotic potentials, a significantly smaller $\Delta\Psi_\pi$, and a lower $RWC_{(TLP)}$ were recorded for treatment SL-1-P1. There were no apparent similarities between the fall or spring lifted treatments for any of the selected shoot-tissue water relations parameters. The greatest similarity between lifting seasons occurred for treatments FL-48-P2 and SL-48-P2. Both treatments had a statistically similar $\Psi_{\pi(sat)}$, $\Psi_{\pi(TLP)}$, and $\Delta\Psi_\pi$.

Thirteen days after potting, the water stressed seedlings had visually lost turgor (i.e. the current shoots were drooping) and the experiment was terminated. At this time, the soil water content averaged between 8 % and 14 % by weight (i.e. $\Psi_{soil} < -1.5$ MPa) (Appendix IV, Figure IV.1, Appendix V, Figure V.1b). Osmotic potentials had decreased substantially since potting for the freshly lifted seedlings and generally increased for the fall and spring lifted, stored seedlings under both watering regimes. Under well-watered conditions, treatment FL-48-P2 had the lowest osmotic potentials, treatment FL-7-P2 had the largest $\Delta\Psi_\pi$, and treatment SL-1-P2 had the lowest $RWC_{(TLP)}$. Treatment FL-7-P2 had the highest $\Psi_{\pi(sat)}$ and $RWC_{(TLP)}$ and treatment SL-48-P2 had the highest $\Psi_{\pi(TLP)}$ and the smallest $\Delta\Psi_\pi$. There were no consistent trends of decreased or increased post-potting shoot-tissue water relation parameters across all water stressed treatments. Under conditions of declining Ψ_{soil}, treatment SL-1-P1 had the lowest osmotic potentials and the lowest $RWC_{(TLP)}$ while treatment FL-7-P2 had a significantly greater $\Delta\Psi_\pi$. Treatment FL-7-P2 had the highest $\Psi_{\pi(sat)}$, treatment FL-48-P2 had the highest $\Psi_{\pi(TLP)}$ and $RWC_{(TLP)}$, and treatment SL-48-P2 had the smallest $\Delta\Psi_\pi$.

Root Growth Capacity Response

RGC indices suggested that root activity was strongly influenced by lifting-storage treatment (Figure 1.7b). The treatments are ranked in descending order by their mean modified Burdett code in Table 1.4. In comparison with Potting Time 1, RGC increased for the fall and spring lifted, stored seedlings and decreased for the freshly lifted seedlings. The fall lifted treatments, particularly FL-7-P2, had the best new root growth at the end of the 14 day RGC test period. SL-48-P2 was the only treatment that did exceptionally poorly with eight of the 25 seedlings potted producing no new white roots. Two SL-1-P2 seedlings also produced no new roots.

DISCUSSION

Reforestation by planting, from the standpoint of the seedling, is an unnatural process during which a juvenile plant with limited carbohydrate and water reserves is transplanted from the luxurious nursery environment to a comparatively harsh outplanting site and expected to grow vigorously. To ensure survival, the outplant must avoid water stress and the accompanying growth disruptions by controlling transpirational losses while accessing additional water by expanding its limited root system. There is a growing realization that consistent reforestation success is contingent on a thorough understanding of the impact of all nursery cultural and handling techniques on seedling physiology (Duryea and Brown 1984, Duryea and Landis 1984, Duryea 1985). Furthermore, an increased understanding of the effects of current nursery practices on early seedling physiology will lead to improved reforestation programs and ultimately increase future forest yields. Fall lifting and overwinter frozen storage have gained widespread usage but their effects on early seedling physiology have not been extensively researched. The following discussion addresses the hypothesis that the date of lifting and the temperature and duration of storage affects seedling physiology and thereby influences the physiological response during early establishment. Response variables examined include gaseous exchange of water vapour, selected components of shoot-tissue water potential known to influence drought tolerance, and RGC.

POTTING TIME 1 (MAY 21)

Water Relations Response

Stomatal Conductance and Transpiration

The distinct differences in g_s and E_t response that occurred between the lifting-storage treatments regardless of soil water condition (Figures 1.1 to 1.4) clearly show that nursery lifting and storage practices influence seedling water relations during early establishment. Unfortunately, sample sizes were often insufficient and variation among replicates frequently prevented the assumption of significance at α=0.05 (Appendix III, Table III.1). This discussion will therefore be primarily concerned with differences, similarities, and trends apparent through a visual inspection of treatment means (Appendix III, Table III.1) and the provided figures. Obtaining a sufficiently large sample to reduce the within treatment variability is a common problem in plant water relations research because the time interval over which comparable measurements can be taken is frequently limited by atmospheric factors (e.g. amount,

duration, and quality of light, temperature and water vapour deficit) and factors of the plants themselves (e.g. Ψ_{plant} and concentration changes in endogenous growth regulators such as ABA, auxins, and cytokinins) (Mansfield and Davies 1985). Consequently, sample sizes have historically been determined by the number of g_s and E_t measurements it is feasible to make over a predetermined time interval without regard for variation between the measurements (Jarvis 1981).

With one notable exception, the effects of lifting date and temperature and duration of storage on early plant water relations do not appear to have been quantified in the literature. Blake (1983) determined the water relations response within 2 hours of midday for fall lifted, overwinter frozen stored and spring lifted 2+0 white spruce seedlings in a controlled environment chamber under: (1) well-watered conditions over a 48 day period, and (2) simulated drought conditions imposed by the osmoticum polyethylene glycol 4000 over a 6 day period. Blake argued that frozen stored seedlings were better adapted to survive the weeks following planting because of: (1) their greater degree of bud dormancy, (2) the absence of a marked decline in g_s following potting, and (3) their ability to reduce water loss after planting and when soil water became limited without reducing the stomatal aperture, and thus, the photosynthetic capacity when soil water was adequate. Blake measured gaseous exchange rates separately for current and year-old foliage and it is therefore difficult to compare water relations patterns between studies. However, Blake's conclusions are not supported by the results of this thesis.

Additional problems arise when comparing the results of similar studies since early seedling response varies with species, provenance, stock type, age class, size of stock, time of lifting, nursery, cultural regime (especially root culture, irrigation, and fertilization regimes), condition of stock entering storage (especially bud dormancy status), size of bundle or package, etc., rate of cooling, humidity and temperature of storage, plant water status, light conditions during storage, and possibly, the rates of warming of stock leaving storage (Hocking and Nyland 1971, Sutton 1980, Venn 1980, Sutton 1982a, Duryea and McClain 1984, Lavender 1984, Kennedy *et al.* 1987). Furthermore, sampling methods and growing environments varied widely amongst studies. Consequently, directly relevant information on any given combination of species/provenance/stock type/etc. factors is very limited. Moreover, only a few studies have been replicated in time and even these have limited inference because of planting stock, geographic location, and climatic differences (Sutton 1982a,b). Therefore, conclusions have often been based on incomplete data (Sutton 1982a).

Response patterns are very similar for g_s and E_t regardless of soil water condition although isolated differences occurred. This similarity occurred because the driving force for E_t (the absolute humidity difference between the bulk air and the air within the substomatal cavity, which is assumed to be saturated) varied little under the controlled environment conditions. Consequently, the resistance due to the size of the stomatal opening (stomatal resistance, which is inversely proportional to the diameter of the stomatal aperture) largely controlled E_t. The similarities that were apparent between the fall lifted

seedlings and the spring lifted seedlings indicate that treatment effects were greater between the fall and spring lifting seasons than between storage temperatures (for the fall lifted treatments) or lifting dates within a season (for the spring lifted treatments). The SNK mean separation tests (Appendix III, Table III.1) verified this observation for a number of sample times.

The gaseous exchange patterns recorded for the well-watered fall and spring lifted seedlings indicate that inherent response differed between groups. The generally greater g_s and E_t rates exhibited by the fall lifted treatments suggests that these seedlings exercised poor stomatal control over transpirational losses. This is supported by the Δg_s values which indicate that partial stomatal closure occurred by the daytime measurement period during the first twelve days of the study (Figure 1.5a). Partial stomatal closure occurs during high stress periods to conserve internal water reserves and maintain a more favourable internal water balance (Meidner and Mansfield 1968). This response is not normal for healthy, vigorous seedlings growing in a moist environment under moderate atmospheric stress. Rather, g_s would be expected to increase under such conditions as illumination and temperature increased (Woods and Turner 1971, Running 1976, Pereira and Kozlowski 1977, Hinckley *et al.* 1978). This inability to control g_s is not detrimental to field planted seedlings if soil water is adequate and may even favour rapid growth by maximizing carbon dioxide (CO_2) uptake. However, under conditions of soil or atmospheric drought, the fall lifted seedlings would rapidly experience water stress and become poorly established or die. On the other hand, the spring lifted seedlings quickly gained stomatal control after potting and minimized water loss at the expense of CO_2 uptake as evidenced by the overall lower rates of g_s. This response promoted a more favourable internal water balance since positive Δg_s values were observed over the entire experimental period (Figure 1.5a). Although partial stomatal closure limits water loss to a greater degree than CO_2 assimilation (Hsiao and Acevedo 1974, Kramer 1983), this response presumably reduced growth in the short run. In particular, root growth, which has been shown to depend on current photosynthate production (Etter and Carlson 1973, Ritchie 1982, van den Driessche 1987), may have been limited.

The greater overall rates of g_s and E_t recorded for the fall lifted seedlings can not be explained by the available data. Possibly, endogenous ABA concentrations were greater for this treatment following overwinter frozen storage (Blake 1983) which should have reduced stomatal response in comparison with the spring lifted seedlings (Jones and Mansfield 1970, Davies *et al.* 1981, Mansfield and Davies 1985). It is also possible that the high rates of first light g_s and E_t measured for the fall lifted seedlings are in part, a consequence of incomplete stomatal closure during darkness. Grossnickle and Blake (1985) found that stomata on mature foliage of $1^1/_2 + 1^1/_2$ white spruce seedlings did not fully close during darkness after removal from cold storage, but the initially low values recorded for the fall lifted seedlings on the first two measurement days do not support their finding. Cold storage may also damage the CO_2 fixation process and reduce the photosynthetic capacity (McCracken 1978) which might indirectly affect stomatal

response to first light. However, considerable evidence reviewed by Jarvis and Morison (1981) suggests that g_s is largely independent of the rate of carbon fixation in the leaf as a whole.

The increased g_s and E_t rates recorded with time out of cold storage for the fall lifted seedlings of the present study agree with the results of other investigations (Grossnickle and Blake 1985, Grossnickle 1987, Grossnickle 1988b). These increases have been attributed to reduced water flow resistances through the soil-plant-atmosphere continuum (SPAC), presumably throughout the plant and at the soil-root interface, and a higher Ψ_{plant} contingent on increased root development. The importance of new root development for increased water absorption has also been demonstrated for other conifers (Chung and Kramer 1975, Carlson 1986, Johnsen *et al.* 1988, Colombo and Asselstine 1989). Since the factors of the aerial environment known to affect g_s and E_t were constant during the present study, it is probable that the increased rates observed here also resulted from increases in Ψ_{plant} that followed a reduced SPAC resistance through the seedling and at the soil-root interface as the seedling initiated new roots. A decreased SPAC resistance is coincident with new root growth because new unsuberized roots are more permeable to soil water than older suberized roots (Chung and Kramer 1975, Sands *et al.* 1982) and because of an increase in water absorbing area. Presumably, the increased daytime values recorded for the spring lifted treatments occurred for similar reasons.

The initially greater gaseous exchange rates followed by the more abrupt decline in g_s under conditions of declining Ψ_{soil} suggests that stomata of the fall lifted seedlings were less sensitive to the associated declines in Ψ_{plant} (not measured but known to occur). In many outplanting situations, the ability to maintain greater rates of g_s over a wide range of Ψ_{plant} is likely advantageous since it allows for CO_2 influx and fixation (and subsequent growth) over the normal diurnal range in Ψ_{plant} gradients (Jarvis and Jarvis 1963a, 1963b). In drought prone environments, however, greater rates of g_s may be counterproductive if rapid transpirational water loss depletes available soil water reserves and cell extension is limited by a loss of turgor (Tyree 1976, Jarvis 1980). Grossnickle and Blake (1986) demonstrated that spring lifted $1^1/_2 + 1^1/_2$ black spruce seedlings outplanted onto boreal cutover sites were very sensitive to increased needle water deficits and showed a gradual stomatal closure in response to declining Ψ_{soil} and increased evaporative demands. The differences in stomatal response suggest that overwinter frozen storage disrupts the stomatal mechanism that normally responds to decreasing Ψ_{plant} and further suggests that the fall lifted seedlings are unable to effectively regulate gaseous exchange following planting. Thus, the fall lifted seedlings are at a greater risk to plant moisture stress following field planting onto sites with low available soil water. Indeed, a comparison between water relations patterns of the well-watered (Figures 1.1a and 1.2a) and water stressed (Figures 1.1b and 1.2b) treatments suggests that under conditions of declining Ψ_{soil}, partial stomatal closure at first light occurred sooner for the fall lifted (around Day 6), than the spring lifted treatments (between Days 8 and 10). This

indicates that nighttime water absorption partially alleviated transpirational losses over a longer period for the spring lifted than the fall lifted seedlings.

Shoot-Tissue Water Relations

Shoot-tissue water relations suggest that nursery lifting and storage practices affected the inherent ability of the variously treated seedlings to avoid water stress (i.e. to maintain turgor as Ψ_{plant} decreased) during establishment (Table 1.3). The similar pre-potting osmotic potentials recorded for the spring lifted seedlings indicate a similar physiological condition, presumably a consequence of their similar pre-storage history. The dissimilar values determined for the fall lifted seedlings are likely a consequence of the different levels of bud dormancy and/or different storage methods. Indeed, the higher (less negative) osmotic potentials recorded for treatment FL-48-P1 likely reflect lower reserve carbohydrate levels consistent with the greater respirational losses that would have occurred over the longer conditioning period at above freezing temperatures (van den Driessche 1979).

A comparison of the pre-potting shoot-tissue water relations characteristics reveals a lack of agreement between the selected parameters making it difficult to rank drought tolerance amongst treatments at this time. For example, the lower (more negative) $\Psi_{\pi(sat)}$ and $\Psi_{\pi(TLP)}$ observed for treatment FL-7-P1 indicate a greater initial drought resistance for these seedlings (Cheung *et al.* 1975, Roberts and Knoerr 1977). However, these low values were not reflected by a lower $RWC_{(TLP)}$ or a greater $\Delta\Psi_{\pi}$ which would also indicate a greater drought resistance. These discrepancies may be explained wholly or in part by differences in cell wall elasticities that presumably occurred between the treatments because of their different physiological stages. Since greater elasticities (i.e. a lower bulk modulus of elasticity [ε]) would result in a lower $RWC_{(TLP)}$ and a larger $\Delta\Psi_{\pi}$ (because elastic walls shrink and maintain turgidity as water is lost [Kramer 1983]) it seems reasonable to suppose that ε decreased as the seedlings of the present study became physiologically active and the lower $RWC_{(TLP)}$ and greater $\Delta\Psi_{\pi}$ exhibited by the SL-1-P1 seedlings are primarily a consequence of a lower ε. However, elasticity-turgor relationships do not always show clear seasonal trends (Parker *et al.* 1982). For example, tissue elasticity increased (i.e. ε decreased) during shoot elongation for 2 to 3-year old Douglas-fir (*Pseudotsuga menseizeii* [Mirb.] Franco) seedlings (Ritchie and Shula 1984), decreased for 1-year old black spruce (Colombo 1987) and $1^1/_2 + 1^1/_2$ white spruce (Grossnickle 1988c) seedlings, and remained unchanged for 2+0 jack pine (*Pinus banksiana* Lamb.) seedlings (Grossnickle 1988c).

Post-potting osmotic potentials increased (became less negative) under conditions of unlimited soil water as the fall lifted treatments became phenologically active and spring lifted treatments increased their level of phenological activity. This response pattern, noted to occur for other conifers during bud swell and shoot elongation (Ritchie and Shula 1984, Tyree *et al.* 1978, Colombo 1987, Grossnickle 1988c), indicates an overall reduction in foliar sugars (i.e. osmotic solute concentrations) as they are

metabolized at a greater rate than they are produced (Ritchie and Shula 1984). Osmotic potentials may also increase during this phenological stage as cells enlarge to enclose greater water volumes and effectively decrease the concentration of the osmoticum. The succulent new foliage and the high osmotic potentials render the seedlings especially prone to desiccation at this time (Ritchie *et al.* 1985). The increased $RWC_{(TLP)}$ and decreased $\Delta\Psi_\pi$ following the 13 day experimental period further suggest a reduced tolerance to water stress for the well-watered treatments at this time.

Post-potting osmotic potentials were generally lower for the water stressed than the well-watered seedlings. While the precise reasons for these lower values cannot be determined for the present study, they are known to occur in response to water stress because of: (1) an increase in cell wall elasticity, (2) an increase in solute concentrations as cells are dehydrated, and/or (3) an active accumulation of solutes (Hsiao *et al.* 1976, Turner 1979). In comparison with the pre-potting values, only the fall lifted treatments exhibited lower osmotic potentials and a greater $\Delta\Psi_\pi$ suggesting that they had become better adapted to the drought conditions (Kandiko *et al.* 1980). These lower potentials may account for the greater gaseous exchange rates exhibited by the fall lifted seedlings as Ψ_{soil} declined, since both water relations parameters indicate a lower threshold leaf water potential (Ψ_{leaf}) for stomatal closure (Kramer 1983). Thus, assuming Ψ_{plant} declined at the same rate for all treatments, the fall lifted seedlings were able to maintain positive turgor at low Ψ_{leaf} and therefore maintain a more favourable turgor balance between the guard cells and the epidermal cells under drier soil conditions (Bradford and Hsiao 1982).

Root Growth Capacity Response

New root development was strongly influenced by lifting-storage treatment (Table 1.4, Figure 1.7a). The greater RGC indices recorded for the fall and freshly lifted seedlings suggest that they would extend new roots and re-establish intimate root-soil contact following field planting. This ability is essential to establishing seedlings which must offset transpirational losses through increased water absorption to assure survival and rapid early growth (Sands 1984, Grossnickle and Blake 1987a,b). In contrast, the low RGC indices recorded for SL-14-P1 seedlings suggest that they could not maintain a favourable water balance and would be prone to desiccation after outplanting, especially under conditions of high evaporative demand and low soil water content. Indeed, three of the seedlings potted to assess RGC for this treatment died under well-watered conditions. It should be noted that RGC indices determined under optimum conditions indicate inherent response patterns only and are highly dependent on the growing environment (Sutton 1988). Moreover, the implied correlation between new root development measured under optimum and field conditions has not been extensively proven (Ritchie 1985, Burdett 1987, Sutton 1987). However, it seems reasonable to suppose that seedlings with an inherent ability to produce roots under optimum conditions would be more competitive for available soil

water over the field conditions that might prevail following planting and, thus, less prone to desiccation during times of seasonal water stress.

The precise reasons for the observed differences cannot be deduced from the available data since many of the endogenous (e.g. growth regulating hormones) and exogenous (e.g. soil water content, temperature, and aeration and atmospheric conditions) factors (Ritchie and Dunlap 1980) affecting the expression of RGC were not investigated. However, several previous studies have suggested that lifting date and temperature and duration of storage affect early root growth through interactions with bud dormancy status and carbohydrate availability (Ritchie and Dunlap 1980). It is quite likely that the response patterns of the present study occurred for similar reasons. Moreover, it is probable that winter injury had a detrimental effect on RGC for the spring lifted seedlings.

Bud dormancy status varied between treatments (as indicated by differences in phenological development) and presumably interacted with the expression of RGC by affecting RGC periodicity. In nature, RGC increases progressively as chilling sums accumulate during deep dormancy and then decreases more rapidly as dormancy is released during quiescence. Roots are the major metabolic sink in the seedling prior to bud break. However, with renewed shoot activity, there is a sink strength reversal favouring shoot elongation and root growth declines rapidly (Ritchie and Dunlap 1980). While the sub-freezing storage temperatures satisfied the chilling requirement for the fall lifted seedlings (Lavender 1964, van den Driessche 1977), dormancy was released at a slower rate than for the seedlings remaining in the nursery beds (Jorgensen and Stanek 1962, Blake 1983, Ritchie 1984b, Ritchie *et al.* 1985). This delayed response is apparently due to the following storage conditions: (1) a less than optimum temperature for dormancy release (Nienstaedt 1967, van den Driessche 1975), (2) a lack of temperature fluctuation (Campbell and Sugano 1975, Campbell 1978), and (3) the absence of light (Lavender and Waring 1972, Lavender 1978). RGC periodicity was subject to further variations between treatments because of the different storage periods at above freezing temperatures and the different spring lifting dates.

Carbohydrate reserves may stimulate RGC directly (Krueger and Trappe 1967, Stone and Jenkinson 1971, Ritchie and Dunlap 1980) or initiate the production of current photosynthate, which in turn stimulates root growth (Etter and Carlson 1973, Ritchie 1982, van den Driessche 1987). Reserve carbohydrate concentrations were not determined during the present study, but it is reasonable to suppose that treatment differences occurred. It is well documented that reserves are depleted in cold storage and that the rate of depletion increases with temperature (Hocking and Nyland 1971, Ronco 1973, McCracken 1979, Venn 1980, Ritchie 1982, Ritchie *et al.* 1985, Marshall 1985, Mattsson and Troeng 1986). It is therefore likely that FL-48-P1 seedlings, which had been conditioned at above freezing temperatures longer than FL-7-P1 seedlings, had lower reserve carbohydrates. Moreover, the spring lifted seedlings were subject to fluctuating temperatures over the winter and may have re-initiated photosynthesis and accumulated additional reserves prior to lifting. Several studies have shown that additional reserves are

rapidly accumulated once photosynthesis begins and starch concentrations can increase dramatically prior to bud break (Glerum 1980, Mattsson 1982, Ericsson *et al.* 1983, Marshall 1985). Bud swell was evident for treatment SL-1-P1 at the time of lifting and indicates that photosynthesis had begun and the significantly greater top dry weight measured upon lifting (Table 1.2) may indicate increased carbohydrate concentrations (Mattsson and Troeng 1986). Current photosynthate may also have supplemented carbohydrate stores for treatment SL-14-P1 prior to lifting or reserves may had been invested in the preparation of foliage for photosynthesis and buds for elongation (Marshall 1985), but the seedlings lifted prior to significant photosynthate accumulations. In this case, additional carbohydrate losses to maintenance respiration while in storage may have seriously depleted reserves and contributed to the low levels of root development recorded for this treatment.

Upon lifting, many of the spring lifted seedlings showed symptoms consistent with winter drying. This damage occurs during periods of inadequate snow cover when mild days interrupt cold weather and expose seedlings to warm temperatures and dry winds. Under such conditions, water loss from exposed foliage cannot be replaced by the frozen root system. In essence, this type of damage is similar to that caused by soil drought during the growing season (Singh 1976). Winter drying was found to be detrimental to RGC for black spruce and jack pine container seedlings (Colombo 1982, Colombo and Glerum 1984). It is therefore possible that winter drying affected RGC for the spring lifted seedlings, particularly, treatment SL-14-P1, which had less time to recover from the negative effects prior to lifting.

POTTING TIME 2 (JUNE 24)

Water Relations Response

Stomatal Conductance and Transpiration

Gaseous exchange patterns clearly differed between treatments and thereby lend additional support to the hypothesis that the date of lifting and the temperature and duration of storage influence seedling physiology during early establishment (Figures 1.8 to 1.11). The differences that occurred between trials for the fall and spring lifted, stored seedlings can be partly attributed to the further physiological changes (e.g. bud dormancy status, carbohydrate or hormonal imbalances, and tissue desiccation) and/or pathological deterioration that occurred during the extended storage periods. Such changes are well documented and known to cause an overall reduction in seedling vigour (Hocking and Nyland 1971, Navratil 1973, Venn 1980) but the precise mechanisms governing post-storage stomatal response are currently unclear (Blake 1983). The freshly lifted seedlings were not subjected to extensive storage but were more phenologically advanced during Potting Time 2. This effect would certainly influence seedling physiology (Lavender 1981, 1988) and, presumably, stomatal response following the lifting-storage-potting sequence, but the relationship does not appear to have been investigated. It is also probable that

variation between seedlings, within lifting-storage treatments attributed to differences between trials since samples were necessarily small due to limited sampling time and equipment constraints. This is particularly evident from the response hierarchy recorded for the fall lifted seedlings during Potting Time 2; prior to a noticeable decline in Ψ_{soil}, g_s and E_t rates differed between seedlings designated as well-watered and water stressed. However, these differences were not significant at α=0.05 (Appendix III, Table III.2).

In spite of the forementioned treatment differences, the salient results of Potting Time 2 generally support those of Potting Time 1 and thereby provide additional evidence that response patterns are inherent to the selected lifting-storage methods. Most importantly, the g_s and E_t response patterns indicate that the fall lifted seedlings, particularly treatment FL-48-P2, maximized CO_2 influx at the expense of water vapour efflux and presumably, a more favourable internal water balance. This is supported by the Δg_s values which indicate that partial stomatal closure, presumably in response to internal water deficits (Meidner and Mansfield 1968), occurred by the daytime measurement period during the first 11 days of the study (Figure 1.12a). As previously noted, this response is atypical of healthy, well-watered seedlings experiencing only moderate atmospheric stress (Woods and Turner 1971, Running 1976, Pereira and Kozlowski 1977, Hinckley *et al.* 1978). In contrast, the spring lifted seedlings, particularly treatment SL-1-P2, achieved a more favourable water balance soon after potting by limiting water loss through a reduced stomatal opening, presumably at the expense of CO_2 assimilation. This is evidenced by the consistently lower g_s rates for SL-1-P2 seedlings and the positive Δg_s values observed 4 days after potting for both spring lifted treatments. Moreover, the spring lifted seedlings reached minimal levels of first light g_s and E_t by Day 8 while rates declined for the fall lifted seedlings over the entire experimental period. These results suggest that the fall lifted seedlings are less likely to become established than the spring lifted seedlings following outplanting onto drought prone soils where water absorption may not be sufficient to meet the transpirational demand. Under such conditions, internal water reserves would rapidly decline and prevent biochemical reactions that result in growth from occurring.

The high first light g_s and E_t rates exhibited by all treatments on Day 1 indicate that stomata were open during storage or responded profusely to first illumination. Previous investigations with $1^1/_2 + 1^1/_2$ black spruce seedlings (Blake and Sutton 1987, Grossnickle 1987, Grossnickle and Blake 1987b) and the first light rates recorded during Potting Time 1 and the remainder of Potting Time 2 suggest that such extreme rates are atypical of normally functioning seedlings. These values may indicate the maximum attainable stomatal aperture since all seedlings were well-watered and held in darkness under low atmospheric stress during the 24 hour period preceding first illumination. Under such conditions, seedling tissue pressure potentials would approach a maximum as Ψ_{plant} equilibrated with Ψ_{soil} (i.e. $\Psi_{plant} \cong 0.0$ MPa) resulting in a high turgor pressure within the plant cells. Thus, g_s would not be

limited by available plant water (i.e. a low Ψ_{plant}), the fundamental factor regulating the degree of stomatal opening (Larcher 1980). It is also possible that the high gaseous exchange rates may indicate physiological, pathological, and/or physical (e.g. stem and needle abrasion, bending and breaking of needles and roots, drying of roots) damage to the stomatal mechanism that occurred during the lifting-storage-potting sequence.

First light g_s and E_t declined abruptly for all treatments following potting and then increased, possibly in response to improved cellular water relations effected through increased root development and/or reduced waterflow resistances throughout the seedlings. A similar transient decrease observed for freshly lifted but not frozen stored white spruce seedlings was attributed to planting shock (Blake 1983). Blake's data were collected within 2 hours of midday and the daytime rates of the present study do not corroborate his findings. Nonetheless, the Δg_s values indicate that all treatments exhibited partial stomatal closure by the daytime measurement period on Days 1 to 3. A similar result may have occurred on Day 1, Potting Time 1; daytime values were precluded by equipment failure but measurements gathered prior to failure indicated that g_s gradually decreased following first light. Thus, the results of both trials suggest that all treatments experienced water stress during establishment in spite of the favourable growing environment and careful handling practices. Furthermore, they emphasize the importance of strict quality control during all phases of the reforestation process, particularly during late spring and summer when sub-optimal edaphic and atmospheric conditions frequently prevail.

The commonly greater g_s and E_t rates recorded for the fall lifted seedlings can not be explained by the available data, but presumably occurred for reasons similar to those discussed for the corresponding treatments of Potting Time 1. Daytime rates were greater for all treatments at the end of the experimental period than at the beginning but only the spring lifted seedlings showed the gradual increase that characterized all treatments during Potting Time 1. Increased gaseous exchange rates with time since potting were noted to indicate reduced water flow resistances through the SPAC and a higher Ψ_{plant} contingent on increased root development. The mid-study increase exhibited by the fall lifted seedlings, particularly FL-48-P2, probably indicate a decreased SPAC resistance interacting with better stomatal control. In contrast to Potting Time 1, the magnitude of daytime g_s and E_t rates was frequently more comparable between fall lifted and SL-48-P2 seedlings than between the spring lifted seedlings, particularly during daytime. These differences clearly reflect the varied synchrony of seedling physiology that occurred for the spring lifted treatments of Potting Time 2.

The initially greater gaseous exchange rates followed by the more abrupt decline in g_s under conditions of declining Ψ_{soil} suggests that stomata of the fall lifted seedlings were less sensitive to the associated declines in Ψ_{plant}. As previously discussed, a reduced stomatal sensitivity to declines in Ψ_{plant} (i.e. wider pore widths as Ψ_{plant} becomes increasingly negative) assures CO_2 assimilation over the normal diurnal range in Ψ_{plant}. However, this response may be counterproductive if soil water

reserves are depleted and growth is limited by internal plant water deficits. The differences in stomatal response support the results of Potting Time 1 and further indicate that the fall lifted seedlings are unable to effectively control water loss following planting.

Gaseous exchange rates were minimal for all water stressed seedlings by Day 12 and probably indicate complete stomatal closure at or near this time. This result, consistent with those of Potting Time 1, is substantiated by the Δg_s values which were near zero for all treatments thereafter (Figure 1.12b). Gaseous exchange patterns recorded between Days 12 and 21 are misleading and only indicate differences that arose after the very low g_s and E_t rates recorded for each seedling were corrected for foliage area. Those seedlings with the smallest transpirational surface area, typically FL-7-P2 seedlings, had their measured rates increased to a greater extent than those seedlings with the largest transpirational surface area, typically SL-1-P2 seedlings. The manufacturer has since suggested that the CS-102 porometer's ability to detect changes in water vapour density over time may be limited under conditions of minimal water vapour flux.

The demonstrated ability of the spring lifted seedlings to reduce their rate of water loss during both trials under conditions of limited and unlimited Ψ_{soil} might explain the greater survival of spring lifted in comparison with fall lifted black spruce transplants following outplanting during hot dry periods (Day and Harvey 1984, K. M. McClain, unpublished data, R. J. Day, unpublished data). Furthermore, the approximately two week delay in phenological development reported for fall lifted in comparison with spring lifted seedlings (K. M. McClain, unpublished data, Day and Harvey 1984, and the results of Chapter 2) may have been due partly to an initial period of water stress similar to that shown for the fall lifted seedlings of the present study (Figures 1.5 and 1.12). It is worth noting that the response observed for the well-watered spring lifted seedlings early in each study is adopted by the well-watered fall lifted seedlings after about a three week acclimatization period. The inability of the fall lifted seedlings to reduce g_s and subsequent water loss after planting is not, in itself, detrimental to field planted seedlings, provided soil water conditions are adequate and atmospheric stress is low. However, if such stock was outplanted onto a droughty site, or if water absorption is reduced by cold soil temperatures (Kaufmann 1975, 1977, Grossnickle and Blake 1985) or flooding (Coutts 1981, Grossnickle 1987), its survival chances may be limited.

Shoot-Tissue Water Relations

Less similarity occurred between trials for shoot-tissue water potential components than gaseous exchange rates or root development and may indicate water relations differences that occurred between treatments but were only discernible at the bulk tissue level (Table 1.5). Pre-potting osmotic potentials differed for the spring lifted treatments reflecting the underlying physiological changes associated with the advanced phenology of the freshly lifted seedlings. The dissimilar values determined for the fall lifted

seedlings substantiate those recorded during Potting Time 1 and are likely a consequence of different levels of bud dormancy and/or different storage methods. Indeed, the higher (less negative) osmotic potentials recorded for treatment FL-48-P2 likely reflect reduced carbohydrate concentrations consistent with the greater respirational losses that would have occurred over the longer conditioning period at above freezing temperatures (van den Driessche 1979).

The higher pre-potting osmotic potentials recorded for the fall and spring lifted, stored seedlings during Potting Time 2 can be attributed to further respirational losses of reserve carbohydrates (Ronco 1973, Ritchie 1982, 1984a). The more pronounced decrease observed for the spring lifted seedlings occurred because they had broken dormancy (as evidenced by bud swell) prior to lifting. Active plant tissues have greater respiration rates and a higher consumption of carbohydrate reserves than non-active tissues (Navratil 1973). The lower (more negative) pre-potting potentials recorded for treatment FL-7-P2 agree with the results of Potting Time 1 and indicate a greater initial drought resistance for these seedlings. The higher pre-potting osmotic potentials recorded for the freshly lifted seedlings during Potting Time 2 can be attributed to a decrease in the amount of osmotically active solute coincident with the rapid shoot elongation observed for this treatment. This decrease occurred as foliar sugar metabolization outpaced production (Ritchie and Shula 1984) and cells enlarged to enclose greater volumes of water. The succulent new foliage and the high osmotic potentials indicate that these seedlings were especially prone to desiccation at this time (Ritchie *et al.* 1985). However, the low pre-potting $RWC_{(TLP)}$ suggests that plant tissues were very elastic and maintained lower osmotic than pressure potentials and, thus, positive turgor as Ψ_{plant} decreased.

Post-potting osmotic potentials generally increased for the fall and spring lifted, stored seedlings under both watering regimes. These increases can presumably be attributed to decreased osmotic solute concentrations coincident with renewed bud and shoot activity. The differences that occurred between trials and treatments may reflect different sink/source priorities for stored carbohydrates that resulted from different bud dormancy intensities or root growth periodicities following the extended storage periods. Moreover, variations in bud dormancy intensity, seedling vigour, and subsequent growth rates may have influenced carbohydrate production/metabolization balances within the seedlings and resulted in different osmoticum concentrations. In contrast, osmotic potentials decreased and $\Delta\Psi_{\pi}$ increased substantially for the freshly lifted seedlings suggesting that carbohydrates had accumulated since potting. This may have occurred because the physiological shock associated with the lifting-storage-potting sequence retarded growth processes and current photosynthate had accumulated since potting. Indeed, increments of leader extension determined for Potting Time 2 and concurrent outplantings (Chapter 2) indicate that shoot growth virtually ceased following potting and outplanting. In comparison with the pre-potting values, only the freshly lifted treatments exhibited lower osmotic potentials, a lower $RWC_{(TLP)}$ and a greater $\Delta\Psi_{\pi}$ suggesting that they had become better adapted to the drought conditions (Kandiko *et al.* 1980).

This suggests that the reduced rates of gaseous exchange recorded for this treatment were not a consequence of insufficient turgor for stomatal opening. Rather, these seedlings likely controlled water loss more effectively than the others because their physiological integrity was less affected by the lifting-storage-potting disturbances.

Studies with shoots and roots of water stressed and well-watered western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) (Kandiko *et al.* 1980) and English oak (*Quercus robur* L.) (Osonubi and Davies 1978) seedlings indicated that osmotic adjustment in shoots of droughted seedlings was reflected by a lowering of root osmotic potentials. It is, therefore, reasonable to suggest that root water relations differed between the lifting-storage methods of the present study and may have influenced the response patterns of the droughted seedlings. One possible effect might be to favour root growth over shoot growth during periods of water stress (Hsiao and Acevedo 1974). However, this effect must be limited to relatively high Ψ_{soil} since Day and MacGillivray (1975) have shown new root development and elongation to be negligible for $1^1/_2 + 1^1/_2$ white spruce seedlings when Ψ_{soil} was held at -0.15 MPa.

Root Growth Capacity Response

New root development was strongly influence by lifting-storage treatment (Table 1.4, Figure 1.7b). The greater RGC indices recorded for the fall and freshly lifted seedlings suggest that they would expand their limited root systems to exploit additional water and nutrient reserves and become rapidly established following planting. On the other hand, the low RGC indices recorded for SL-48-P2 seedlings suggest that they could not maintain a favourable water status and would be prone to desiccation after outplanting, especially during hot dry periods. The similarities and differences that occurred between trials cannot be fully explained because they are subject to a myriad of interdependent and interrelated factors (previously discussed) not specifically addressed during the present study.

Previous studies with both coniferous and deciduous forest tree seedlings showed RGC to vary widely following storage depending on lifting date, storage conditions, and the duration of storage (Ritchie and Dunlap 1980). As discussed earlier, these variations suggested that the lifting-storage method affects RGC through its interactions with bud dormancy and carbohydrate reserves (Ritchie and Dunlap 1980). Although carbohydrate reserves were lower for the fall lifted seedlings during Potting Time 2, RGC increased dramatically. Perhaps, carbohydrate levels were sufficient for root development during both potting trials and the extended storage period promoted a more uniform achievement of the chilling requirement which in turn increased RGC. The slight increase in average RGC recorded for the spring lifted, stored seedlings is probably due to variation between test seedlings since it is unlikely that RGC would increase during storage for non-dormant seedlings. On the other hand, the slight decreases that

occurred for the freshly lifted seedlings can presumably be related to differences in root growth periodicity that occurred between trials.

CONCLUSIONS

The central hypothesis under test in this study was that the date of lifting and the temperature and duration of storage affects seedling physiology and thereby influences the physiological response during early establishment. The results indicate that this hypothesis should be accepted. In particular, they showed the selected lifting-storage treatments to affect early plant water relations through interactions with both RGC and stomatal function.

The fall lifted seedlings showed similar response patterns regardless of the varied storage periods at above freezing temperatures. They exhibited prolific root growth but ineffectively controlled water loss from the needle surface. This suggests that they would maintain a favourable internal water status following field planting onto moist sites where transpirational demand could be satisfied through water absorption from the expanding root system. Moreover, this response may favour early rapid growth under such conditions by maximizing CO_2 assimilation. However, if outplanted onto a droughty site, or if water absorption is reduced by cold soil temperatures or flooding, the fall lifted seedlings may become poorly established and grow slowly for several years, or die.

The spring lifted treatments reduced water loss at the expense of CO_2 uptake soon after potting. However, the low RGC indices recorded for the spring lifted, stored seedlings suggests that they would not access soil water outside the immediate vicinity of their existing root systems and would be prone to desiccation following outplanting, especially during hot dry periods. Although the level of RGC necessary to establish an outplant is subject to environmental conditions (Burdett 1983), the intermediate indices recorded for the freshly lifted seedlings, coupled with their inherent ability to reduce transpirational losses suggests that they would become successfully established over the range of field conditions that might prevail following planting.

CHAPTER 2

ESTABLISHMENT AND EARLY GROWTH OF BLACK SPRUCE (*Picea mariana* [Mill.] B.S.P.) IN RELATION TO SELECTED NURSERY LIFTING AND STORAGE PRACTICES. 2. PHYSIOLOGICAL AND MORPHOLOGICAL RESPONSE FOLLOWING OUTPLANTING.

ABSTRACT

Butson, R. G. 1989. Establishment and early growth of black spruce (*Picea mariana* [Mill.] B.S.P.) in relation to selected nursery lifting and storage practices. 2. Physiological and morphological response following outplanting. M. Sc. F. Thesis. Lakehead Univ., Sch. For., Thunder Bay, Ont.

KEYWORDS: bareroot nursery practice, black spruce, field performance, *Picea mariana*, root growth capacity, seedling establishment, storage practices, stomatal conductance, transpiration, water relations

Problems associated with the establishment and early growth of outplanted black spruce (*Picea mariana* [Mill.] B.S.P.) seedlings led to research on the effects of selected nursery lifting and storage practices on post-planting performance. The broad objective was to evaluate important physiological and morphological response attributes of fall lifted, overwinter frozen stored, spring lifted, cool stored, and freshly lifted $1\frac{1}{2} + 1\frac{1}{2}$ black spruce transplants during concurrent field trials established in early May and mid-June, 1987, on a cultivated nursery soil and the scarified soil of a regional outplanting site. The nursery trial included undisturbed (i.e. not planted, thinned *in situ*), control seedlings as an additional treatment.

Physiological response differences were not readily apparent from measurements of xylem pressure potential. However, stomatal and root growth response indicated that nursery lifting-storage practices influence the seedling's ability to achieve and maintain a favourable internal water balance during establishment. Most importantly, the fall lifted seedlings exhibited prolific root growth but poorly regulated transpirational losses during establishment. In contrast, the spring lifted seedlings showed poorer root growth but maintained better stomatal control over transpirational losses. This response difference may have contributed to the generally greater growth response determined for the fall than spring lifted seedlings by increasing both their photosynthetic capacity and internal water reserves. However, under conditions of limited soil water, it is probable that the inability of the fall lifted seedlings to control transpirational losses would place them at an increased risk to desiccation. After one growing season, the undisturbed seedlings were clearly larger than any of the outplants, particularly the spring lifted, stored seedlings. Regardless of variations in physiological and morphological response, all seedlings showed acceptable growth and survival after one growing season.

INTRODUCTION

Ontario's forest tree nurseries are responsible for producing high quality seedlings capable of meeting minimum performance expectations under the constraints of the planting site. To ensure growth and survival, a newly planted seedling must replenish its limited water reserves as quickly as possible (Kozlowski and Davies 1975, Burdett 1987). The attainment of a favourable water balance is primarily dependent on the outplants inherent ability to control its initial rate of water loss and to access additional water by regenerating new roots and extending existing roots (Chung and Kramer 1975, Sands *et al.* 1982, Burdett *et al.* 1983, Nambiar 1984, Ritchie 1985, Johnsen *et al.* 1988). A seedling that is unable to expand its limited root system and re-establish intimate root-soil contact is subject to desiccation because soil water outside the immediate vicinity of the existing roots must be exploited to meet the high evaporative demands that frequently characterize atmospheric conditions at the time of planting (Sands 1984, Grossnickle and Blake 1987a,b). Nursery cultural and handling techniques have therefore been developed to prepare seedlings physiologically and morphologically to respond favourably to the edaphic, physiographic, biological, and climatic limitations (Greaves *et al.* 1978, Chapin *et al.* 1987) that impede survival and rapid early growth (Duryea and McClain 1984, Duryea and Landis 1984).

A number of nursery practices are also applied primarily for logistic reasons and their effect on early plantation performance is less well known (Sutton 1982a, McClain 1986). An increased understanding of the physiological plant processes governing these effects may lead to improved cultural and handling practices. Furthermore, only through clearer insights into the physiological response following planting will future management decisions become less intuitive. Towards this end, a number of outplanting trials have been established to investigate the effect of transplanting shock on early growth and physiological response. Since the limitations imposed by the planting site are varied and often interact in complex ways (Spurr and Barnes 1980, Hobbs 1984), research has largely focused on water stress which is considered to be the primary cause of plantation failure (Kozlowski and Davies 1975, Cleary *et al.* 1978, Burdett 1987). In particular, recent investigations have focused on the ability of seedlings to maintain a favourable internal water balance through stomatal control and root development (Hallman *et al.* 1978, Sands 1984, Örlander 1986, Blake and Sutton 1987, Grossnickle and Blake 1987a,b).

Simply stated, transpiration (E_t) is the loss of water vapour from plants. E_t is regarded as the dominant process in plant water relations because it controls the rate of water absorption and the ascent of sap. The rate of E_t is determined by the supply of energy available to vaporize water, the vapour pressure

gradient between the evaporating leaf surfaces and the surrounding air (which is the driving force), and the magnitude of the resistances to diffusion. Energy is supplied to the leaves from solar radiation (direct, reflected, and reradiated) and the advective flow of sensible heat from the surroundings. The vapour pressure gradient is primarily controlled by leaf and air temperature and atmospheric humidity. The resistances to diffusion include those of the boundary layer, cuticle, and stomata. The boundary layer is a thin region of unstirred air around the leaf through which the vapour density gradient between the leaf and the atmosphere changes linearly. This region is thinnest and offers the least resistance to diffusion at high wind velocities. The cuticular resistance is seldom considered because it is fairly constant and always relatively high (Ting 1982, Kramer 1983, Salisbury and Ross 1985). On the other hand, the exchange of water vapour between the intercellular spaces within the leaf and the aerial environment is largely controlled by the resistance of the stomata (Meidner and Mansfield 1968, Larcher 1980, Jarvis and Morison 1981, Kaufmann and Fiscus 1985).

Stomatal conductance (g_s), the inverse of stomatal resistance, is directly proportional to pore width; when the pore width is large, g_s is large and *vice versa*. The degree of stomatal opening is more commonly expressed as conductance rather than resistance because the former term has more biological meaning than the latter, and because conductances are proportional to fluxes of carbon dioxide (CO_2) and water vapour (Burrows and Milthorpe 1976, Ludlow 1980). By varying the pore width, a seedling simultaneously controls the entry of CO_2 and the exit of water vapour. Changes in stomatal opening are not immediate, but can occur within just a few minutes, rapidly enough for the seedling to adjust its resistance to diffusion in response to environmental fluctuations (e.g. sudden changes in wind speed) that could impose severe water stress. Such rapid response is necessary because a seedling's water reserves are limited in comparison with the potential rate of E_t (Mansfield and Davies 1985).

Stomatal movements are affected by numerous environmental factors, both past and present, including light (amount, duration, and quality), plant water potential (Ψ_{plant}), atmospheric humidity (vapour pressure deficit), temperature, CO_2 concentration, and wind (Burrows and Milthorpe 1976, Jarvis and Mansfield 1981, Willmer 1983). In the natural environment, these variables interact to affect g_s in complex ways making it difficult to determine the influence of any single cause (Burrows and Milthorpe 1976, Jarvis 1976, Squire and Black 1981). For example, high light intensities are frequently accompanied by high temperatures, which affect seedling water status, and an increased photosynthetic rate which affects the intercellular CO_2 levels. Stomata will, therefore, respond to all of these variables in concert (Willmer 1983). In addition to environmental factors, stomatal response and, therefore, the rate of E_t, vary with factors of the plant itself, including leaf age, location, and arrangement, growth regulators (especially phytohormones, i.e. abscisic acid, phaseic acid, cytokinins, and gibberellins), and past treatment (Burrows and Milthorpe 1976, Larcher 1980, Kramer 1983). The interaction among the

controlling factors generally results in an intermediate stomatal opening; maximum conductance is rarely achieved because the conditions that promote opening infrequently coincide (Larcher 1980).

Stomata open and close in response to light. Opening is relatively rapid at low levels of light intensity, but becomes more gradual at higher levels (Burrows and Milthorpe 1976). Closure is generally faster than opening (Willmer 1983). The stomata close in response to increasing vapour pressure deficits, especially at lower levels of Ψ_{plant} (Jarvis 1980, Larcher 1980). Conifers exhibit a distinct optimum temperature for maximum stomatal opening while g_S approaches zero at low and high temperature extremes (Jarvis 1980, Jarvis and Morison 1981). In general, stomata open and close as ambient CO_2 concentrations decrease and increase over the physiological range (Willmer 1983). Ambient CO_2 concentration had no apparent effect on stomatal response for several conifer species grown under field conditions (Jarvis 1980). However, partial stomatal closure in response to increased wind speed may be triggered by the associated CO_2 concentration increases at the leaf surface (Burrows and Milthorpe 1976, Mansfield and Davies 1985).

The pore width is ultimately determined by seedling water status and maximum g_S can only occur when turgor potential is high; if it should fall below a critical threshold value, all other factors that stimulate opening become ineffective (Larcher 1980). Seedling water status expresses the condition of water in a seedling (Spomer 1985). It is often quantified in terms of water potential (i.e. the difference between the chemical potential of pure, free water [assumed to equal zero] and water in the seedling, when both are measured under identical conditions of temperature, elevation, and atmospheric pressure) (Slatyer 1967, Kramer 1983). As well as quantifying the physiochemical availability of water for plant processes, gradients in Ψ_{plant} largely determine the direction of water movement within the plant. Ψ_{plant} is primarily determined by the water potential of the soil (Ψ_{soil}) and the E_t rate. Ψ_{plant} varies both diurnally and seasonally in response to temperature, humidity, wind speed, light intensity, daylength, and Ψ_{soil} (Cleary *et al.* 1978, Greaves *et al.* 1978). Those factors which increase the rate of E_t decrease Ψ_{plant} when soil water is limited. However, very negative Ψ_{plant} values can also occur in soils of high water content if the seedling experiences a physiological drought as a result of root damage or other factors (e.g. cold soil temperatures and flooding) that limit absorption (Cleary *et al.* 1978).

Cold storage of planting stock is commonly practiced in Ontario and known to influence seedling physiology during the post-planting period (Hocking and Nyland 1971, Sutton 1979, Venn 1980, Burdett and Simpson 1984). However, there is no reliable information on how this practice affects early growth and survival (McCracken 1978, Ericsson *et al.* 1983, Duryea and McClain 1984). Cold storage involves the holding of fall lifted seedlings at sub-freezing temperatures over the winter months or the holding of spring lifted seedlings within a narrow range just above freezing until planting. Although coniferous seedlings have been successfully stored overwinter at above freezing temperatures (Mullin and Bunting 1970, 1972) and after lifting in early spring at below freezing temperatures (Mullin 1976, Mullin

and Forcier 1976, Mullin and Reffle 1980, Sutton 1982b), neither of these methods are practiced operationally in Ontario. The former places seedlings at an increased risk to physiological (particularly the consumption of carbohydrate reserves) and pathological deterioration (Hocking and Nyland 1971, Navratil 1973, Venn 1980) while the latter is detrimental to seedlings lifted following dormancy release (Mullin 1976, Mullin and Forcier 1976, 1979, Mullin and Reffle 1980), a condition that occurs prior to any visible evidence of renewed growth (Ryker 1976).

Several studies have revealed that the physiological quality of seedlings changes during cold storage. Most importantly, carbohydrate concentration (Hellmers 1962, Winjum 1963, Ronco 1973, McCracken 1979, van den Driessche 1979, Ritchie 1982, Ritchie *et al.* 1985), seedling dry weight (Aldhous 1964, Navratil 1976, Navratil *et al.* 1976, McCracken 1979, DeWald and Feret 1988), root growth capacity (Sutton 1980, Ritchie 1982, Carlson 1985, Ritchie *et al.* 1985), stomatal response (Blake 1983, Grossnickle and Blake 1985, Grossnickle 1987, 1988b), and photosynthetic activity (McCracken 1978, Mattsson and Troeng 1986) have been influenced by storage treatment.

Unfortunately, experimental outplantings conducted to investigate the early water relations and growth response of cold stored seedlings are limited for Ontario's boreal conifers (Grossnickle and Blake 1987b, Grossnickle 1988a, 1988b) and no trials have been conducted to compare the effects of varied storage methods on plant water relations under field conditions. Under controlled environment conditions, Blake (1983) found that frozen storage at -3±1 ° C conditioned the stomata of 2+0 white spruce (*Picea glauca* [Moench] Voss) seedlings to reduce water loss after potting under simulated drought conditions (imposed by the osmoticum polyethylene glycol 4000). This occurred without markedly reducing the stomatal aperture and, thus, the photosynthetic capacity under well-watered conditions. The physiological mechanisms underlying the greater stomatal responsiveness of the frozen stored seedlings could not be fully explained, although it was suggested that it might be due to greater endogenous abscisic acid (ABA) concentrations (either total ABA or the ratio of free form of ABA relative to bound ABA) that presumably followed frozen storage. This suggestion was based on previous research which indicated that: (1) freezing plants induces a high degree of moisture stress (Cleary and Tinus 1980), a condition that would be intensified during overwinter frozen storage, (2) free ABA levels increased with stressful cold temperatures in tomato plants (Daie and Campbell 1981) and during bud dormancy of *Vitis vinifera* L. (Düring and Bachmann 1975), and (3) drought stress increases ABA concentrations (Wright 1978). This altered stomatal response, in addition to an observed delay in flushing and lower leaf water potentials in the post-planting period, prompted Blake to propose that frozen stored stock was better adapted to survive outplanting than freshly lifted stock. However, the results of Chapter 1 do not support Blake's conclusions. Rather, they suggest that overwinter frozen stored seedlings ineffectively control transpirational losses making them especially prone to atmospheric and soil drought during establishment. These effects must be further investigated because of the importance of maintaining

favourable water relations after outplanting and because growth rhythms are becoming increasingly disrupted as non-conventional lifting and storage practices gain widespread use (Sutton 1977, 1979).

The research presented in this chapter tests the hypothesis that the date of lifting and the temperature and duration of storage affects seedling physiology and thereby influences the physiological and morphological response during early establishment. This hypothesis was tested on the cultivated soil (semi-controlled environment) of the Ontario Ministry of Natural Resources (OMNR) Thunder Bay Forest Nursery (TBFN) and the scarified soil (uncontrolled environment) of a regional outplanting site near Raith, Ontario. Black spruce (*Picea mariana* [Mill.] B.S.P.) transplants ($1^1/_2 + 1^1/_2$) were chosen as the experimental material. Prior to outplanting in early May and mid-June, the seedlings were subjected to the following lifting-storage treatments: (1) fall lifted (October 29, 1986), overwinter stored at $-2 \pm 1^\circ$ C and conditioned at $+2 \pm 1^\circ$ C for 7 or 48 days, (2) spring lifted (May 6, 1987), stored at $+2 \pm 1^\circ$ C until removed, and (3) spring lifted, stored at $+2 \pm 1^\circ$ C for 1 day (i.e. freshly lifted). The physiological response attributes of stomatal conductance (g_s), transpiration (E_t), xylem pressure potential (Ψ_{xylem}), and new root development were evaluated for the variously conditioned seedlings outplanted at the TBFN only because of time, labour and equipment constraints. Moreover, the proximity of the experiments to Thunder Bay facilitated more intensive monitoring of water relations and growth increments and the proposed research included an undisturbed (i.e. not planted, thinned *in situ*) treatment. The morphological response attributes of height, ground caliper and leader extension increment, and seedling top and root dry weight and first season survival were evaluated at both sites.

The objectives of the research conducted at the TBFN outplanting site were as follows:

1. To determine seedling response in terms of gaseous exchange (i.e. rates of g_s and E_t) and Ψ_{xylem} for a nine week period following outplanting.
2. To determine new root development 14 days after planting.
3. To monitor growth increments of leader extension and ground caliper for an 84 day period following outplanting.
4. To determine the height, leader extension, ground caliper, top and root dry weight, and survival at the end of the first growing season (late October).

The objectives of the research conducted at the Raith outplanting site were as follows:

1. To determine growth increments of leader extension and ground caliper 60 days after planting.
2. To determine the height, leader extension, ground caliper, top and root dry weight, and survival at the end of the first growing season (late October).

METHODS AND MATERIALS

In 1986-87, experimental planting trials were established on the cultivated soil (semi-controlled environment) of the OMNR TBFN and the scarified soil (uncontrolled environment) of a regional outplanting site near Raith, Ontario. At each study area, experimental seedlings were outplanted on two dates, the first during May and the second during June. These studies were conducted to evaluate the early growth response and survival of fall and spring lifted $1^1/_2 + 1^1/_2$ black spruce transplants that were conditioned prior to planting as described in Tables 2.1 and 2.2. The physiological response attributes of g_s, E_t, Ψ_{xylem}, and new root development were evaluated for the variously conditioned seedlings at the TBFN. The morphological response attributes of height, ground caliper and leader extension increment, and seedling top and root dry weight and first season survival were evaluated at both sites.

EXPERIMENTAL MATERIAL

The origin, lifting, packaging, storage, and gross morphology of the $1^1/_2 + 1^1/_2$ black spruce transplants (seed source 34-25-0-00)[1] used in the study were described in Chapter 1. Briefly, all treatments, with the exception of SL-1-P2 seedlings, were lifted using a shaker lifting blade (Egedal). SL-1-P2 seedlings were lifted with planting shovels to minimize damage to current growth that had developed since earlier lifting. The average morphological characteristics determined upon lifting, their associated standard errors, and significant differences between the average values determined using Student-Newman-Keuls' (SNK) multiple range test (Steel and Torrie 1980) are presented for the nursery trial in Table 2.3 and the Raith trial in Table 2.4. Due to time limitations, average morphological characteristics were not determined for SL-1-P2 seedlings of the Raith trial. Rather, the values reported in Table 2.4 were determined 7 days later for SL-1-P2 seedlings of the nursery trial (i.e. lifted on June 14). Therefore, the average morphological characteristics reported in Table 2.4 may deviate slightly from those of the freshly lifted seedlings outplanted at the Raith site (i.e. lifted on June 8).

All seedlings were assigned to the various experiments at random with the exception of those selected to determine g_s and E_t response which were of similar morphological description (i.e. within 10 % of the mean root collar diameter and mean height determined for each lifting-storage treatment [Day *et al.* 1985]). Mean trees were chosen in this way to study gaseous exchange because it was reasoned that

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[1] seed source information code: 34 = site region code (3W), 25 = geographic location code (Thunder Bay District), 0 = agency code (OMNR), 00 = collection type code (general collection) (O.M.N.R. 1986b).

Table 2.1. The treatments evaluated at the Thunder Bay Forest Nursery during 1987. Black spruce transplants ($1^1/_2 + 1^1/_2$) from the Thunder Bay Forest Nursery were tested (seed source 34-25-0-00).

Treatment Code[1]	Treatment Description	Lifting Date	Duration and Temperature of Storage	Planting Date
Planting Time 1 (May 14)				
FL-48-P1	Fall lifted, frozen stored for 148 days, conditioned in cold storage for 48 days	October 29, 1986	148 days at - 2 ± 1°C 48 days at +2 ± 1°C	May 14, 1987
FL-7-P1	Fall lifted, frozen stored for 189 days, conditioned in cold storage for 7 days	October 29, 1986	189 days at - 2 ± 1°C 7 days at +2 ± 1°C	May 14, 1987
SL-7-P1	Spring lifted, cold stored for 7 days	May 6, 1987	7 days at +2 ± 1°C	May 14, 1987
SL-1-P1	Spring lifted, cold stored for 1 day	May 13, 1987	1 day at +2 ± 1°C	May 14, 1987
Planting Time 2 (June 15)				
FL-48-P2	Fall lifted, frozen stored for 180 days, conditioned in cold storage for 48 days	October 29, 1986	180 days at - 2 ± 1°C 48 days at +2 ± 1°C	June 15, 1987
FL-7-P2	Fall lifted, frozen stored for 221 days, conditioned in cold storage for 7 days	October 29, 1986	221 days at - 2 ± 1°C 7 days at +2 ± 1°C	June 15, 1987
SL-39-P2	Spring lifted, cold stored for 39 days	May 6, 1987	39 days at +2 ± 1°C	June 15, 1987
SL-1-P2	Spring lifted, cold stored for 1 day	June 14, 1987	1 day at +2 ± 1°C	June 15, 1987
Not Planted				
Undisturbed	Control, not planted, thinned *in situ*	not applicable	not applicable	not applicable

[1] Treatment Code: FL = fall lifted; SL = spring lifted; 48, 39, 7, 1 = number of days stored at +2 ± 1°C; P1 = Planting Time 1 (May 14, 1987); P2 = Planting Time 2 (June 15, 1987).

Table 2.2. The treatments evaluated at a regional outplanting site near Raith, Ontario during 1987. Black spruce transplants ($1^1/_2 + 1^1/_2$) from the Thunder Bay Forest Nursery were tested (seed source 34-25-0-00).

Treatment Code[1]	Treatment Description	Lifting Date	Duration and Temperature of Storage	Planting Date
Planting Time 1 (May 8)				
FL-48-P1	Fall lifted, frozen stored for 142 days, conditioned in cold storage for 48 days	October 29, 1986	142 days at - 2 ± 1°C 48 days at +2 ± 1°C	May 8, 1987
FL-7-P1	Fall lifted, frozen stored for 183 days, conditioned in cold storage for 7 days	October 29, 1986	183 days at - 2 ± 1°C 7 days at +2 ± 1°C	May 8, 1987
SL-1-P1	Spring lifted, cold stored for 1 day	May 7, 1987	1 day at +2 ± 1°C	May 8, 1987
Planting Time 2 (June 9)				
FL-48-P2	Fall lifted, frozen stored for 173 days, conditioned in cold storage for 48 days	October 29, 1986	173 days at - 2 ± 1°C 48 days at +2 ± 1°C	June 9, 1987
FL-7-P2	Fall lifted, frozen stored for 214 days, conditioned in cold storage for 7 days	October 29, 1986	214 days at - 2 ± 1°C 7 days at +2 ± 1°C	June 9, 1987
SL-32-P2	Spring lifted, cold stored for 32 days	May 6, 1987	32 days at +2 ± 1°C	June 9, 1987
SL-1-P2	Spring lifted, cold stored for 1 day	June 8, 1987	1 day at +2 ± 1°C	June 9, 1987

[1] Treatment Code: FL = fall lifted; SL = spring lifted; 48, 32, 7, 1 = number of days stored at +2 ± 1°C; P1 = Planting Time 1 (May 8, 1987); P2 = Planting Time 2 (June 9, 1987).

Table 2.3. Morphological measurements ($\bar{x}$, S.E. [in brackets], n = 100 seedlings) by treatment for $1^1/_2 + 1^1/_2$ black spruce transplants outplanted at the Thunder Bay Forest Nursery during 1987. These characteristics were determined upon lifting from randomly selected samples using the mean and standard deviation method (Day *et al.* 1985). Unless otherwise noted, all determinations are derived from methods described by Day *et al.* Means within a column without a common letter are significantly different ($\alpha = 0.05$).

Treatment Code[1]	Treatment Description	Root Collar Diameter (mm)	1986 Height[2] (cm)	1987 Leader Extension[3] (cm)	Top Dry Weight (g)	Root Dry Weight (g)	Root Area Index (cm^2)	Root Volume (cm^3)
Planting Time 1 (May 14)								
FL-48-P1	Fall lifted, frozen stored for 148 days, conditioned in cold storage for 48 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
FL-7-P1	Fall lifted, frozen stored for 189 days, conditioned in cold storage for 7 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
SL-7-P1	Spring lifted, cold stored for 7 days	4.662a (0.138)	24.7a (0.55)	n/a	5.150a (0.3042)	1.608ab (0.1151)	56.3bc (2.97)	5.8a (0.40)
SL-1-P1	Spring lifted, cold stored for 1 day	5.28b (0.134)	28.3b (0.64)	n/a	6.523b (0.3161)	1.822b (0.0904)	63.6c (3.53)	6.1a (0.30)
Planting Time 2 (June 15)								
FL-48-P2	Fall lifted, frozen stored for 180 days, conditioned in cold storage for 48 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
FL-7-P2	Fall lifted, frozen stored for 221 days, conditioned in cold storage for 7 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
SL-39-P2	Spring lifted, cold stored for 39 days	4.662a (0.138)	24.7a (0.55)	n/a	5.150a (0.3042)	1.608ab (0.1151)	56.3bc (2.97)	5.8a (0.40)
SL-1-P2	Spring lifted, cold stored for 1 day	5.50b (0.138)	23.8a (0.54)	11.3 (0.37)	8.335c (0.4548)	1.429a (0.0732)	46.9a (2.22)	4.8b (0.26)

[1] Treatment Code: FL = fall lifted; SL = spring lifted; 48, 39, 7, 1 = number of days stored at $+2 \pm 1\,^{\circ}C$; P1 = Planting Time 1 (May 14, 1987); P2 = Planting Time 2 (June 15, 1987).

[2] Defined as the distance from the root collar to the base of the terminal bud on the tallest leader.

[3] Defined as the distance from the base of the previous years growth node to the tip of the growing dominant terminal or lateral.

Table 2.4. Morphological measurements ($\bar{x}$, S.E. [in brackets], n = 100 seedlings) by treatment for $1^1/_2 + 1^1/_2$ black spruce transplants outplanted at a regional outplanting site near Raith, Ontario during 1987. These characteristics were determined upon lifting from randomly selected samples using the mean and standard deviation method (Day *et al.* 1985). Unless otherwise noted, all determinations are derived from methods described by Day *et al.* Means within a column without a common letter are significantly different ($\alpha = 0.05$).

Treatment Code[1]	Treatment Description	Root Collar Diameter (mm)	1986 Height[2] (cm)	1987 Leader Extension[3] (cm)	Top Dry Weight (g)	Root Dry Weight (g)	Root Area Index (cm^2)	Root Volume (cm^3)
Planting Time 1 (May 8)								
FL-48-P1	Fall lifted, frozen stored for 142 days, conditioned in cold storage for 48 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
FL-7-P1	Fall lifted, frozen stored for 183 days, conditioned in cold storage for 7 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
SL-1-P1	Spring lifted, cold stored for 1 day	4.662a (0.138)	24.7a (0.55)	n/a	5.150a (0.3042)	1.608ab (0.1151)	56.3bc (2.97)	5.8a (0.40)
Planting Time 2 (June 9)								
FL-48-P2	Fall lifted, frozen stored for 173 days, conditioned in cold storage for 48 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
FL-7-P2	Fall lifted, frozen stored for 214 days, conditioned in cold storage for 7 days	4.55a (0.115)	24.0a (0.54)	n/a	4.987a (0.2747)	1.441a (0.0765)	50.0ab (2.25)	6.3a (0.33)
SL-32-P2	Spring lifted, cold stored for 32 days	4.662a (0.138)	24.7a (0.55)	n/a	5.150a (0.3042)	1.608ab (0.1151)	56.3bc (2.97)	5.8a (0.40)
SL-1-P2	Spring lifted, cold stored for 1 day	5.50b (0.138)	23.8a (0.54)	11.3 (0.37)	8.335b (0.4548)	1.429a (0.0732)	46.9a (2.22)	4.8b (0.26)

[1] Treatment Code: FL = fall lifted; SL = spring lifted; 48, 32, 7, 1 = number of days stored at +2 ± 1 °C; P1 = Planting Time 1 (May 8, 1987); P2 = Planting Time 2 (June 9, 1987).

[2] Defined as the distance from the root collar to the base of the terminal bud on the tallest leader.

[3] Defined as the distance from the base of the previous years growth node to the tip of the growing dominant terminal or lateral.

the use of such would: (1) reduce the response variability as much as possible, particularly in light of the necessarily small sample size, and (2) render the results of the nursery trials and the approximately concurrent potting trials (Chapter 1) more comparable. The choice of undisturbed seedlings was limited to those in the proximity of the g_s and E_t experiments. They were chosen on the basis of ease of measurement (i.e. single stemmed trees were chosen over multiple stemmed trees) and vigour (i.e. trees with winter damage were not selected).

TREATMENTS

Each experiment investigated the physiological or morphological response of the selected seedlings subjected to the the following date of lifting - temperature and duration of storage treatments:

1. Fall lifted and overwinter frozen stored at - 2 ± 1 ° C, conditioned at +2 ± 1 ° C for 7 or 48 days.
2. Spring lifted and stored at +2 ± 1 ° C until planting.
3. Spring lifted and stored at +2 ± 1 ° C for 1 day (i.e. freshly lifted).

The specific lifting dates, temperatures, storage durations, and planting dates are presented along with treatment codes and treatment descriptions in Table 2.1 for the nursery trial and Table 2.2 for the Raith trial. The nursery trial included undisturbed (i.e. not planted, thinned *in situ*), control seedlings as an additional treatment. Fall lifted seedlings were stored in OMNR freezers at Thunder Bay until April when they were removed for further storage at Lakehead University (Treatments FL-48-P1, FL-7-P1, FL-48-P2, FL-7-P2; see Tables 2.1 and 2.2 for code descriptions and lengths of conditioning periods). Spring lifted seedlings (Treatments SL-7-P1, SL-1-P1, SL-32-P2, SL-39-P2, SL-1-P2; see Tables 2.1 and 2.2 for code descriptions) were stored at Lakehead University. The rationale that guided the selection of lifting-storage treatments was discussed in Chapter 1.

STUDY AREA LOCATIONS AND DESCRIPTIONS

Nursery Trial

The TBFN is located within the Rosslyn Land Type (Hills and Morwick 1944) on reclaimed farmland within the outer limits of Thunder Bay at latitude 48 ° 22 ' N, longitude 89 ° 22 ' W (Appendix VI, Figure VI.1). The site originally supported pure, or nearly pure stands of jack pine (*Pinus banksiana* Lamb.) on fresh, weakly developed, deep podzol soils of glaciolacustrine origin. The landform is broadly flat (Mollard 1979, Mollard and Mollard 1983). All experiments were located in the three most northerly beds of Compartment 113 because its east-west orientation minimized partial shading of the experiments. Uniform shading was particularly important during the first light measurements of g_s, E_t, and Ψ_{xylem}.

The soil texture of the plough layer (0 to 23 cm depth) within this area was determined as a loamy sand (86 % sand, 11.2 % silt, 2.8 % clay) using the Bouyoucos hydrometer method (Wilde *et al.* 1979). A characteristic soil water retention curve is presented in Appendix VII, Figure VII.1a. This curve was developed according to the procedures outlined in the operating manual for the ceramic plate extractor (Soil Moisture Equipment Corp., Santa Barbara, Calif.). Soil texture and water retention determinations were based on nine soil samples taken at random locations across the study area. Prior to determinations, the samples were air dried, sifted through a 2 mm sieve, and well mixed.

The soil chemical properties determined for Compartment 113 by the TBFN staff from the fall of 1985, through to the fall of 1987 are presented in Table 2.5. Unfortunately, no data were collected for the compartment during 1986. Total fertilizer applied by the nursery during 1986 was approximately 87.1 kg/ha elemental nitrogen (8 applications of ammonium nitrate top dressing at a rate of 33 kg/ha) and approximately 52.5 kg/ha elemental phosphorus (5 applications of mono ammonium phosphate top dressing at a rate of 50 kg/ha). Total nitrogen from both sources was approximately 117.1 kg/ha (Tisdale 1975). No standard cultural treatments used at the nursery (i.e. irrigation, pesticide, and fertilizer applications) were applied to the experiments. All plots were weeded by hand as required.

Table 2.5. Soil chemical properties compiled for Compartment 113 at the Thunder Bay Forest Nursery from the fall of 1985 through to the fall of 1987.

	Date Sampled		
	Fall 1985	Fall 1986	Fall 1987
pH	5.40	not sampled	5.40
Organic Carbon (%)	not sampled	not sampled	1.89
Phosphorus (mg/100 g)	17.13	not sampled	9.13
Potassium ($cmol \cdot kg^{-1}$)	0.41	not sampled	0.36
Calcium ($cmol \cdot kg^{-1}$)	not sampled	not sampled	0.38
Magnesium ($cmol \cdot kg^{-1}$)	0.72	not sampled	0.41

Soil tensiometers were installed across the experimental trial on June 3 (after the risk of frost) at a depth of 15 to 18 cm. Seasonal macroclimatic data (i.e. precipitation, daily maximum and minimum temperatures) recorded by the Atmospheric Environment Service of Environment Canada at the Thunder Bay airport (latitude 48 ° 22 ' N, longitude 89 ° 19 ' W) are appended for the months of April through October, 1987 (Appendix VIII, Figures VIII.1 to VIII.7). From these data, cumulative degree growing days (base 5 ° C) have been calculated separately for the undisturbed seedlings (accumulated since March 1, 1987) and for the seedlings outplanted on each of the two planting dates (Appendix VIII, Figures VIII.1 to VIII.7). In addition, site environmental conditions (i.e. relative humidity (RH) (%), vapour pressure deficit (VPD) (kPa), temperature) were recorded at a height of 10 cm during each sampling period for g_s,

E_t, and Ψ_{xylem} using a model 566 psychrometer (Bendix, Environmental Science Division, Baltimore, Maryland).

Raith Trial

The Raith outplanting site is located approximately 80 km northwest of Thunder Bay near Raith, Ontario on Abitibi-Price private land, Block 3 (Appendix VI, Figure VI.1). The planting site is within the B9 section of the Boreal Forest Region (Rowe 1972) at latitude 48° 56' N, longitude 89° 58' W, and originally supported a mixture of jack pine and black spruce. The landform is gently rolling. Fresh, deep sandy till with cobbles of ground moraine origin are representative of those occurring on the site (Mollard 1979, Mollard and Mollard 1983). The soil texture was determined as a silty loam (33.2 % sand, 61.6 % silt, 5.2 % clay). A characteristic soil water retention curve is presented in Appendix VII, Figure VII.1b. These determinations were made from nine well-mixed soil samples (three samples were collected at random from each of the three experimental blocks) according to the previously discussed procedures. Each sample was taken to a depth of 20 cm after the organic layer had been scraped away.

The area was cutover in 1982, scarified with a TTS disk trencher in mid-summer and sprayed with 2.154 kg a.i./ha of glyphosate in 6 L/ha of Round-up® in August, 1986. The site contained little slash, few residuals and little advanced growth. At the time of planting, competition was light and comprised mainly of grasses and sedges. However, by mid-summer it became apparent that a portion of the planting trial, in particular, most of block 3, had been almost entirely missed by the herbicide application. By that time, this area was under moderate competition from grasses, sedges, and some shrubs.

ESTABLISHMENT OF EXPERIMENTS

Nursery Trial

In September, 1986, randomly assigned control plots of undisturbed seedlings were located and marked with steel assessment pins (Appendix VI, Figures VI.2 and VI.3) to ensure that they remained intact during fall and spring lifting operations by nursery personal. At the ends of each control plot, a 0.8 linear meter buffer was reserved to allow for root system development of undisturbed seedlings contained within the plot boundaries. Trees within the buffer zone that were disturbed by the 'Egedal' blade while lifting adjacent plots were heeled back into place. Trees within the buffer zone were not measured. No trees were planted into the buffer zone. Consequently, trees contained in the undisturbed plots were virtually unaffected by lifting or planting in surrounding plots. In addition, experimental seedlings potted

(Chapter 1) or outplanted during the present study were located within the northernmost bed and marked for fall and spring lifting.

All randomly assigned plots within six experimental designs were located and marked with assessment pins after the spring lift on May 6, 1987 (Appendix VI, Figures VI.2 and VI.3). It was necessary to locate g_s and E_t experiments on the end of an undisturbed plot reserved for Ψ_{xylem} measurements in order to provide experimental control seedlings for g_s and E_t measurements. Undisturbed seedlings reserved for Ψ_{xylem} and morphological measurements were chosen to approximate the spacing of the outplanted seedlings. Seedlings surrounding the chosen undisturbed seedlings were cut off at ground level to reduce competition effects and shading to a level approximating that of the outplants. All outplant locations were marked with steel assessment pins immediately prior to planting. (Experimental designs, plot dimensions, and seedling spacing intervals are discussed later in this section.) On each planting date (Table 2.1), trees were removed from cold storage, and transported in storage containers (sealed polyethylene bags in waxed kraft boxes) to the TBFN. The containers were then placed in the shade of a drainage ditch culvert until planting. All trees were planted with planting shovels using the L-slit method at previously marked locations to assure uniform spacing.

Raith Trial

The experimental design and plot boundaries were located and staked with steel posts in April, 1987 (Appendix VI, Figure VI.4). (Experimental designs, plot dimensions, and seedling spacing intervals are discussed later in this section.) Each plot contained 4 to 6 TTS trenches. On each planting date (Table 2.2), trees were removed from cold storage and transported in storage containers (sealed polyethylene bags in waxed kraft boxes) to the Raith outplanting site. The containers were then placed in the shade of a mature stand of jack pine until planted. All trees were planted with planting shovels in the bottom of the TTS trenches using the L-slit method.

MEASUREMENT OF SEEDLING PHYSIOLOGICAL RESPONSE

Plant water relations and root growth response were monitored at the TBFN only because of time, labour, and equipment constraints. Moreover, the proximity of the experiments to Thunder Bay facilitated more intensive monitoring of seedling water relations and the proposed research included an undisturbed (i.e. not planted, thinned *in situ*) treatment.

Water Relations Response

Stomatal Conductance and Transpiration

Experimental Design

The experiment was planned as a randomized complete block design with four blocks, each comprised of five treatments (four lifting-storage treatments and an undisturbed, control treatment) (Table 2.1). A single seedling per lifting-storage treatment, per block, was planted. Since it was not possible to locate the undisturbed seedlings randomly, one undisturbed seedling was sampled per block at a sampling time randomly determined at the start of each study. Thus, 20 seedlings in total were measured during the experiment. The blocks were arranged as four rows of five trees. There were 0.32 m between rows and seedlings of adjacent rows and 0.4 m between seedlings within each row.

Sampling Procedure

The g_S ($cm \cdot sec^{-1}$) and E_t ($mg \cdot cm^{-2} \cdot sec^{-1}$) rates of each individual seedling were measured using the model CS-102 whole seedling transient type porometer (Micromet Systems Inc., Vancouver, B. C.), the design and calibration of which are described by Livingston *et al.* (1984). The entire measurement process required approximately 90 seconds per seedling. Each seedling was measured once every 30 minutes over the sample day. Since porometers give erroneous readings when foliage is wet, each sample day began when visual inspection under 10 X magnification indicated that all dew had evaporated. Stomatal conductance and E_t were monitored from May 15 to July 4 for Planting Time 1 and from June 16 to August 13 for Planting Time 2. These response variables where monitored most intensively for the first three weeks following outplanting (daily when weather conditions permitted) and then once every two to three weeks depending on weather and scheduling considerations. The sampling dates and times are appended for Planting Time 1 (Appendix IX, Table IX.1) and 2 (Appendix IX, Table IX.2). Between 3000 and 4000 individual seedling measurements of g_S and E_t were taken during each trial.

To minimize the error related to changing g_S and E_t during the day, particularly the sharp rise at dawn, each experiment was consistently sampled in a block by block, left to right pattern. In this manner, each treatment was measured for g_S and E_t at least once every 7.5 minutes. As previously discussed, the undisturbed seedlings could not be located randomly within each block. Therefore, one undisturbed seedling was sampled per block at a sampling time randomly determined at the start of each trial. To further minimize variability in g_S and E_t over the sample period, the measurements from the four seedlings representing each treatment (one seedling per block) were averaged after being corrected for projected foliage area (Appendix I). Therefore, approximately 750 to 1000 measurements of average g_S and E_t were recorded during each trial.

Xylem Pressure Potential

Experimental Design

The experiment was a randomized complete block design with three blocks, five treatments per block (four lifting-storage treatments and an undisturbed, control treatment [Table 2.1]), and 80 seedlings per plot (Appendix VI, Figure VI.2). Thus, 1200 seedlings in total were measured during each experiment. Each block occupied 21.6 linear meters of one of three adjacent nursery beds and was composed of five randomly located treatment plots four meters in length. Each treatment plot contained eight rows of ten seedlings. There was 0.17 m between rows, 0.4 m between seedlings within each row, and 0.26 m between seedlings of adjacent rows.

Sampling Procedure

Ψ_{xylem} measurements were taken on excised lateral branch tips using a pressure chamber and a hand held lens. This technique was thoroughly reviewed by Ritchie and Hinckley (1975). Briefly, each lateral branch tip was severed using a single scalpel stroke and stripped of needles, phloem. and cambium for a short distance back from the cut. The shoot was then inserted into a slotted rubber stopper with the cut end protruding. The stopper was fitted into the pressure chamber cap so that the cut end protruded through the cap hole. With the chamber tightly capped, compressed air was introduced at a slow, even rate while the cut end was observed at 10 X magnification. At the instant water appeared at the cut surface, the chamber air pressure was noted and recorded. Precautions were taken to minimize measurement errors following the recommendations of Ritchie and Hinckley.

The entire measurement process required approximately 60 seconds per seedling. Three seedlings per treatment per block were randomly chosen and measured during each 60 minute sample period. Each sample day began at dawn. Ψ_{xylem} was monitored from May 15 to July 4 for Planting Time 1 and from June 16 to August 13 for Planting Time 2. Ψ_{xylem} was monitored most intensively for the first three weeks following outplanting (daily when weather conditions permitted) and then once every two to three weeks depending on weather and scheduling considerations. The sampling dates and times are appended for Planting Time 1 (Appendix IX, Table IX.1) and 2 (Appendix IX, Table IX.2). Between 4000 and 5000 individual seedling measurements of Ψ_{xylem} were taken during each trial.

To minimize the error related to changing Ψ_{xylem} during the day (particularly the sharp decrease at dawn), each experiment was consistently sampled in a block by block, left to right pattern. In this manner, each treatment was measured for Ψ_{xylem} at least once every 15 minutes. If the range in Ψ_{xylem} among lateral branch tips measured within each plot exceeded 0.15 MPa, and time allowed, additional samples were collected. Time constraints frequently prevented additional sampling during diurnal measurement periods and Ψ_{xylem} values occasionally varied by as much as 0.30 MPa. As each

seedling was sampled, it was marked with an assessment pin until each seedling within a plot was sampled. Pins were then removed and the procedure was repeated. To further minimize variability in Ψ_{xylem} over the sample period, the measurements from the nine seedlings representing each treatment (three seedling per block) were averaged. Therefore, approximately 450 to 550 measurements of average Ψ_{xylem} were recorded during each trial.

Root Growth Response

Experimental Design

A completely randomized design with eight lifting-storage treatments (Table 2.1) and 32 seedlings per treatment was established (Appendix VI, Figure VI.2). Each treatment plot contained eight rows of four seedlings. There was 0.17 m between rows, 0.4 m between seedlings within each row, and 0.26 m between seedlings of adjacent rows.

Sampling Procedure

Fourteen days after outplanting, 25 of the 32 trees planted per treatment were randomly selected, carefully excavated, and transported to the laboratory at Lakehead University. The roots were then carefully washed in running water until free of soil. New root growth was evaluated using the root growth capacity coding system developed by Burdett (1979) for lodgepole pine (*Pinus contorta* Dougl.) and modified for black spruce to include two additional classes (Appendix II). This coding system is based on the assumption that the first new roots to develop increase drought resistance to a greater degree than the last new roots (Burdett 1987).

MEASUREMENT OF SEEDLING MORPHOLOGICAL RESPONSE

Morphological seedling response was monitored most intensively at the TBFN because of time, labour, and equipment constraints. Moreover, the proximity of the experiments to Thunder Bay facilitated more intensive monitoring of growth increments and the proposed research included an undisturbed (i.e. not planted, thinned *in situ*) treatment.

Nursery Trial

Experimental Design

A randomized complete block design with unequal replication was established to determine growth and development at the TBFN. Each of the nine treatments (Table 2.1) was replicated once in one

of the three blocks. Each block occupied 50 linear meters of one of three adjacent nursery beds and was composed of 11 to 13 randomly located treatment plots 2.8 m in length (Appendix VI, Figure VI.3). Each treatment plot contained six rows of seven seedlings. Thus, 1512 seedlings in total were measured during the experiment. There was 0.17 m between rows, 0.4 m between seedlings within each row, and 0.26 m between seedlings of adjacent rows.

Sampling Procedure

Immediately following outplanting, each seedling was marked at ground level with a latex paint ring and tagged for identification. Ground caliper, height and leader extension were determined for each seedling on the day of outplanting, 21, 42, 63 and 84 days after outplanting, and at the end of the growing season (Appendix IX, Figures IX.1 and IX.2). The undisturbed seedlings was marked and measured concurrently with the seedlings outplanted on May 14 (Table 2.1).

Ground caliper was determined immediately above the paint ring to 0.01 mm precision using digital electronic calipers. To reduce measurement error, calipers were always held in the same relative position (i.e. on the south side of the stem parallel to an adjacent cedar hedge). Height, defined as the distance from the root collar to the base of the terminal bud on the tallest leader, was measured to 0.1 cm precision using a ruler. Leader extension, defined as the distance from the base of the previous years growth node (identified by the occurrence of bud scale scars) to the tip of the growing dominant terminal or lateral, was measured to 0.1 cm precision with a ruler.

Outplants were carefully excavated and taken to the laboratory at Lakehead University at the end of the growing season (October 21). Each seedling was carefully washed in running water to remove the soil from the root system. Each seedling was severed at the root collar and tops and roots were bagged separately, placed in a forced air convection oven, and dried for 48 hr at 70 ° C. The tops and roots were then weighed separately to 0.001 g precision on a electronic digital balance.

Raith Trial

Experimental Design

A randomized complete block design with unequal replication was established to determine growth and development at the Raith outplanting site (Appendix VI, Figure VI.4). With the exception of SL-1-P1, each of the treatments (Table 2.2) was replicated once in one of the three blocks. Treatment SL-1-P1 was replicated once in blocks 1 and 3 and three times in block 2. The additional replication occurred because no spring lifted, stored seedlings were available during the first planting time. Each block was 36 m by 48 m in size and was composed of 16 randomly located treatment plots. Each

treatment plot was 9 m by 12 m in size and contained four to six TTS trenches. Trees were spaced at approximately 1.6 m by 1.6 m and 40 trees were planted per plot. Thus, 1280 seedlings in total were measured during the experiment.

Sampling Procedure

Each tree was tagged for identification and its location marked with an assessment pin immediately following outplanting. Ground caliper, height, and leader extension were determined for each seedling on the day of outplanting, 60 days after planting, and at the end of the growing season. Ground caliper was determined where the soil met the stem. Height and leader extension were measured according to the previously discussed procedures. At the end of the planting season (October 23), seedlings were carefully excavated, taken to the laboratory at Lakehead University, and measured for top and root dry weight according to the previously discussed procedures.

DATA EVALUATION AND ANALYSIS

Seedling Physiological Response

Water Relations Response

First measurement and diurnal patterns of g_s, E_t, and Ψ_{xylem} were plotted to visually assess treatment similarities, differences, and trends during early establishment and to compare patterns of behaviour among trials. According to Matin *et al.* (1989), treatment similarities and differences in g_s, E_t, and Ψ_{xylem} response are readily apparent at times of low (first measurement) and high (diurnal) environmental stress. First measurement patterns were plotted over each three week post-planting period. Diurnal patterns were plotted immediately following planting and after approximately 3 and 7 weeks.

The data were not analysed statistically because the sample sizes were insufficient to reduce the within treatment variability. This problem is common in plant water relations research because the time period over which comparable measurements can be taken is frequently limited by factors of the aerial environment (e.g. amount, duration, and quality of light, water vapour saturation deficit, and CO_2 concentration) and factors of the plants themselves (e.g. leaf water potential and concentration changes in endogenous growth regulators such as ABA, auxins, and cytokinins) (Mansfield and Davies 1985). Consequently, sample sizes have historically been determined by the number of g_s and E_t measurements it is feasible to make over a predetermined time interval without regard for variation between the measurements (Jarvis 1981).

Water flow through the soil-plant-atmosphere continuum (SPAC) was estimated using the following Ohm's law analogy (Hinckley *et al.* 1978):

$$\Psi_{xylem} = \Psi_{soil} - R_{SPAC}\,(E_t) \qquad (2.1)$$

where Ψ_{xylem} is the xylem pressure potential, Ψ_{soil} is the soil water potential, R_{SPAC} is the total resistance to waterflow in the liquid phase from the soil to the leaf, and E_t is the transpiration rate. According to equation (2.1), Ψ_{xylem} will become increasingly negative with decreases in Ψ_{soil} or increases in the rate of E_t or soil to atmosphere resistances. This analogy assumes steady state conditions (i.e. water absorption $\cong E_t$) which clearly do not occur. However, since water flux through a seedling is usually greater than changes in seedling water content, the diurnal $\Psi_{xylem} : E_t$ relationship can be described as a sequence of steady states, even in the variable natural environment (Cowan and Milthorpe 1968, Elfving *et al.* 1972). While equation (2.1) does not clearly account for the effects of growth partitioning (Fiscus *et al.* 1983) or coupled solute flow on Ψ_{xylem} (Kaufmann 1976), most evidence suggests that it is adequate for interpreting many field responses (Kaufmann and Fiscus 1985). Linear regression analysis was used to interpret the $\Psi_{xylem} : E_t$ relationship for each treatment as the experimental period progressed. Thus, the regression coefficients (β_1) provided an estimate of R_{SPAC} and the y-intercept (β_0) estimated the Ψ_{soil} perceived by the seedling at the start of the measurement day (Jarvis 1976, Hinckley *et al.* 1978). E_t was assumed to equal zero when wet foliage prevented its determination concurrent with the first measurement of Ψ_{xylem}. Regression analyses were performed using the Cricket software package on an Apple® Macintosh™ Plus personal computer at Lakehead University.

Root Growth Response

The results of the experimental design established to assess the new root growth of the outplanted treatments were not analysed statistically because the nature of the response variables did not lend themselves to strict statistical test procedures. The data were therefore analysed graphically.

Seedling Morphological Response

Ground caliper increment was plotted over degree growing days accumulated since planting for both nursery planting times. Periodic ground caliper increment and periodic leader extension increment were plotted over growth period for both the nursery and the Raith trials. As well, significant differences were determined for end of season height, leader extension, ground caliper, and top and root dry weight by conducting an analysis of variance (ANOVA) or an analysis of covariance (ANCOVA). The latter analysis was chosen if the covariate (1986 height) increased the relative precision of the experiment (i.e. reduced the effective error mean square) (Steel and Torrie 1980). The block X treatment interaction (within cells error) was combined with the residual error if the former was not significant at α=0.25. When either procedure indicated at least one significant difference (α=0.05) between treatment means,

single degree of freedom F tests were used to make planned comparisons between treatments and planting times (Milliken and Johnson 1984). ANOVA's, ANCOVA's, and the single degree of freedom F tests were performed using the SPSS^{X}™ MANOVA procedure on a MICROVAX II computer at Lakehead University.

RESULTS

ENVIRONMENTAL CONDITIONS AND SEEDLING PHYSIOLOGICAL RESPONSE

Nursery Trial - Planting Time 1 (May 14)

Water Relations Response

First Measurement Patterns (1 to 22 Days After Planting)

Snowfall during the 1986-87 winter months and rainfall during a six week period prior to planting was well below normal for the Thunder Bay area and it is likely that soil drought caused unfavourable internal seedling water relations and impaired establishment immediately following planting (Appendix VIII, Figures VIII.1 and VIII.2). However, edaphic conditions improved following a heavy rain on May 16 (Day 2) (Figure 2.2). The 22 day period following planting (May 15 to June 5) was cool and wet (Appendix VIII, Figures VIII.2 and VIII.3). Weather data recorded by Environment Canada (1987) indicated that effective insolation averaged 6.1 hours per day. Maximum temperatures ranged from 6.4 ° C to 25.5 ° C and averaged 16.3 ° C. Minimum temperatures ranged from -3.0 ° C to 10.8 ° C, averaged 4.9 ° C, and fell below zero on 4 nights. A total of 80.7 mm of rain were recorded over 11 days and a trace of rain fell on an additional 5 days. At the time of first g_S and E_t measurement (Appendix IX, Table IX.1), the atmospheric conditions recorded at the site at a height of 10 cm differed considerably between sample days. However, temperature, RH, and VPD were generally greater during the latter half of the 22 day post-planting period (Figure 2.1).

Gaseous exchange patterns indicate that the fall lifted treatments (FL-48-P1, FL-7-P1) and the spring lifted treatments (SL-7-P1, SL-1-P1) behaved similarly (Figure 2.2) although similarities were less evident in the more variable nursery than controlled environment (Chapter 1). As well, g_S and E_t response patterns were less similar under field conditions. For example, g_S increased and then decreased for all treatments between Days 1 and 4 while E_t generally decreased over the same period. However, day to day fluctuations in g_S and E_t were generally in the same direction for all treatments and although they most closely followed fluctuations in RH and temperature, respectively, a clear correlation was not evident.

First measurement g_S and E_t ranged by a maximum of 0.513 $cm \cdot sec^{-1}$ and 0.226 $mg \cdot cm^{-2} \cdot sec^{-1}$, respectively on Day 17 to a minimum of 0.070 $cm \cdot sec^{-1}$ on Day 10 and 0.048 $mg \cdot cm^{-2} \cdot sec^{-1}$ on Day 1, respectively (Figure 2.2). Rates were greater for the spring lifted seedlings, particularly SL-7-P1,

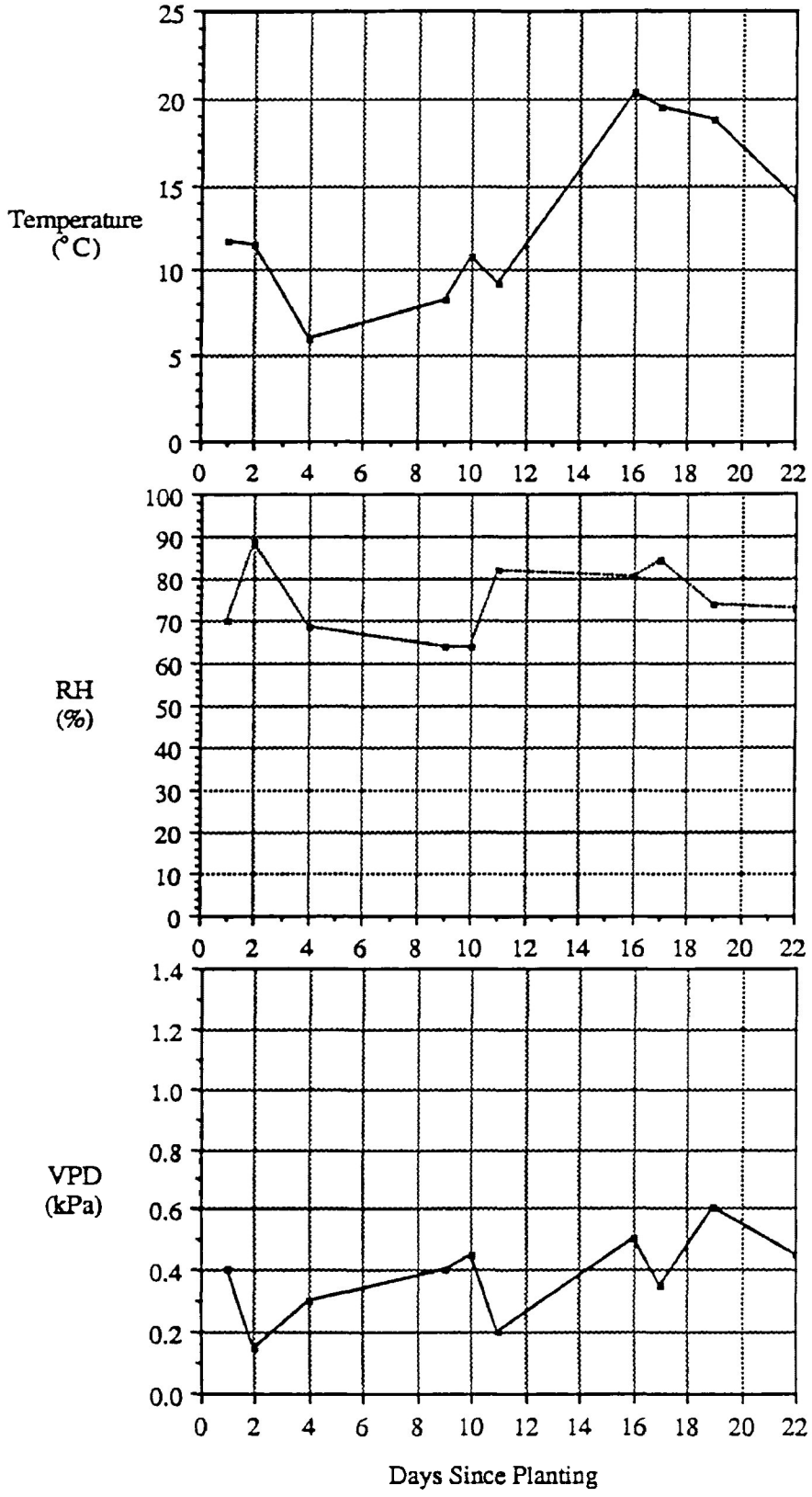

Figure 2.1. Temperature, relative humidity (RH) and vapour pressure deficit (VPD) recorded near the soil surface at the time of the first stomatal conductance and transpiration measurement at the Thunder Bay Forest Nursery from May 15 (Day 1) to June 5, 1987 (Day 22). See Appendix IX, Table IX.1 for sample times.

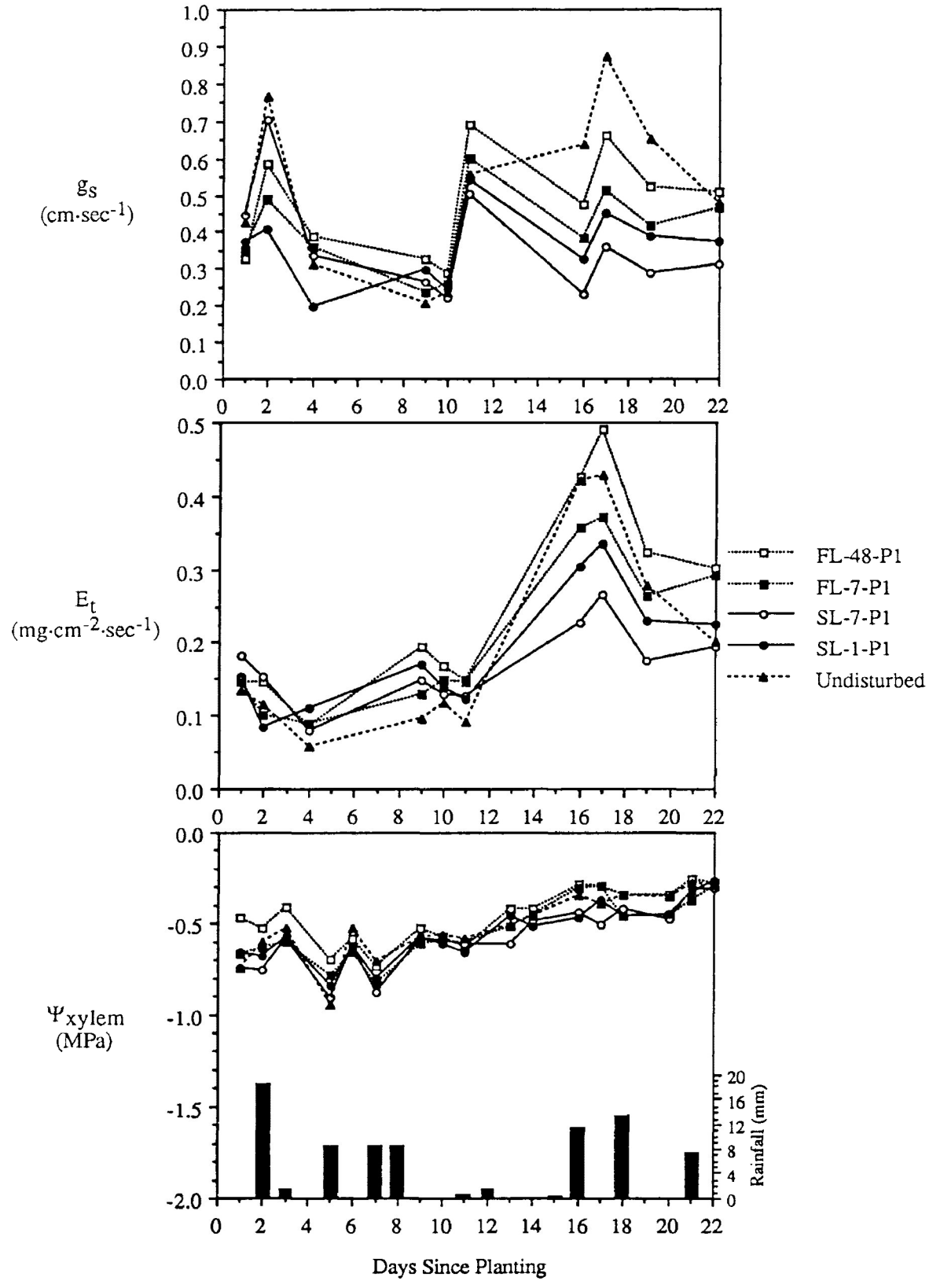

Figure 2.2. First measurement rates of stomatal conductance (g_S), transpiration (E_t) and xylem pressure potential (Ψ_{xylem}) for Nursery Trial: Planting Time 1 seedlings and daily rainfall from May 15 (Day 1) to June 5, 1987 (Day 22). See Table 2.1 for treatment code descriptions and Appendix IX, Table IX.1 for sample times.

than for the fall lifted seedlings on Day 1. There was considerable variation between treatments on Days 1 to 10 inclusive. Thereafter, the fall lifted seedlings, particularly treatment FL-48-P1, showed greater rates than the spring lifted seedlings. SL-7-P1 seedlings generally had greater rates than SL-1-P1 seedlings after Day 4. No clear ranking was apparent for the undisturbed seedlings. Not all treatments achieved the greatest rates on the same day, nor did the lowest rates occur on the same day for all treatments. The maximum E_t rates occurred for all treatments on Day 17 and the minimum rates generally occurred on Day 4. Although the vapour pressure gradient at the leaf-air interface provides the driving force for E_t, the VPD differed by only 0.5 kPa between these days.

Treatment hierarchies were less apparent from first measurement Ψ_{xylem} values (Figure 2.2) which increased (became less negative) for all treatments over the 22 day experimental period from an overall average of -0.66 MPa on Day 1 to an overall average of -0.29 MPa on Day 22. The highest (least negative) values were commonly recorded for undisturbed and fall lifted seedlings, particularly treatment FL-48-P1. The lowest (most negative) values usually occurred for treatment SL-7-P1. The greatest differences between treatments occurred during the first week following planting. Between treatment variation was greatest on Day 1 when Ψ_{xylem} ranged by 0.28 MPa and least on Day 22 when Ψ_{xylem} ranged by 0.04 MPa.

Diurnal Patterns

May 15, 1987 (1 day after planting)

May 15 was mostly cloudy with sunny periods during the early afternoon. Sunrise was at 0611 h[1] and sunset was at 2137 h. Temperature, RH, and VPD recorded over the sample day at a height of 10 cm averaged 13.6 ° C, 64 %, and 0.6 kPa, respectively (Figure 2.3). 2.2 mm of rain fell during the previous 48 hours (Appendix VIII, Figure VIII.2). The mean shoot elongation within the 1986 terminal whorl for each treatment is presented by Table 2.6.

The greatest g_s rates were usually recorded for the undisturbed seedlings and the lowest for the FL-7-P1 seedlings (Figure 2.4). The g_s rates rapidly declined for the fall lifted and SL-7-P1 seedlings as the sample day progressed until minimum values averaging 0.171 cm·sec^{-1} were recorded between 1230 h and 1430 h. In contrast, g_s decreased slightly and then increased for the undisturbed and freshly lifted seedlings. The g_s rates then fell rapidly for the freshly lifted seedlings while the undisturbed seedlings showed a very gradual decline. All treatments showed increased rates towards the end of the measurement day as RH increased and temperature and VPD declined.

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[1] All references to time are Daylight Saving Time, Eastern Time Zone (EDT).

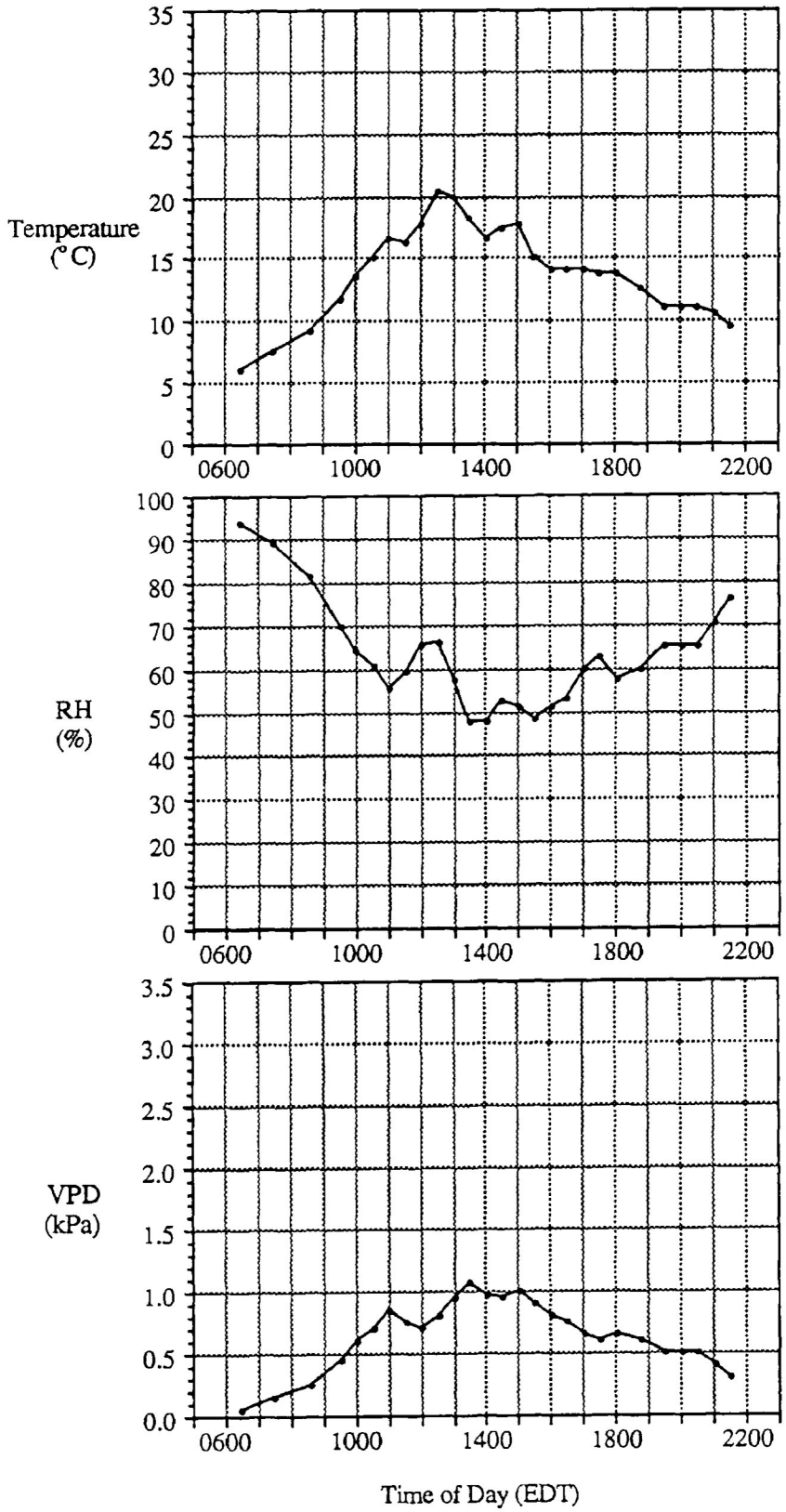

Figure 2.3. Diurnal patterns of temperature, relative humidity (RH) and vapour pressure deficit (VPD) recorded near the soil surface at the Thunder Bay Forest Nursery on May 15, 1987 (1 day after planting).

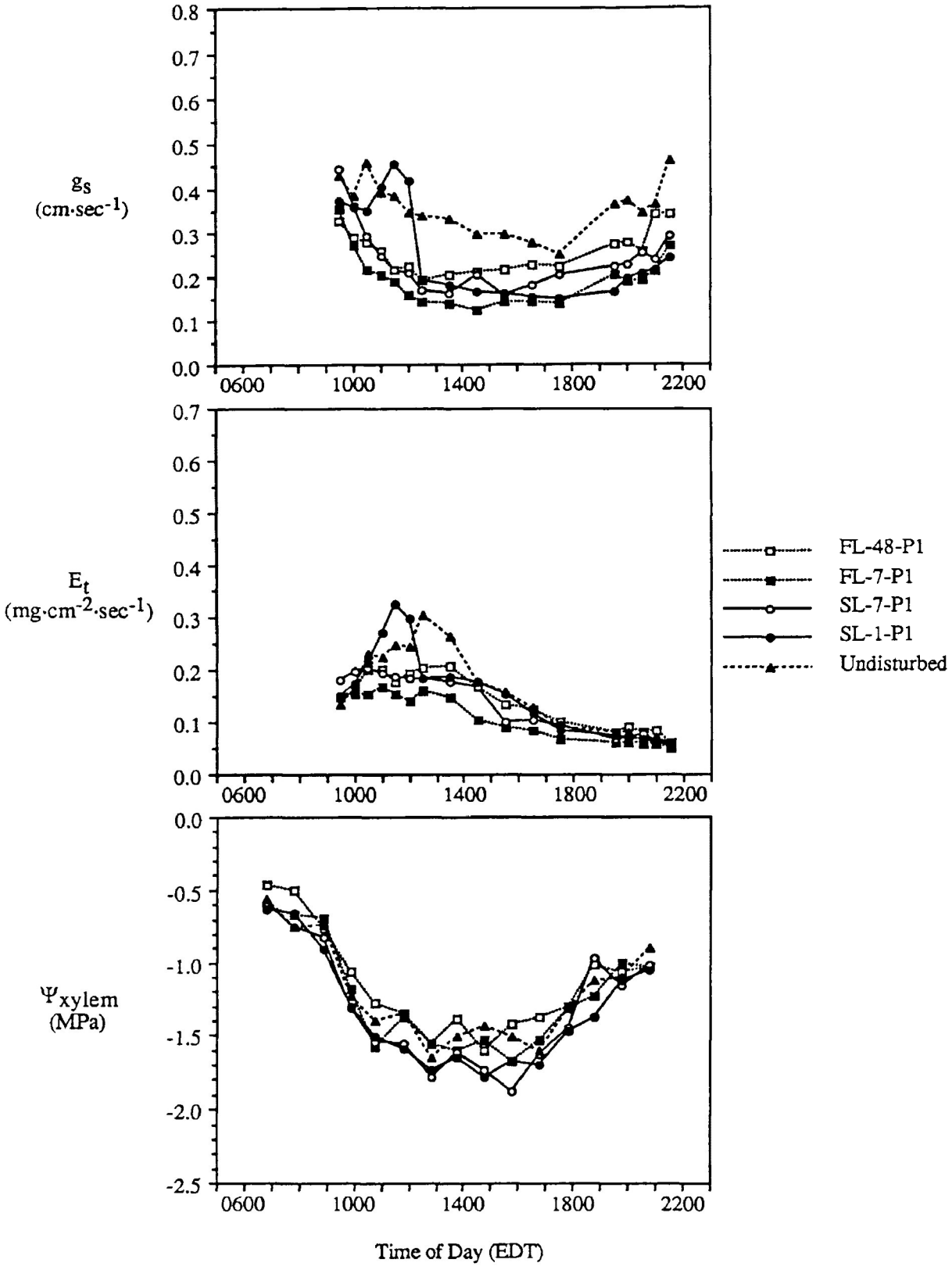

Figure 2.4. Diurnal patterns of stomatal conductance (g_s), transpiration (E_t) and xylem pressure potential (Ψ_{xylem}) for Nursery Trial: Planting Time 1 seedlings on May 15, 1987 (1 day after planting). See Table 2.1 for treatment code descriptions.

Table 2.6. Mean shoot elongation within the 1986 terminal whorl for each treatment evaluated for gaseous exchange on May 15, 1987.

Treatment[1]	Mean Shoot Elongation (cm)
FL-48-P1	0.0
FL-7-P1	0.0
SL-7-P1	0.5
SL-1-P1	0.9
Undisturbed	0.9

[1] See Table 2.1 for treatment code descriptions.

In general, the greatest E_t rates occurred for the undisturbed seedlings and the lowest for treatment FL-7-P1 (Figure 2.4). E_t rates contrasted g_s rates by increasing initially and then decreasing. This was most notable for the freshly lifted and undisturbed seedlings. E_t rates decreased as the evaporative demand decreased after 1330 h. As E_t declined, the variation between treatments was reduced. All treatments had very low rates averaging 0.056 $mg \cdot cm^{-2} \cdot sec^{-1}$ and ranging by only 0.010 $mg \cdot cm^{-2} \cdot sec^{-1}$ at the end of the sample day.

Ψ_{xylem} was commonly higher for FL-48-P1 and undisturbed seedlings and lower for the spring lifted seedlings (Figure 2.4). Ψ_{xylem} was highest and similar for all treatments at the beginning of the sample day when it averaged -0.057 MPa. Thereafter, Ψ_{xylem} fell only slightly over the first hour, more gradually until 1250 h to 1545 h, and then increased. The lowest Ψ_{xylem} value (-1.88 MPa) was recorded at 1545 h for treatment SL-7-P1. At the end of the sample day, Ψ_{xylem} was highest for the undisturbed seedlings (-0.90 MPa) and similar for the outplants averaging -1.03 MPa.

June 5, 1987 (22 days after planting)

June 5 was mostly cloudy becoming mostly sunny after 1800 h. Sunrise was at 0557 h and sunset was at 2154 h. Temperature, RH, and VPD recorded over the sample day at a height of 10 cm averaged 17.0 ° C, 60 %, and 0.9 kPa, respectively (Figure 2.5). 7.4 mm of rain fell during the previous 48 hours (Appendix VIII, Figure VIII.3). The mean shoot elongation within the 1986 terminal whorl for each treatment is presented by Table 2.7.

The greatest g_s rates were commonly recorded for the undisturbed seedlings and the lowest for SL-7-P1 seedlings (Figure 2.6). The fall lifted treatments, particularly FL-48-P1, exhibited greater rates than the spring lifted treatments. All treatments showed their greatest rates at the beginning of the sample day when g_s ranged from 0.310 $cm \cdot sec^{-1}$ for treatment SL-7-P1 to 0.505 $cm \cdot sec^{-1}$ for treatment FL-48-P1. Thereafter, g_s declined rapidly and then more gradually until minimum values were reached

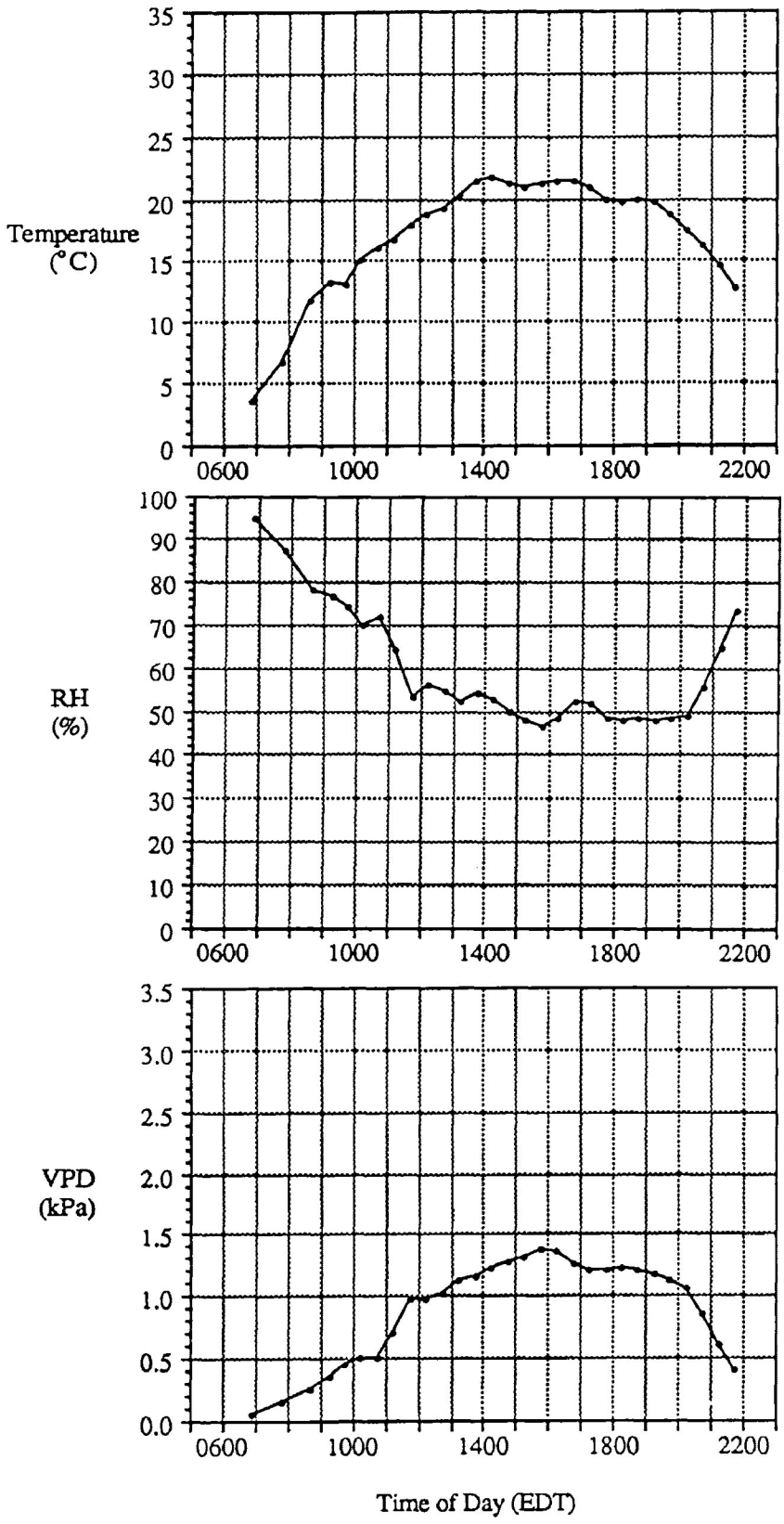

Figure 2.5. Diurnal patterns of temperature, relative humidity (RH) and vapour pressure deficit (VPD) recorded near the soil surface at the Thunder Bay Forest Nursery on June 5, 1987 (22 days after planting).

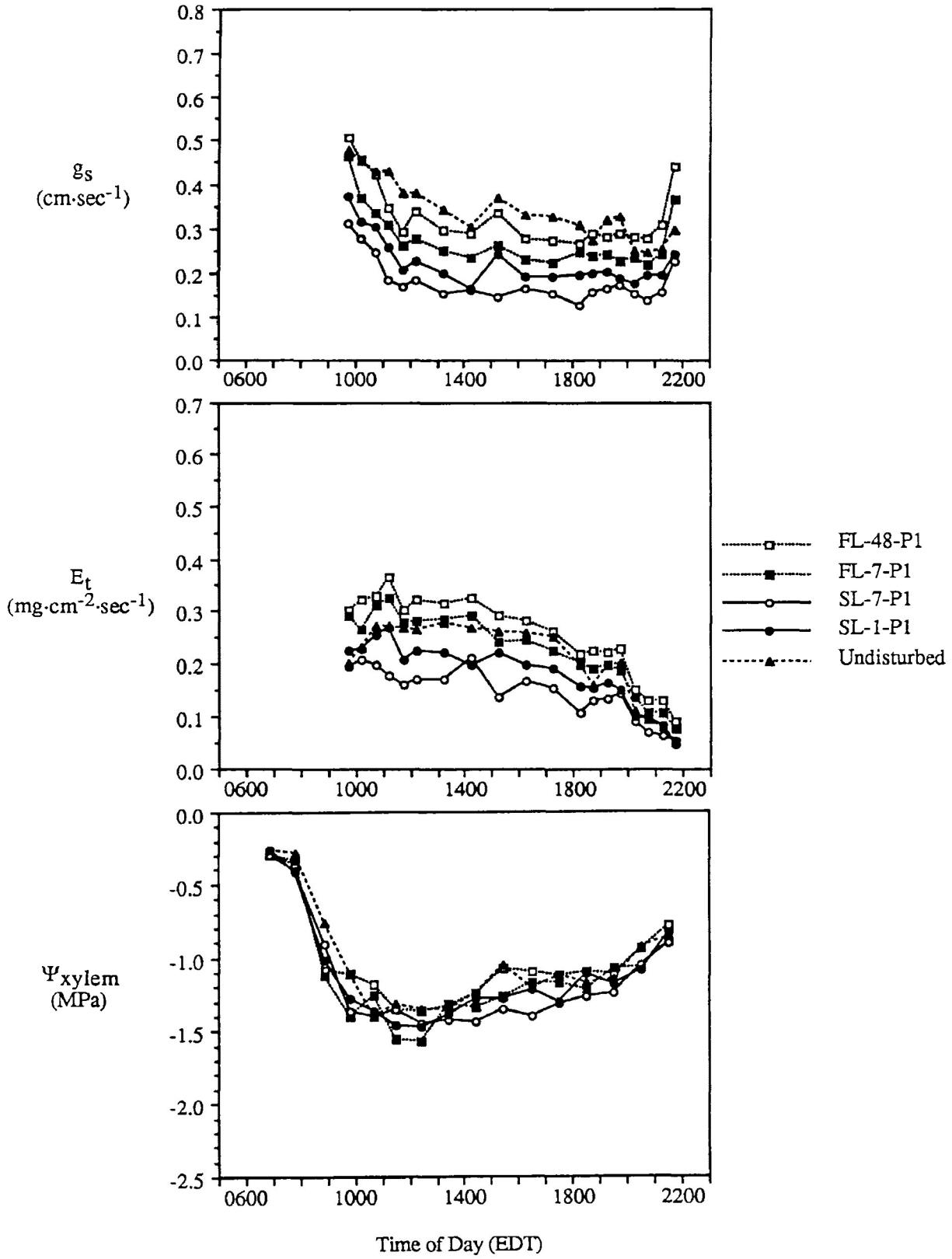

Figure 2.6. Diurnal patterns of stomatal conductance (g_s), transpiration (E_t) and xylem pressure potential (Ψ_{xylem}) for Nursery Trial: Planting Time 1 seedlings on June 5, 1987 (22 days after planting). See Table 2.1 for treatment code descriptions.

between around 1700 h for the outplants and 2045 h for the undisturbed seedlings. The g_s rates increased abruptly for all treatments during the last sample period.

Table 2.7. Mean shoot elongation within the 1986 terminal whorl for each treatment evaluated for gaseous exchange on June 5, 1987.

Treatment[1]	Mean Shoot Elongation (cm)
FL-48-P1	0.6
FL-7-P1	0.2
SL-7-P1	1.2
SL-1-P1	1.4
Undisturbed	2.1

[1] See Table 2.1 for treatment code descriptions.

E_t rates were generally greater for the fall lifted, least for the spring lifted, and intermediate for the undisturbed seedlings (Figure 2.6). E_t increased slightly for all treatments after the first sample period. Thereafter E_t declined gradually until 1930 h and then more rapidly as the evaporative demand decreased. As E_t declined, the variation between treatments was reduced. All treatments exhibited their lowest E_t rates averaging 0.065 $mg \cdot cm^{-2} \cdot sec^{-1}$ and ranging by 0.045 $mg \cdot cm^{-2} \cdot sec^{-1}$ at the end of the sample day.

The highest Ψ_{xylem} values were generally recorded for the undisturbed and FL-48-P1 seedlings (Figure 2.6). Ψ_{xylem} was lowest for treatment FL-7-P1 until 1130 h and treatment SL-7-P1 thereafter. Ψ_{xylem} was greatest for all treatments at beginning of the sample day when it averaged -0.28 MPa and ranged by 0.05 MPa. Thereafter, Ψ_{xylem} declined gradually for all seedlings until 1120 h to 1255 h and then increased. Similar Ψ_{xylem} values averaging -0.87 MPa and ranging by 0.12 MPa were recorded for all treatments at the end of the sample day.

July 4, 1987 (51 days after planting)

July 4 was a clear sunny day. Sunrise was at 0601 h and sunset was at 2201 h. Temperature, RH, and VPD recorded over the sample day at a height of 10 cm averaged 23.8 ° C, 58 %, and 1.4 kPa, respectively (Figure 2.7). 9.0 mm of rain fell during the previous 48 hours (Appendix VIII, Figure VIII.4). The mean shoot elongation within the 1986 terminal whorl for each treatment is presented by Table 2.8.

The g_s response differed 51 days after planting; diurnal rates were generally greatest for the spring lifted, lowest for the fall lifted and intermediate for the undisturbed seedlings (Figure 2.8). All outplants showed their greatest rates at the beginning of the sample day while the undisturbed seedlings

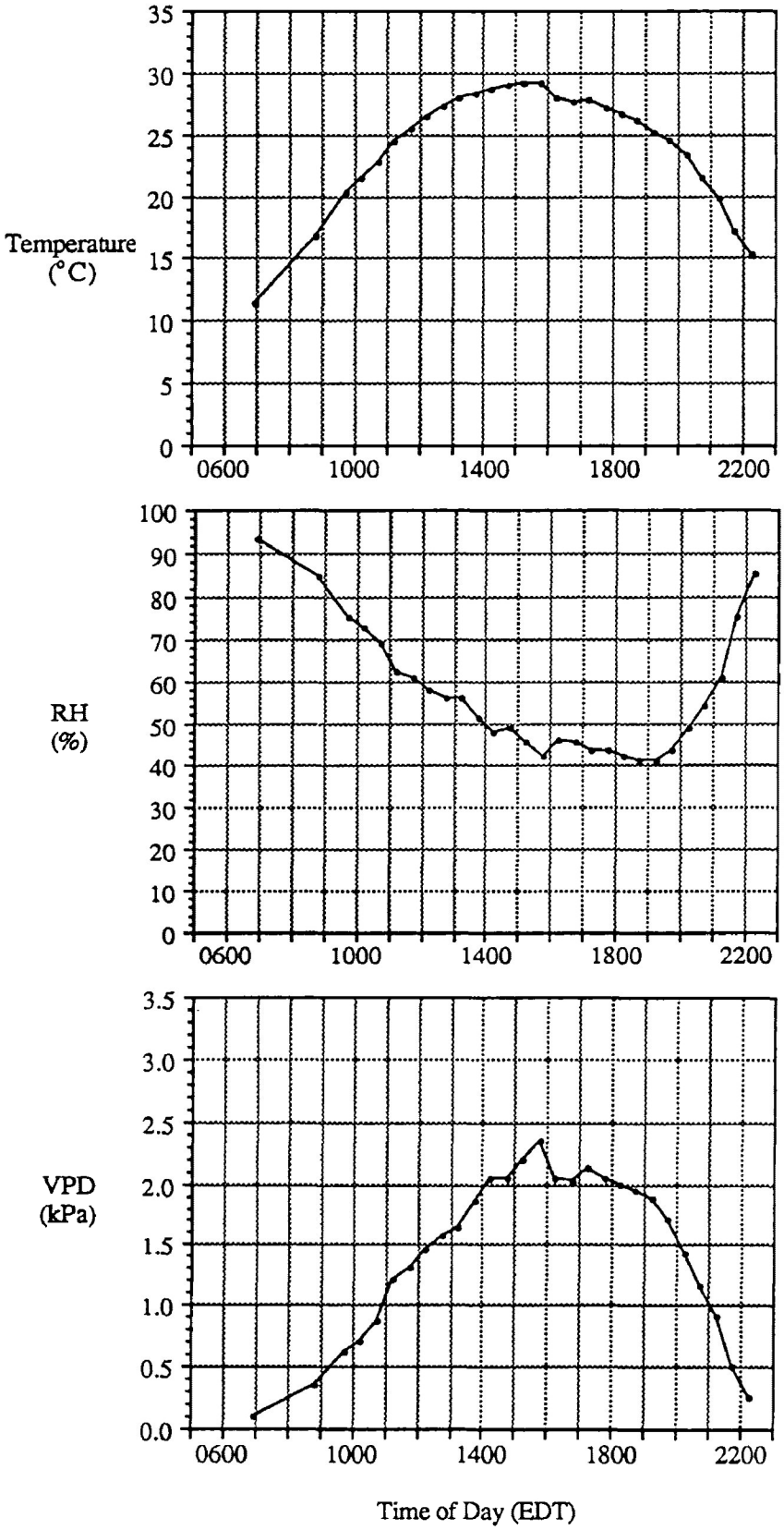

Figure 2.7. Diurnal patterns of temperature, relative humidity (RH) and vapour pressure deficit (VPD) recorded near the soil surface at the Thunder Bay Forest Nursery on July 4, 1987 (51 days after planting).

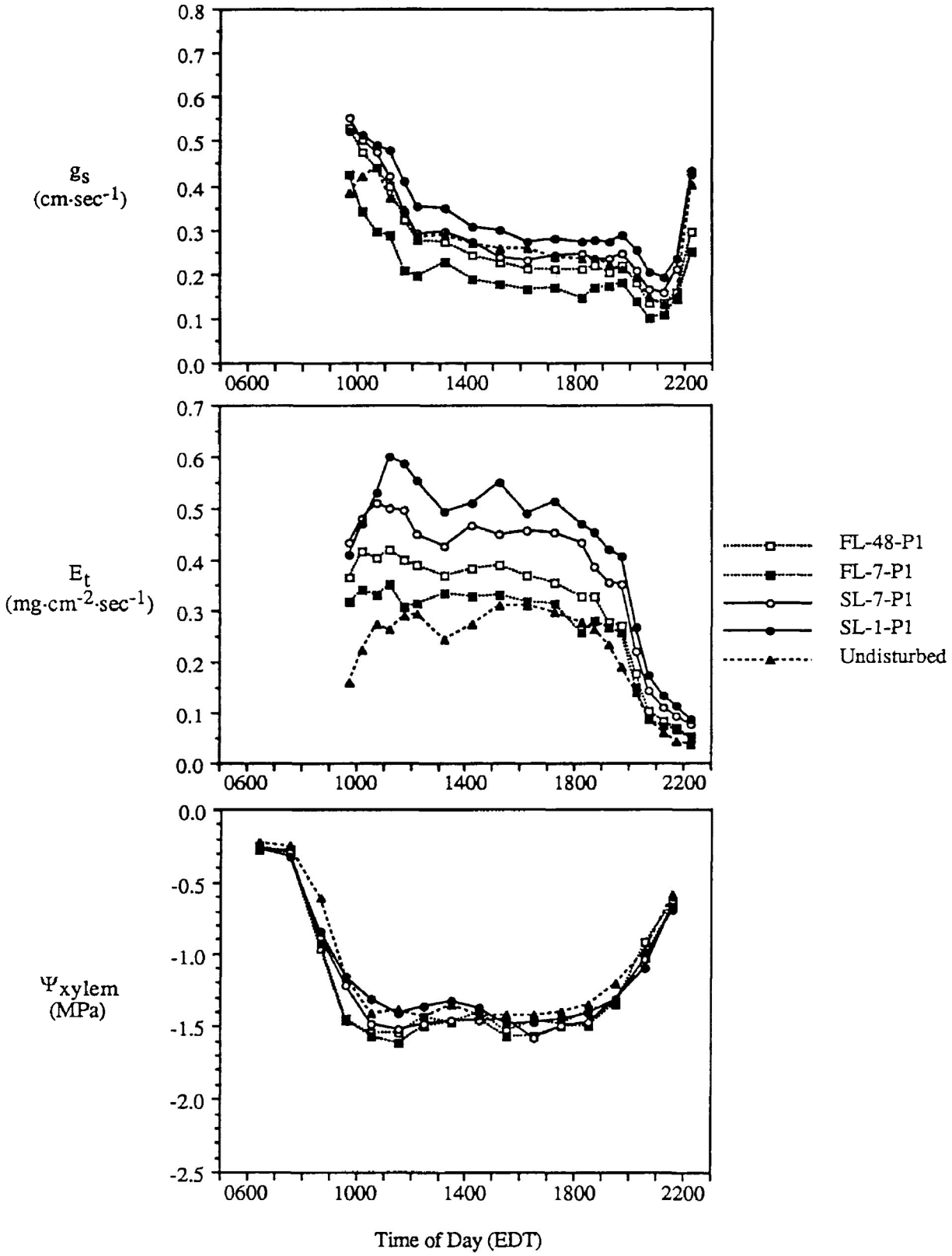

Figure 2.8. Diurnal patterns of stomatal conductance (g_s), transpiration (E_t) and xylem pressure potential (Ψ_{xylem}) for Nursery Trial: Planting Time 1 seedlings on July 4, 1987 (51 days after planting). See Table 2.1 for treatment code descriptions.

showed increased rates until 1045 h. This exception aside, g_s decreased rapidly for all treatments until about 1215 h, more gradually until about 1945 h, and then more rapidly as RH increased and temperature and VPD decreased. The g_s rates increased abruptly for all treatments after 2115 h.

Table 2.8. Mean shoot elongation within the 1986 terminal whorl for each treatment evaluated for gaseous exchange on July 4, 1987.

Treatment[1]	Mean Shoot Elongation (cm)
FL-48-P1	3.1
FL-7-P1	2.4
SL-7-P1	3.5
SL-1-P1	3.1
Undisturbed	5.7

[1] See Table 2.1 for treatment code descriptions.

E_t response hierarchies reflected g_s response hierarchies for the outplants only since the undisturbed seedlings generally exhibited the lowest E_t rates (Figure 2.8). E_t increased for all treatments until about 1045 h, declined gradually until about 1845 h, and then fell sharply as the evaporative demand diminished. The variability between treatments was minimal at the end of the sample day when E_t ranged from 0.089 $mg \cdot cm^{-2} \cdot sec^{-1}$ to 0.037 $mg \cdot cm^{-2} \cdot sec^{-1}$ for the undisturbed and freshly lifted seedlings, respectively.

Ψ_{xylem} rarely differed between treatments by more than 0.20 MPa. Slightly lower values were usually recorded for FL-7-P1 seedlings and slightly higher values for the undisturbed seedlings (Figure 2.8). Ψ_{xylem} was highest, and very similar for all treatments, over the first two measurement periods when it averaged -0.27 MPa and differed by more than 0.06 MPa. Thereafter, Ψ_{xylem} declined rapidly until 1030 h and then stabilized. Ψ_{xylem} increased rapidly after 1830 h. Very similar values were again recorded for all treatments at the end of the day when Ψ_{xylem} averaged -0.65 MPa and ranged by 0.11 MPa.

Water Flow Resistance in the Soil-Plant-Atmosphere Continuum

The stored seedlings, particularly FL-7-P1 (β_1 = -4.39), showed the largest resistances to waterflow through the SPAC immediately after planting (i.e. the R_{SPAC} coefficient [β_1] was the most negative) while the freshly lifted (β_1 = -2.83) and undisturbed seedlings (β_1 = -2.74) showed the smallest resistances (Figure 2.9). The R_{SPAC} coefficient changed as the experimental period progressed and changes differed between treatments in both direction and magnitude. The proportion of variation explained by the Ψ_{xylem} : E_t relationships (i.e. r^2, the coefficient of determination) increased for all

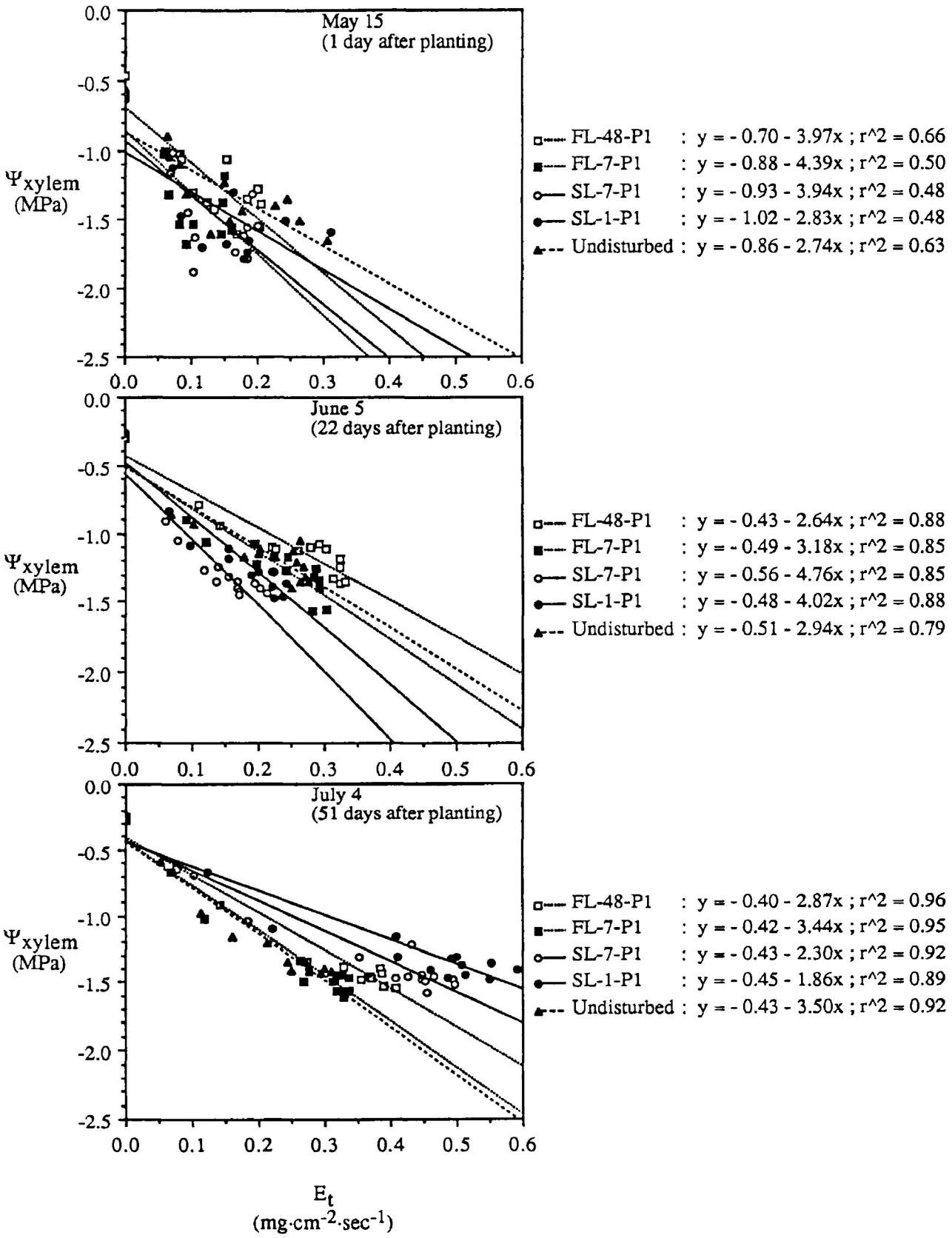

Figure 2.9. Relationship between xylem pressure potential (Ψ_{xylem}) and transpiration (E_t) for Nursery Trial: Planting Time 1 seedlings on May 15 (1 day after planting), June 5 (22 days after planting) and July 4 (51 days after planting). See Table 2.1 for treatment code descriptions.

treatments by the end of the experimental period at which time, the largest and smallest resistances to waterflow occurred for the undisturbed (β_1 = -3.50) and freshly lifted (β_1 = -1.86) seedlings, respectively.

Root Growth Response

The 14 day test period (May 14 to May 28) was cool and wet (Appendix VIII, Figure VIII.2). Weather data recorded by Environment Canada (1987) indicated that effective insolation averaged 5.2 hours per day. Maximum temperatures ranged from 6.4 ° C to 21.8 ° C and averaged 14.1 °C. Minimum temperatures ranged from -3.0 ° C to 10.1 ° C, averaged 3.9 ° C, and fell below zero on 4 nights. A total of 47.9 mm of rain were recorded on 11 days and a trace of rain fell on an additional 5 days.

Classification of root growth response suggested that root activity was strongly influenced by lifting-storage treatment (Table 2.9, Figure 2.10a). FL-7-P1 had the best new root growth at the end of the 14 day experimental period. The spring lifted treatments, particularly SL-1-P1, produced the fewest new white roots. One seedling from each spring lifted treatment produced no new root tips.

Nursery Trial - Planting Time 2 (June 15)

Water Relations Response

First Measurement Patterns (1 to 21 Days After Planting)

Rainfall was adequate and well distributed prior to planting and it is unlikely that Ψ_{soil} limited establishment immediately following planting (Appendix VIII, Figure VIII.3). The 21 day period following planting (June 16 to July 6) was warm and dry (Appendix VIII, Figures VIII.3 and VIII.4). Weather data recorded by Environment Canada (1987) indicated that effective insolation averaged 10.0 hours per day and maximum temperatures averaged 24.7 ° C. Minimum temperatures averaged 11.4 ° C. A total of 19.6 mm of rain were recorded over 9 days, the greater percentage (13.2 mm) falling on July 1 and July 2 (Environment Canada 1987). At the time of first g_s and E_t measurement (Appendix IX, Table IX.2), the atmospheric conditions recorded at the site at a height of 10 cm varied widely between sample days (Figure 2.11).

The fall lifted treatments (FL-48-P2, FL-7-P2) commonly showed greater g_s and E_t rates than the spring lifted treatments (SL-39-P2, SL-1-P2), particularly during the latter half of the 21 day post-planting period (Figure 2.12). However, the similarities that occurred between the fall and spring lifted treatments under controlled conditions (Chapter 1), and to a lesser extent during the 22 day first measurement period following Planting Time 1 (Figure 2.2), were even less apparent during Planting Time 2. Day to day fluctuations in g_s and E_t were generally in the same direction for all treatments;

Table 2.9. The lifting-storage treatments ranked in descending order of average root growth response determined using the Burdett (1979) classification code modified to include two additional classes (Appendix II).

Treatment Code[1]	Treatment Description	Modified Burdett Code
Planting Time 1 (May 14)		
FL-7-P1	Fall lifted, overwinter frozen stored, conditioned at +2 ± 1 °C for 7 days	2.80
FL-48-P1	Fall lifted, overwinter frozen stored, conditioned at +2 ± 1 °C for 48 days	2.32
SL-7-P1	Spring lifted, stored at +2 ± 1 °C for 7 days	1.88
SL-1-P1	Spring lifted, stored at +2 ± 1 °C for 1 day	1.40
Planting Time 2 (June 15)		
FL-7-P2	Fall lifted, overwinter frozen stored, conditioned at +2 ± 1 °C for 7 days	4.64
FL-48-P2	Fall lifted, overwinter frozen stored, conditioned at +2 ±1 °C for 48 days	4.40
SL-39-P2	Spring lifted, stored at +2 ± 1 °C for 39 days	2.60
SL-1-P2	Spring lifted, stored at +2 ± 1 °C for 1 day	1.28

[1] See Table 2.1 for treatment code descriptions, lifting and planting dates, and temperatures and durations of storage.

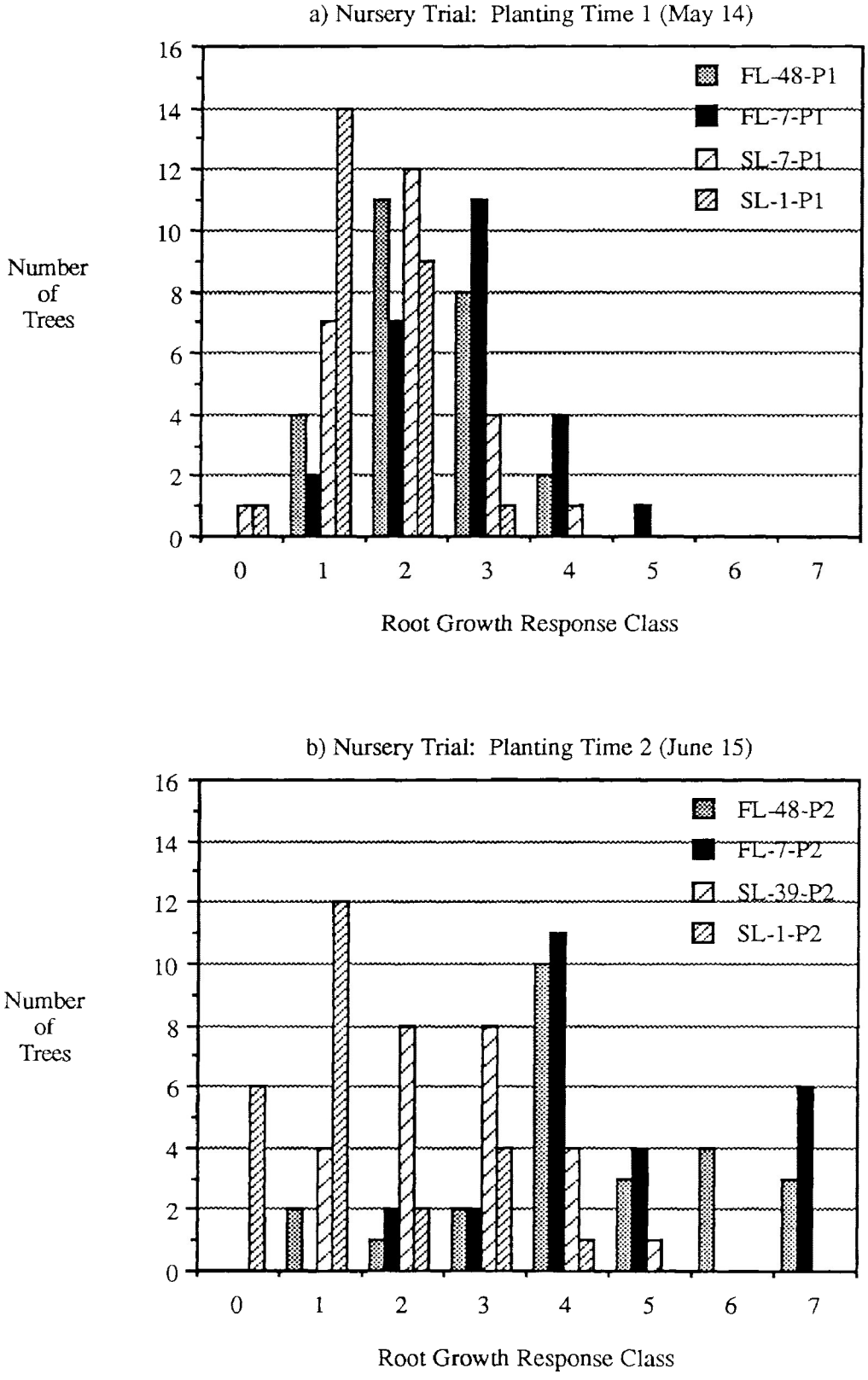

Figure 2.10. Root growth response determined using the Burdett (1979) classification code modified to include two additional classes (Appendix II) for: a) Planting Time 1 (May 14), and b) Planting Time 2 (June 15). A larger class value indicates increased root growth. See Table 2.1 for treatment code descriptions.

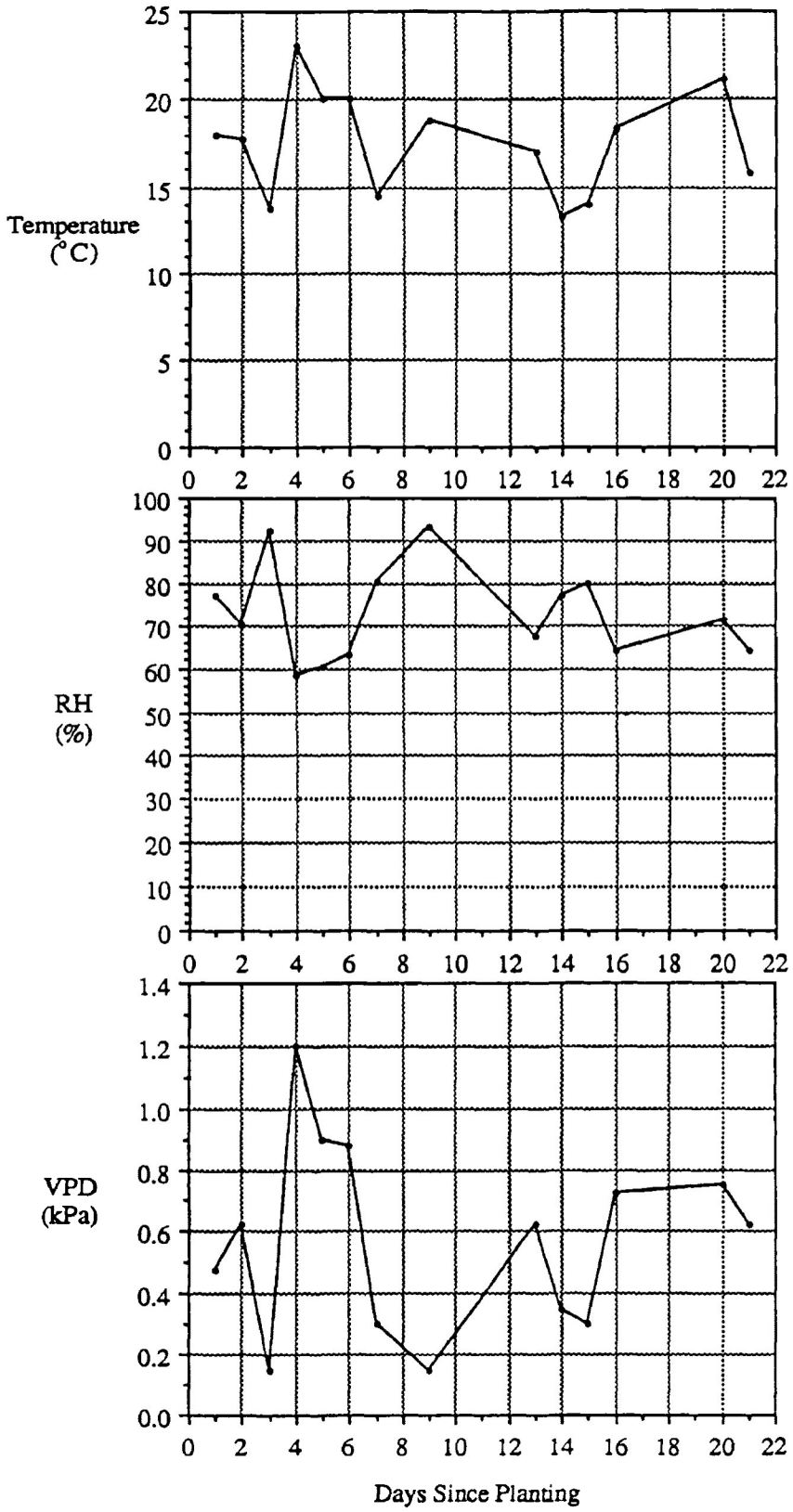

Figure 2.11. Temperature, relative humidity (RH) and vapour pressure deficit (VPD) recorded near the soil surface at the time of the first stomatal conductance and transpiration measurement at the Thunder Bay Forest Nursery from June 16 (Day 1) to July 6, 1987 (Day 21). See Appendix IX, Table IX.2 for sample times.

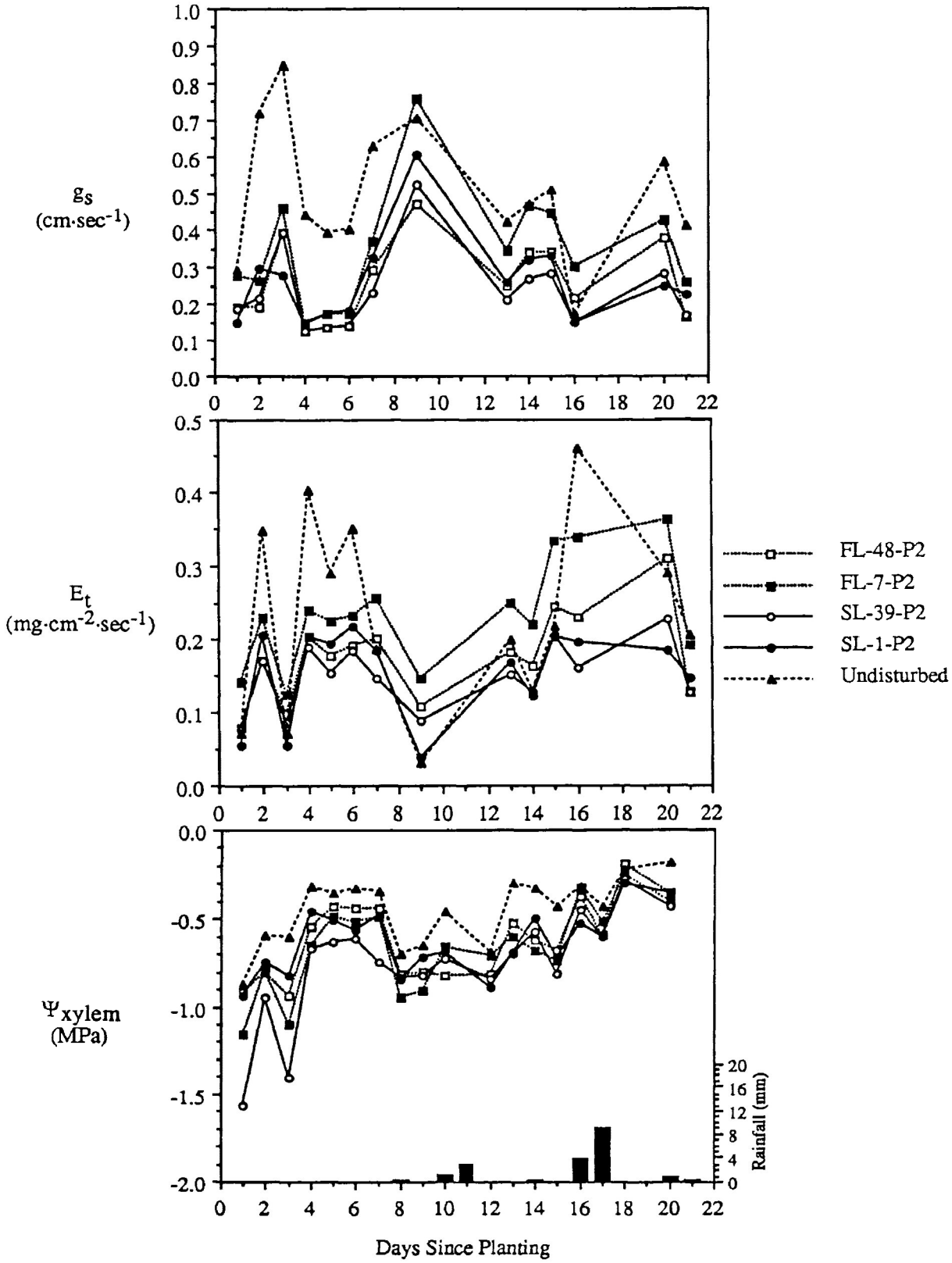

Figure 2.12. First measurement rates of stomatal conductance (g_s), transpiration (E_t) and xylem pressure potential (Ψ_{xylem}) for Nursery Trial: Planting Time 2 seedlings and daily rainfall from June 16 (Day 1) to July 6, 1987 (Day 21). See Table 2.1 for treatment code descriptions and Appendix IX, Table IX.2 for sample times.

fluctuations in g_s most closely followed fluctuations in RH, fluctuations in E_t did not respond similarly for all treatments to any of the selected atmospheric variables.

First measurement g_s ranged by a maximum of 0.568 $cm \cdot sec^{-1}$ on Day 3 to a minimum of 0.155 $cm \cdot sec^{-1}$ on Day 16 (Figure 2.12). The greatest rates were commonly exhibited by the undisturbed seedlings. There was little difference between outplants during the first 6 days following planting. Thereafter, the fall lifted seedlings, particularly treatment FL-7-P2, generally exhibited greater rates than the spring lifted seedlings, particularly treatment SL-39-P2. First measurement E_t ranged by a maximum of 0.299 $mg \cdot cm^{-2} \cdot sec^{-1}$ on Day 16 to a minimum of 0.070 $mg \cdot cm^{-2} \cdot sec^{-1}$ on Day 3 (Figure 2.12). FL-7-P2 seedlings exhibited greater rates than any other outplants and occasionally greater rates than the undisturbed seedlings. The lowest rates were usually recorded for the spring lifted treatments. The most apparent difference between g_s and E_t response occurred on Day 9 and was presumably due to the low VPD at the time of sampling.

Treatment response hierarchies are less apparent from first measurement Ψ_{xylem} (Figure 2.12) which increased for all treatments over the 20 day experimental period from an overall average of -1.09 MPa on Day 1 to an overall average of -0.34 MPa on Day 20. The greatest increases occurred for the outplants, particularly treatment SL-39-P2. The highest values were commonly recorded for undisturbed and fall lifted seedlings, particularly treatment FL-48-P2. The greatest difference between outplants occurred from Days 1 to 7, inclusive over which period the lowest Ψ_{xylem} values were recorded for treatment SL-39-P2. The smallest difference between treatments (0.11 MPa) occurred on Day 18 at which time, the highest Ψ_{xylem} values were recorded for all outplants; 13.2 mm of rain fell during the 48 hour period preceding Day 18.

Diurnal Patterns

June 16, 1987 (1 day after planting)

June 16 was a sunny day with scattered cloud cover. Sunrise was at 0554 h and sunset was at 2201 h. Temperature, RH, and VPD recorded over the sample day at a height of 10 cm averaged 26.1° C, 47 %, and 1.9 kPa, respectively (Figure 2.13). No precipitation was recorded during the previous 48 hours (Appendix VIII, Figure VIII.3). The mean shoot elongation measured within the 1986 terminal whorl was clearly more advanced for the spring lifted and undisturbed seedlings at the second (Table 2.10) than the first planting time (Table 2.6).

The greatest g_s rates were commonly recorded for the undisturbed seedlings (Figure 2.14). The g_s rates increased for the outplants until 0715 h to 0745 h and then decreased rapidly until 1015 h. Thereafter, g_s was low, averaged 0.065 $cm \cdot sec^{-1}$ and variation between treatments was minimal. It is probable that these low values are indicative of stomatal closure. The g_s rates increased over a longer

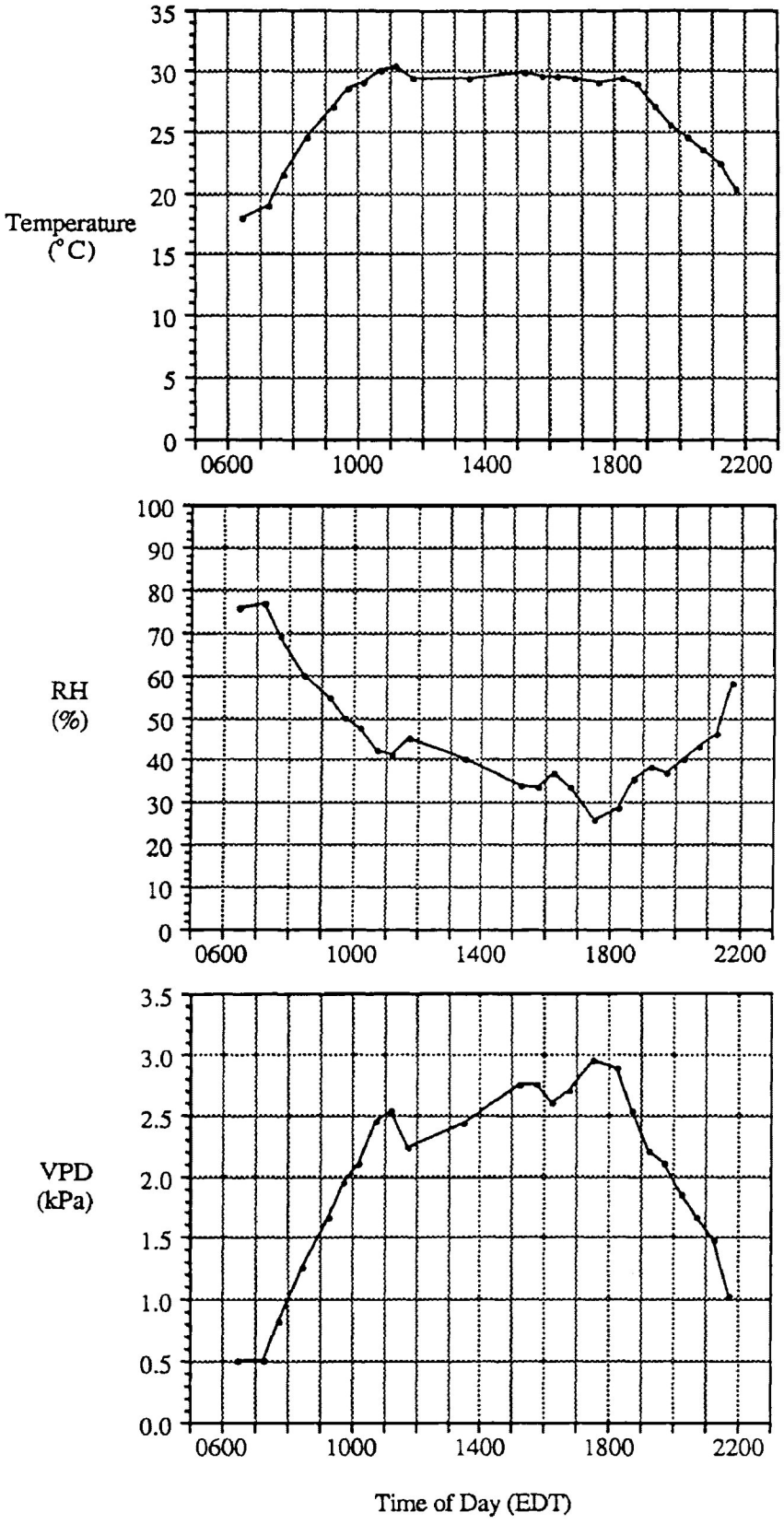

Figure 2.13. Diurnal patterns of temperature, relative humidity (RH) and vapour pressure deficit (VPD) recorded near the soil surface at the Thunder Bay Forest Nursery on June 16, 1987 (1 day after planting).

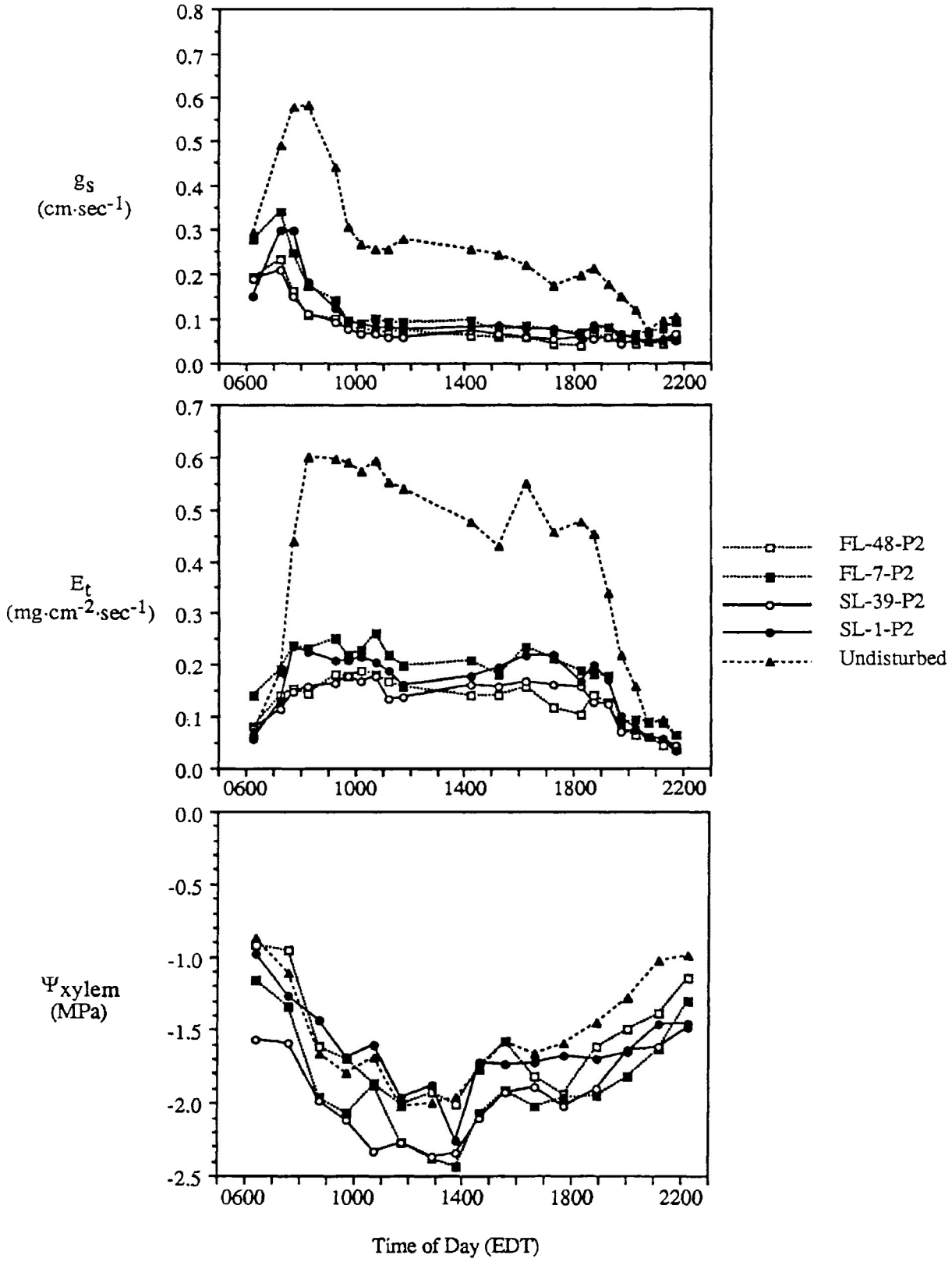

Figure 2.14. Diurnal patterns of stomatal conductance (g_s), transpiration (E_t) and xylem pressure potential (Ψ_{xylem}) for Nursery Trial: Planting Time 2 seedlings on June 16, 1987 (1 day after planting). See Table 2.1 for treatment code descriptions.

period (until 0815 h) for the undisturbed seedlings and there were two periods of rapid decline. The first occurred between 0815 h and 0945 h (when g_s also decreased for the outplants) and the second occurred as the evaporative demand diminished towards the end of the sample day.

Table 2.10. Mean shoot elongation within the 1986 terminal whorl for each treatment evaluated for gaseous exchange on June 16, 1987.

Treatment[1]	Mean Shoot Elongation (cm)
FL-48-P2	0.0
FL-7-P2	0.0
SL-7-P2	0.5
SL-1-P2	5.0
Undisturbed	4.9

[1] See Table 2.1 for treatment code descriptions.

In general, the greatest E_t rates occurred for the undisturbed seedlings and the lowest for treatments FL-48-P2 and SL-39-P2 (Figure 2.14). However, rate differences between outplants were slight. E_t increased initially for all treatments and then stabilized for the outplants but declined gradually over the day for the undisturbed seedlings. After the 1915 h sample period, rates decreased rapidly for all treatments as the evaporative demand diminished. The variability between treatments was minimal during the last sample period when E_t ranged from 0.063 $mg \cdot cm^{-2} \cdot sec^{-1}$ to 0.032 $mg \cdot cm^{-2} \cdot sec^{-1}$ for the undisturbed and freshly lifted seedlings, respectively.

The highest Ψ_{xylem} values were commonly recorded for freshly lifted and undisturbed seedlings (Figure 2.14). The lowest values were generally occurred for treatment SL-39-P2. Ψ_{xylem} was highest for all treatments, with the exception of SL-39-P2, at the beginning of the sample day. The highest Ψ_{xylem} values recorded for SL-39-P2 seedlings occurred during the last sample period. Ψ_{xylem} fluctuated considerably between sample times but generally decreased for all treatments until midday (1250 h to 1345 h) and then increased gradually until the last sample period.

July 8, 1987 (23 days after planting)

July 8 was foggy during the early morning becoming mostly sunny with occasional cloudy periods after 0700 h. Sunrise was at 0603 h and sunset was at 2159 h. Temperature, RH, and VPD recorded over the sample day at a height of 10 cm averaged 27.2 ° C, 51 %, and 2.0 kPa, respectively (Figure 2.15). 0.8 mm of rain fell during the previous 48 hours (Appendix VIII, Figure VIII.4). The mean shoot elongation within the 1986 terminal whorl for each treatment is presented by Table 2.11.

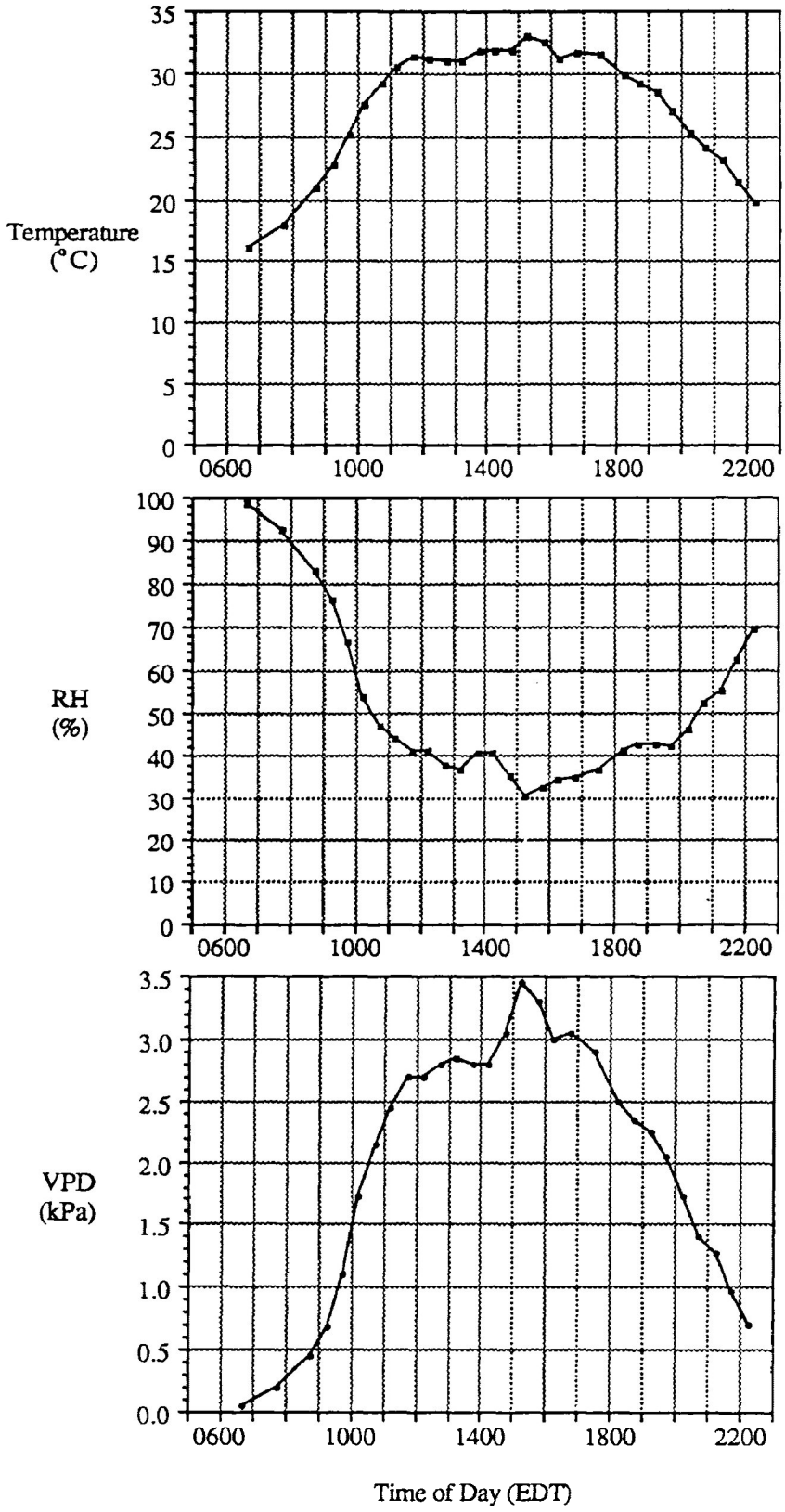

Figure 2.15. Diurnal patterns of temperature, relative humidity (RH) and vapour pressure deficit (VPD) recorded near the soil surface at the Thunder Bay Forest Nursery on July 8, 1987 (23 days after planting).

A clear treatment hierarchy was evident from the g_s patterns (Figure 2.16). The greatest rates were recorded for the undisturbed seedlings and the lowest for SL-39-P2 seedlings. The fall lifted treatments, particularly FL-7-P2, exhibited greater rates than the spring lifted treatments. All treatments showed their greatest rates at the beginning of the sample day when g_s ranged from 0.751 $cm \cdot sec^{-1}$ to 0.336 $cm \cdot sec^{-1}$ for the undisturbed and SL-39-P2 seedlings, respectively. Thereafter, g_s declined rapidly until 1115 h and then more gradually over the remainder of the day.

Table 2.11. Mean shoot elongation within the 1986 terminal whorl for each treatment evaluated for gaseous exchange on July 8, 1987.

Treatment[1]	Mean Shoot Elongation (cm)
FL-48-P2	1.0
FL-7-P2	0.8
SL-7-P2	2.0
SL-1-P2	5.7
Undisturbed	5.3

[1] See Table 2.1 for treatment code descriptions.

E_t response hierarchies reflected g_s response hierarchies (Figure 2.16). In general, E_t rates increased over the day until the evaporative demand declined at about 1800 h. The greatest rates occurred between 1515 h and 1815 h and minimum rates occurred at the end of the sample day. At this time, the variability between treatments was minimal; rates averaged 0.075 $mg \cdot cm^{-2} \cdot sec^{-1}$ and ranged by 0.055 $mg \cdot cm^{-2} \cdot sec^{-1}$.

The treatment ranking that was apparent from the diurnal patterns of gaseous exchange was not evident from the diurnal patterns of Ψ_{xylem} (Figure 2.16). The highest Ψ_{xylem} values were commonly recorded for the undisturbed and fall lifted seedlings. Ψ_{xylem} was highest, and similar for all treatments over the first two measurement periods when it averaged -0.32 MPa and differed by no more than 0.18 MPa. Thereafter, Ψ_{xylem} declined rapidly until 1030 h, very gradually until 1645 h, and then increased until the end of the sample day. Similar Ψ_{xylem} values were recorded for all treatments, excluding SL-1-P2, at the end of the sample day when they averaged -0.77 MPa and ranged by 0.06 MPa. Ψ_{xylem} values recorded for treatment SL-1-P2 were at least 0.21 MPa more negative than any other treatment at this time.

August 13, 1987 (59 days after planting)

August 13 was mostly sunny with scattered cloud cover. Sunrise was at 0647 h and sunset was at 2115 h. Temperature, RH, and VPD recorded over the sample day at a height of 10 cm averaged

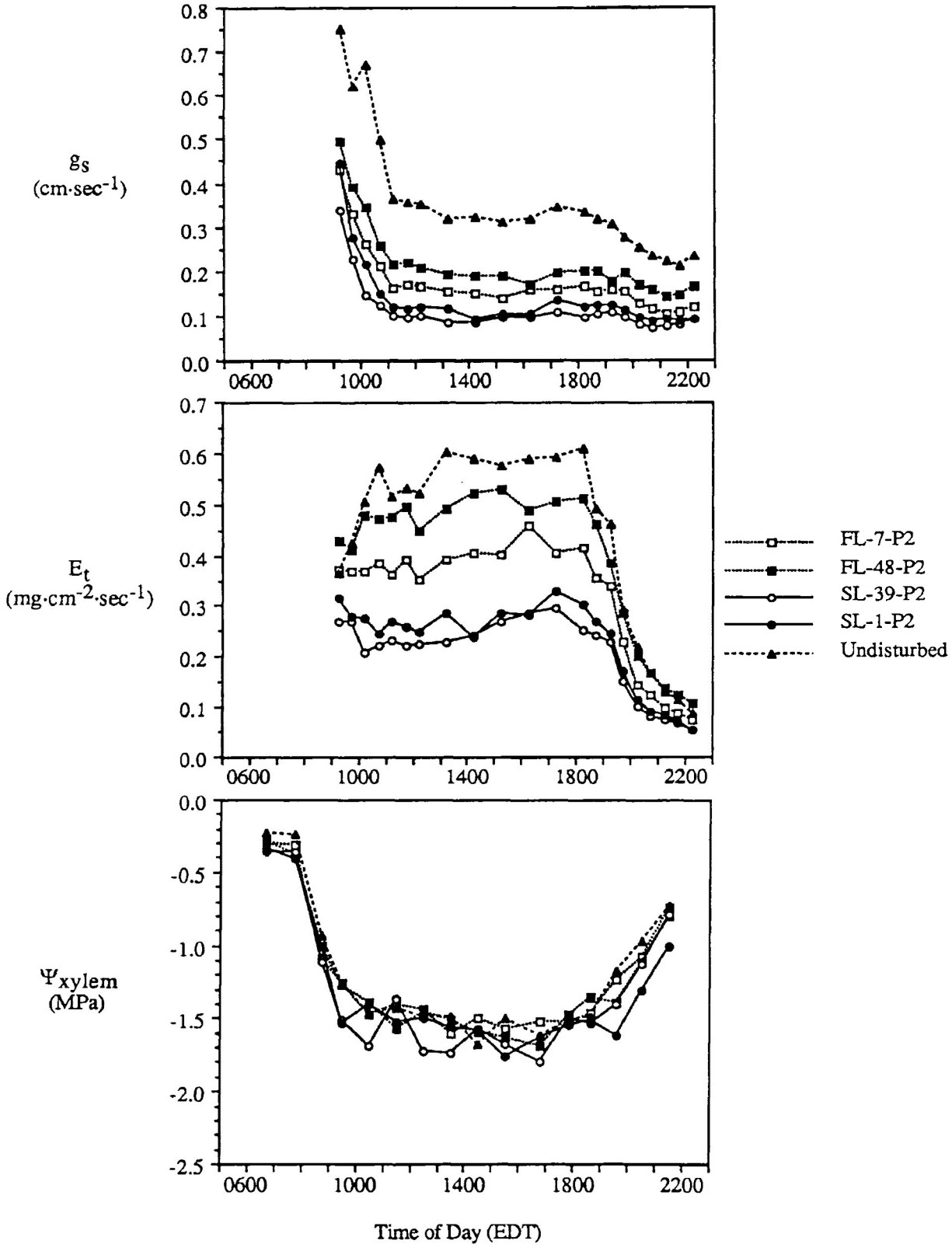

Figure 2.16. Diurnal patterns of stomatal conductance (g_s), transpiration (E_t) and xylem pressure potential (Ψ_{xylem}) for Nursery Trial: Planting Time 2 seedlings on July 8, 1987 (23 days after planting). See Table 2.1 for treatment code descriptions.

22.1° C, 74 %, and 0.7 kPa, respectively (Figure 2.17). 48.2 mm of rain fell during the previous 48 hours (Appendix VIII, Figure VIII.5). The mean shoot elongation within the 1986 terminal whorl for each treatment is presented by Table 2.12.

Table 2.12. Mean shoot elongation within the 1986 terminal whorl for each treatment evaluated for gaseous exchange on August 13, 1987.

Treatment[1]	Mean Shoot Elongation (cm)
FL-48-P2	3.9
FL-7-P2	3.8
SL-7-P2	2.9
SL-1-P2	5.4
Undisturbed	5.6

[1] See Table 2.1 for treatment code descriptions.

The g_S rates generally increased for all treatments until 1515 h, decreased until 1915 h, and then increased with increasing RH and decreasing temperature and VPD towards the end of the sample day (Figure 2.18). No clear g_S response hierarchy was evident. Sample time to sample time fluctuation was particularly extreme for FL-7-P2 seedlings.

The fluctuations that were apparent from the g_S response patterns was also evident from the E_t response patterns (Figure 2.18). However, there was a clearer ranking between E_t rates over most of the day. In general, the spring lifted seedlings, particularly SL-1-P2, exhibited the greatest rates while the undisturbed and fall lifted seedlings exhibited the lowest. E_t rates fell rapidly for all treatments after 1815 h as the evaporative demand diminished.

Ψ_{xylem} values were commonly higher for the undisturbed and lower for the fall lifted seedlings (Figure 2.18). Ψ_{xylem} was highest, and similar for all treatments during the first two measurement periods over which it averaged -0.18 MPa and ranged by 0.06 MPa at 0730 h and 0.12 MPa at 0830 h. Thereafter, Ψ_{xylem} declined rapidly and variability increased between treatments. A transient increase occurred for all treatments between 1330 h and 1630 h after which Ψ_{xylem} increased gradually until 1830 h and then more rapidly until the end of the sample day.

Water Flow Resistance in the Soil-Plant-Atmosphere Continuum

The stored seedlings, particularly SL-39-P2 (β_1 = -5.33), showed the largest SPAC resistances immediately following planting while the freshly lifted (β_1 = -2.05) and undisturbed seedlings (β_1 = -1.69) showed the smallest (Figure 2.19). The R_{SPAC} coefficient changed as the experimental period progressed and changes differed between treatments in both direction and magnitude. The proportion of

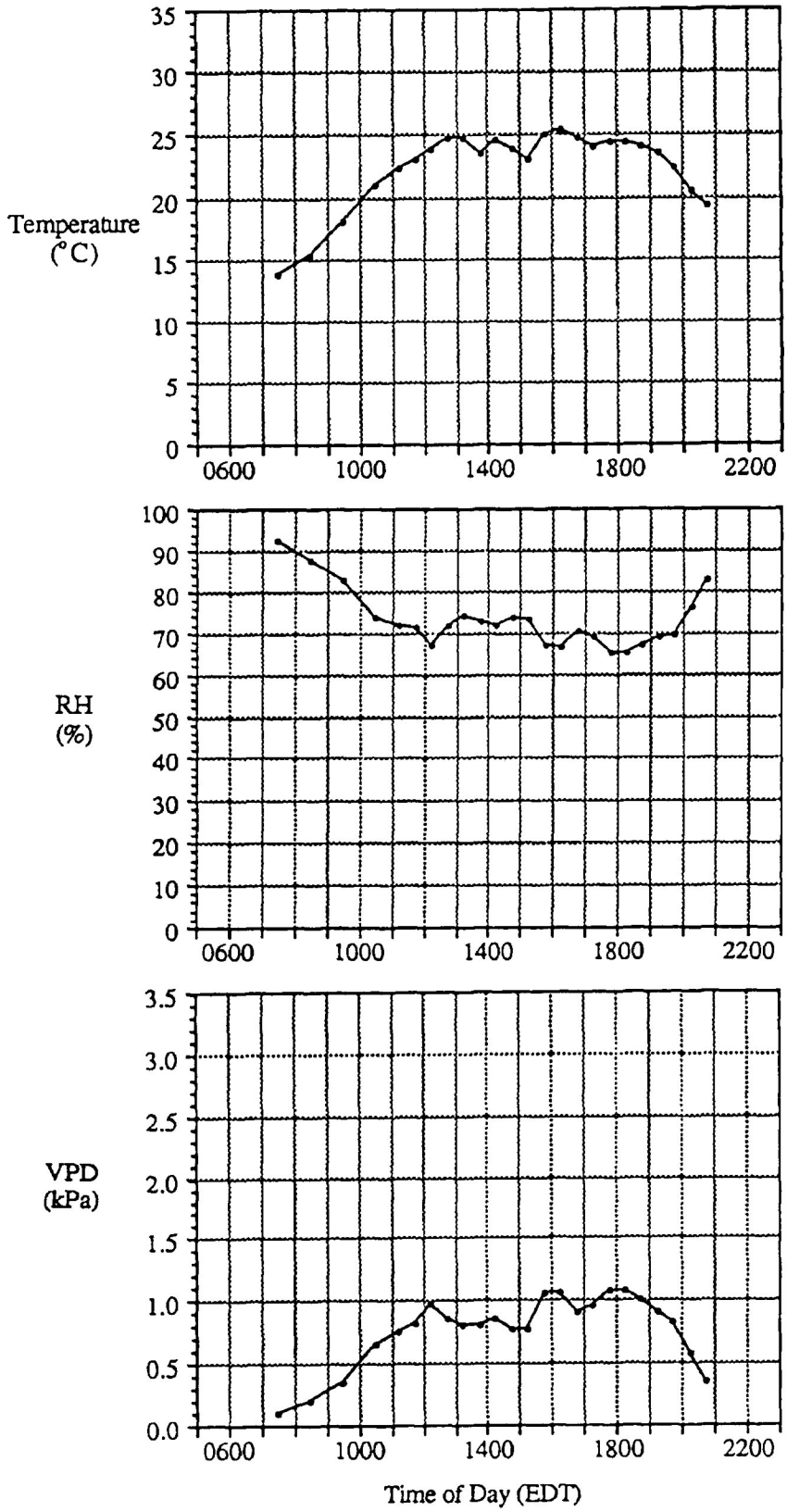

Figure 2.17. Diurnal patterns of temperature, relative humidity (RH) and vapour pressure deficit (VPD) recorded near the soil surface at the Thunder Bay Forest Nursery on August 13, 1987 (59 days after planting).

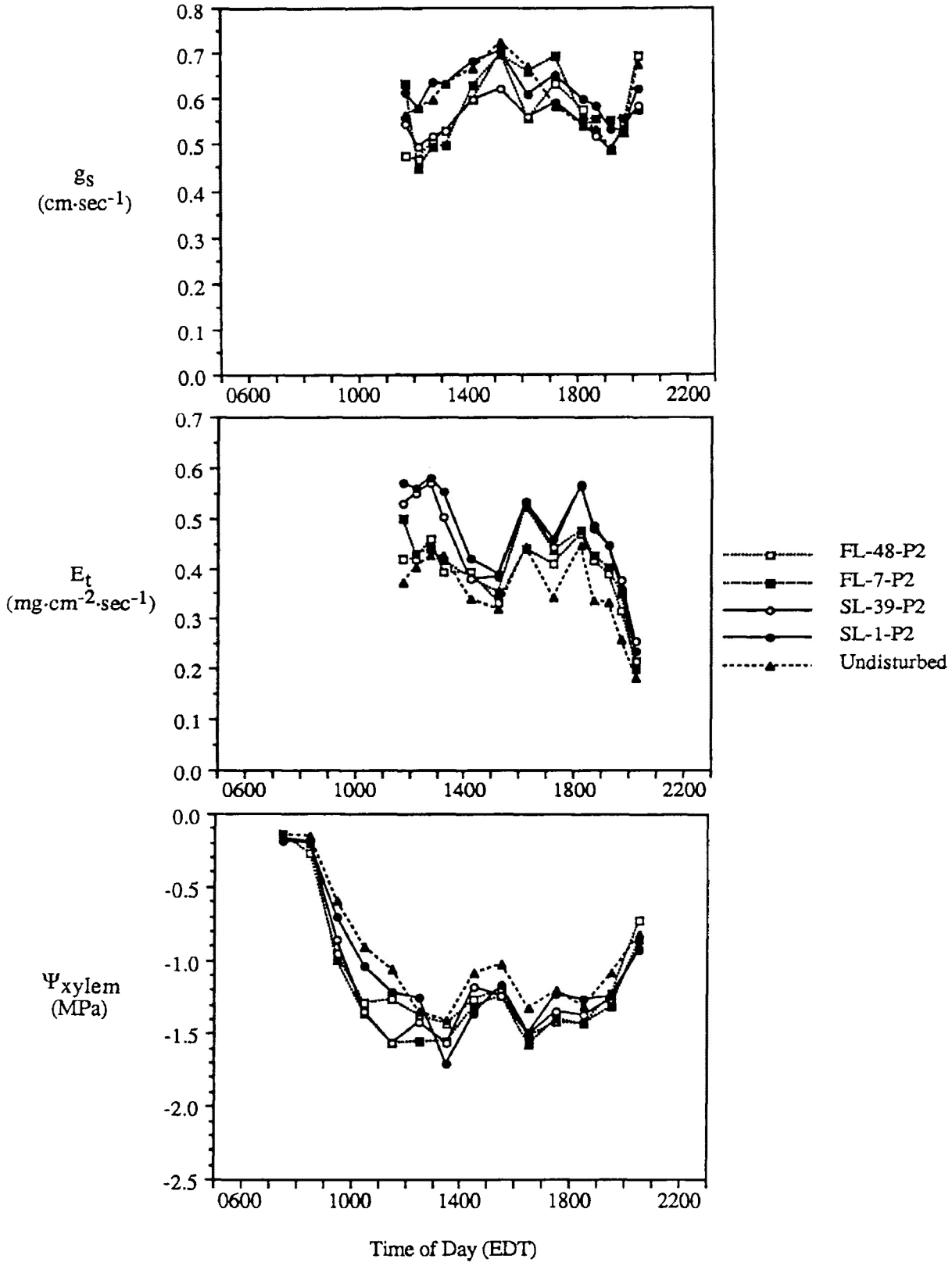

Figure 2.18. Diurnal patterns of stomatal conductance (g_s), transpiration (E_t) and xylem pressure potential (Ψ_{xylem}) for Nursery Trial: Planting Time 2 seedlings on August 13, 1987 (59 days after planting). See Table 2.1 for treatment code descriptions.

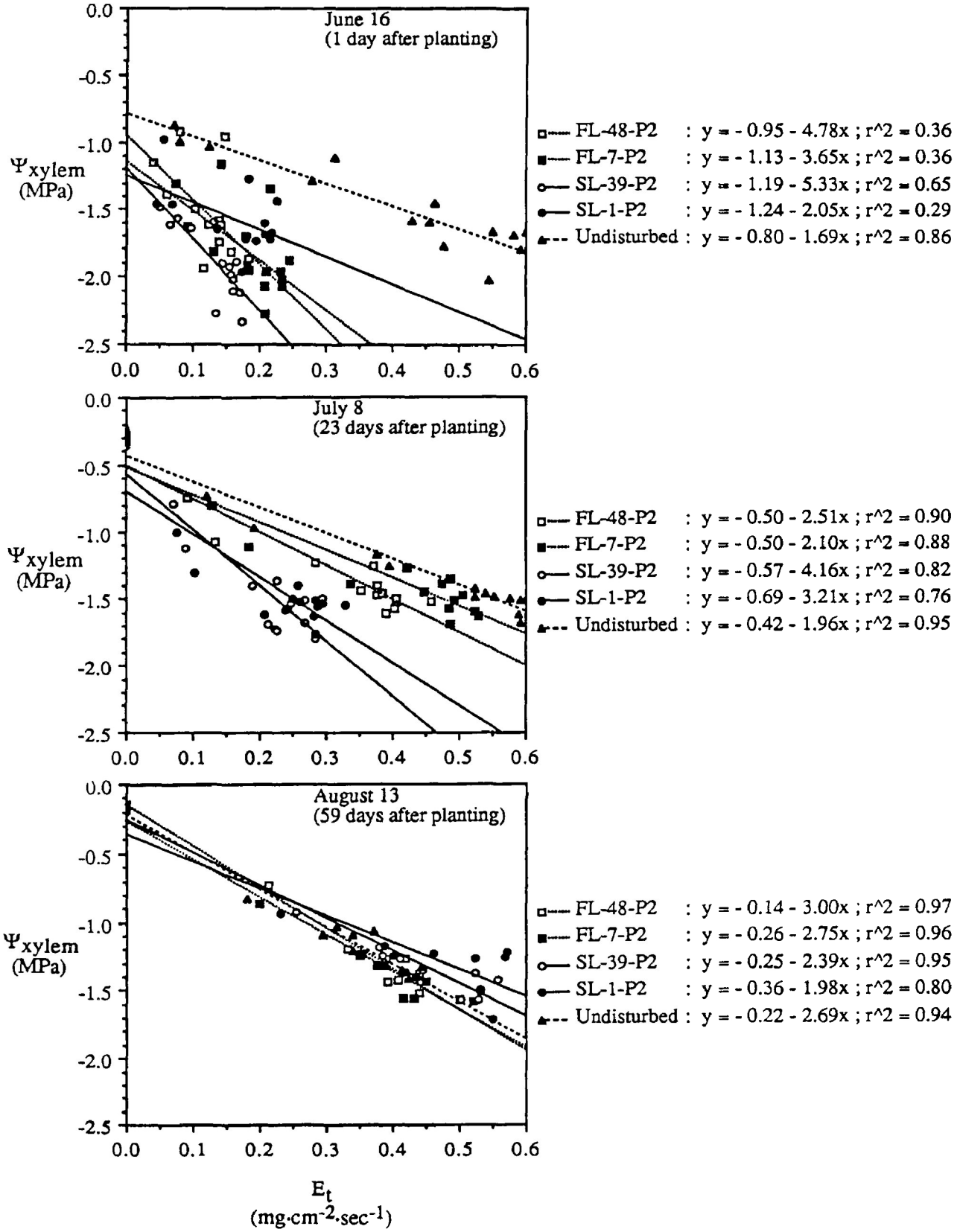

Figure 2.19. Relationship between xylem pressure potential (Ψ_{xylem}) and transpiration (E_t) for Nursery Trial: Planting Time 2 seedlings on June 16 (1 day after planting), July 8 (23 days after planting) and August 13 (59 days after planting). See Table 2.1 for treatment code descriptions.

variation explained by the $\Psi_{xylem} : E_t$ relationships increased for all treatments by the end of the experimental period at which time the largest and smallest SPAC resistances occurred for the FL-48-P2 (β_1 = -3.00) and freshly lifted seedlings (β_1 = -1.98), respectively.

Root Growth Response

The 14 day test period (June 15 to June 29) was warm and dry (Appendix VIII, Figure VIII.4). Weather data recorded by Environment Canada (1987) indicated that effective insolation averaged 11.6 hours per day. Maximum temperatures ranged from 20.5° C to 33.2° C and averaged 26.0° C. Minimum temperatures ranged from 8.4° C to 17.1° C and averaged 12.3° C. A total of 4.8 mm of rain were recorded on 4 days.

Root growth indices suggested that root activity was strongly influenced by lifting-storage treatment (Table 2.9, Figure 2.10b). The fall lifted treatments, particularly FL-7-P2, had the best new root growth at the end of the 14 day experimental period. SL-1-P2 was the only treatment that did exceptionally poorly with six of the 25 seedlings producing no new white roots.

SEEDLING MORPHOLOGICAL RESPONSE

Nursery Trial

Periodic Ground Caliper and Leader Extension Increment

Planting Time 1 (May 14)

The undisturbed seedlings had the largest increments of ground caliper over the first four growth periods (Days 0 to 84) and FL-48-P1 seedlings had the largest increment over the last (Days 85 to 160) (Figure 2.20). With the exception of FL-7-P1 seedlings, all treatments had their smallest ground caliper increments during the period of maximum leader extension (Days 22 to 42). The smallest diameter increases occurred for FL-7-P1 seedlings during the first growth period (Days 0 to 21). All outplants increased diameter at approximately the same rate as growing degree days (base 5° C) accumulated over the first four growth periods (Figure 2.21a). However, the fall lifted seedlings showed the greatest diameter increases by the end of the growing season.

The undisturbed seedlings had the greatest leader extension increments over the first two growth periods (Days 0 to 42) and FL-7-P1 seedlings had the greatest increments over the remaining periods (Days 43 to 160) (Figure 2.20). Leader extension was minimal for all treatments between Days 85 and 160. As indicated by the reduced periodic leader extension between Days 0 to 21, phenological development was delayed for the fall lifted seedlings, particularly treatment FL-7-P1. Maximum leader

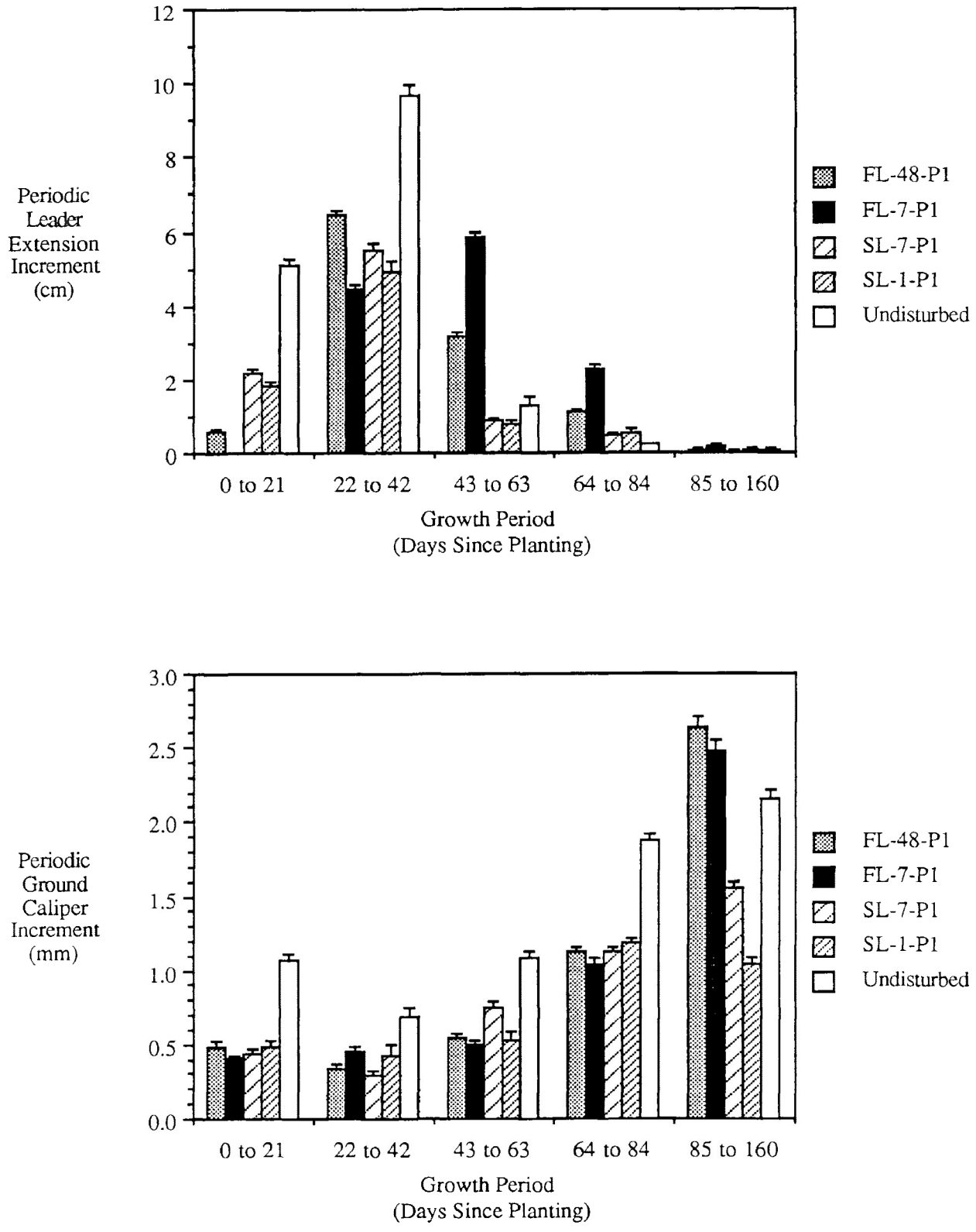

Figure 2.20. Periodic leader extension (above) and ground caliper (below) increment for the lifting-storage treatments and an undisturbed (i.e. not planted, thinned *in situ*) treatment monitored during Nursery Trial: Planting Time 1. All treatments were measured immediately following outplanting (May 14, 1987), after 21 days (June 4), 42 days (June 25), 63 days (July 16), 84 days (August 6), and at the end of the growing season (October 21). Vertical bars show standard error. See Table 2.1 for treatment code descriptions.

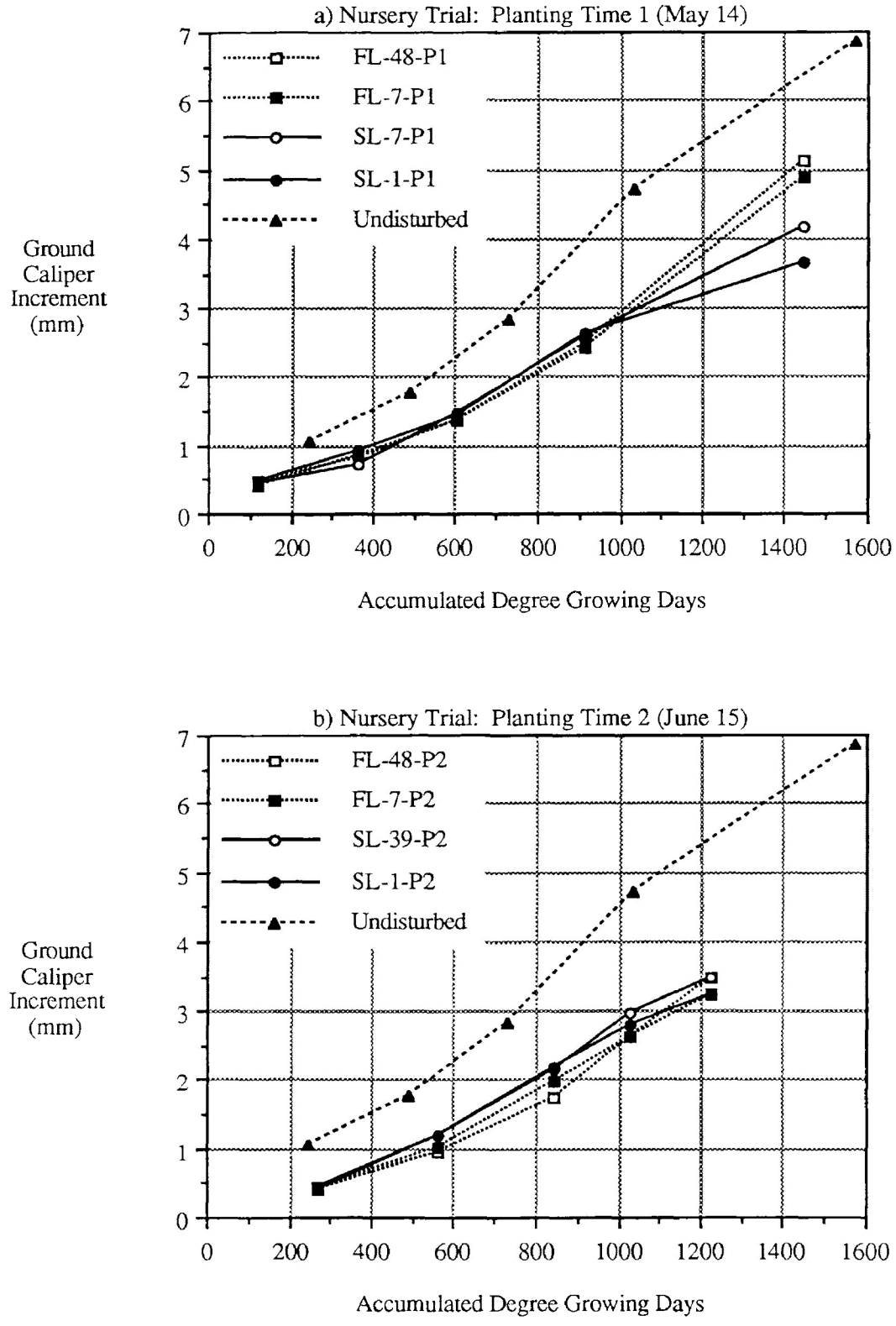

Figure 2.21. Ground caliper increment vs. accumulated degree growing days (base 5 °C) for: a) Nursery Trial: Planting Time 1 outplants and an undisturbed (i.e. not planted, thinned *in situ*), control treatment, and b) Nursery Trial: Planting Time 2 outplants and an undisturbed (i.e. not planted, thinned *in situ*), control treatment All seedlings were measured immediately following planting, after 21, 42, 63, and 84 days and at the end of the growing season. The undisturbed seedlings were measured with those seedlings outplanted during Planting Time 1. See Table 2.1 for treatment code descriptions.

extension occurred for all treatments, excluding FL-7-P1, during the second growth period (Days 22 to 42). Maximum leader extension occurred for FL-7-P1 seedlings during the third period (Days 43 to 63).

Planting Time 2 (June 15)

With the exception of FL-48-P2 seedlings, periodic ground caliper increment increased until the third growth period (Days 43 to 63) for all treatments (Figure 2.22). Periodic ground caliper increment continued to increase for FL-48-P2 seedlings until the fourth growth period (Days 64 to 84). All treatments had their smallest increments of ground caliper during the first growth period (Days 0 to 21). The spring lifted seedlings exhibited greater increments than the fall lifted seedlings between Days 22 and 63 while the fall lifted seedlings had greater increments between Days 85 and 128. All seedlings increased diameter at approximately the same rate as growing degree days (base 5 ° C) accumulated over the entire experimental period (Figure 2.21b). A comparison of Figures 2.21a and 2.21b indicates that diameter increased at a similar rate for both planting times as growing degree days accumulated.

Leader extension was minimal for the freshly lifted seedlings following outplanting. SL-39-P2 seedlings showed the greatest increment during the first growth period (Days 0 to 21) and the fall lifted seedlings showed the greatest increments thereafter. Leader extension was minimal for all treatments during the last two growth periods (Days 64 to 128). The fall lifted seedlings, particularly treatment FL-7-P1, exhibited a delayed phenological response in comparison with the spring lifted, stored seedlings but showed greater leader extension during the first growth period of Planting Time 2 than Planting Time 1.

End of Season Measurements

Planting Time 1 (May 14)

First-year mortality did not exceed 1 % for the undisturbed seedlings or the outplants of Planting Time 1. The undisturbed seedlings were clearly larger than any of the outplants after one growing season (Table 2.13). This was particularly apparent for top dry weight which was 46 % greater than the next largest treatment (FL-7-P1) and 109 % greater than the smallest treatment (SL-1-P2). The fall lifted treatments, particularly FL-7-P1, were larger than the spring lifted treatments after one growing season. This difference was significant or highly significant for many of the paired comparisons tested. A significant difference occurred between the fall lifted treatments for height and leader extension (both were greater for FL-7-P1 seedlings) while no significant differences occurred between the spring lifted treatments.

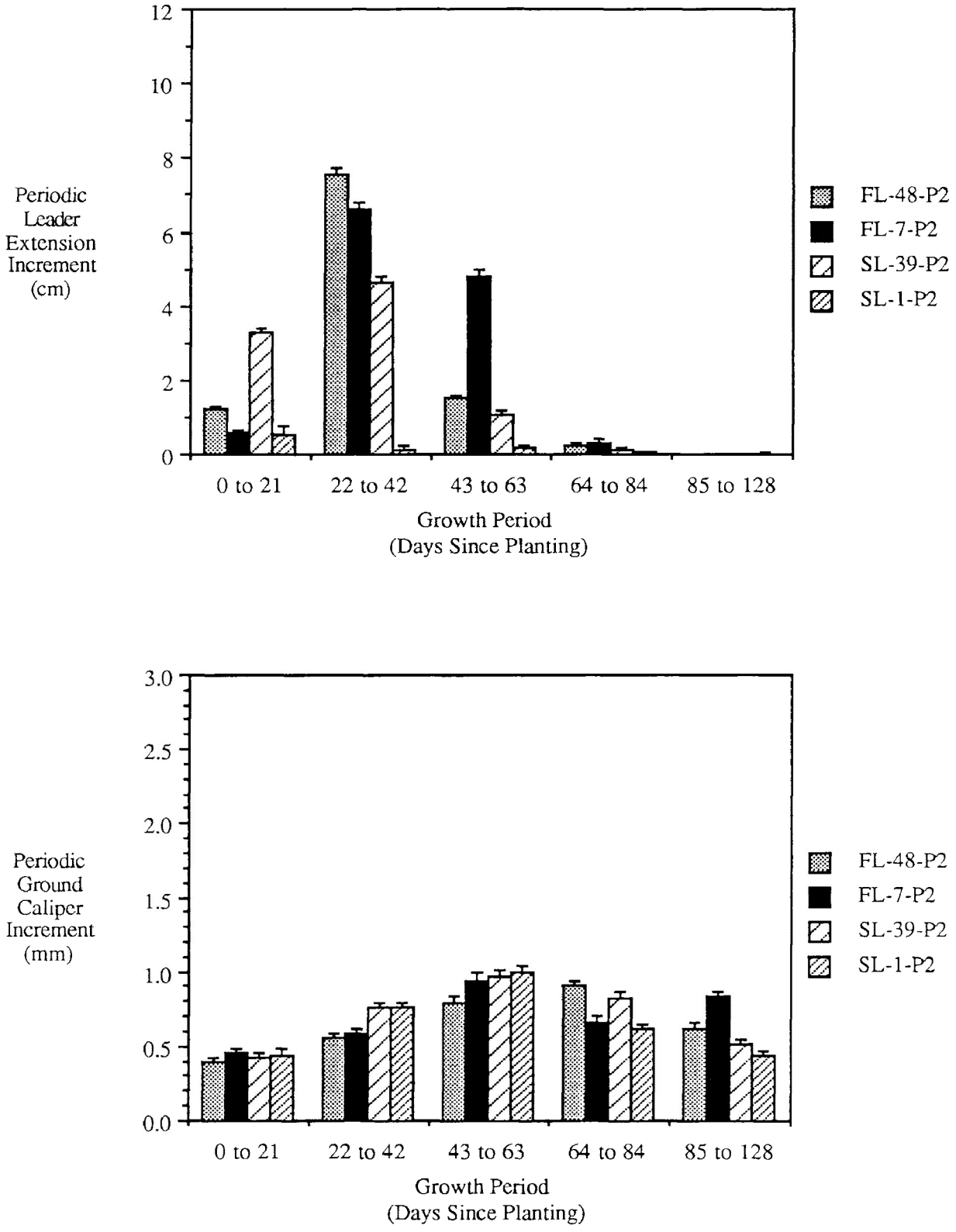

Figure 2.22. Periodic leader extension (above) and ground caliper (below) increment for the lifting-storage treatments monitored during Nursery Trial: Planting Time 2. All treatments were measured immediately following outplanting (June 15, 1987), after 21 days (July 6), 42 days (July 27), 63 days (August 17), 84 days (September 7), and at the end of the growing season (October 21). Vertical bars show standard error. See Table 2.1 for treatment code descriptions.

Table 2.13. Linear contrast information determined for ground caliper, height, leader extension, and top and root dry weight measured in late October, 1987, at the Thunder Bay Forest Nursery outplanting site. The single degree of freedom F tests were based on an analysis of variance for ground caliper, leader extension and root dry weight and an analysis of covariance using 1986 height as a covariate for height and top dry weight.

Dependent Variable	Treatment Number[1] and Mean Values[2]									Dependent Variables and F Values[3]				
	1	2	3	4	5	6	7	8	9					
ground caliper (mm)	9.73	7.54	9.44	7.79	8.98	8.22	8.87	8.36	11.66					
height (cm)	35.8	34.9	37.3	36.5	33.3	33.0	33.7	37.5	41.3					
leader extension (cm)	11.4	10.5	12.8	12.1	9.2	9.1	9.7	13.1	17.9	ground caliper	height	leader extension	top dry weight	root dry weight
top dry weight (g)	16.82	12.26	17.60	14.11	14.43	13.56	12.23	13.66	25.67					
root dry weight (g)	11.27	6.68	12.09	6.39	9.34	7.55	8.62	8.35	14.03					
Contrasts														
Planting Time 1 (May 14)														
Fall lifted seedlings														
1 vs. 3	1	0	-1	0	0	0	0	0	0	1.11 ns	6.66 *	5.37 *	0.39 ns	0.58 ns
Spring lifted seedlings														
5 vs. 7	0	0	0	0	1	0	-1	0	0	0.46 ns	0.30 ns	0.36 ns	2.65 ns	0.84 ns
Fall vs. spring lifted seedlings														
1 vs. 5	1	0	0	0	-1	0	0	0	0	5.38 *	18.21 **	12.77 **	3.66 ns	4.79 *
1 vs. 7	1	0	0	0	0	0	-1	0	0	8.84 **	10.25 *	8.60 **	12.78 **	9.51 **
3 vs. 5	0	0	1	0	-1	0	0	0	0	1.54 ns	42.44 **	34.23 **	6.30 *	8.56 **
3 vs. 7	0	0	1	0	0	0	-1	0	0	3.68 ns	33.62 **	27.52 **	17.44 **	14.77 **
Planting Time 2 (June 15)														
Fall lifted seedlings														
2 vs. 4	0	1	0	-1	0	0	0	0	0	0.19 ns	7.50 *	9.11 **	2.17 ns	0.62 ns
Spring lifted seedlings														
6 vs. 8	0	0	0	0	0	1	0	-1	0	0.80 ns	53.59 **	43.62 **	0.01 ns	1.39 ns
Fall vs. spring lifted seedlings														
2 vs. 6	0	1	0	0	0	-1	0	0	0	2.36 ns	10.82 *	6.29 *	1.07 ns	0.09 ns
2 vs. 8	0	1	0	0	0	0	0	-1	0	5.91 *	19.05 **	16.78 **	1.25 ns	2.16 ns
4 vs. 6	0	0	0	1	0	-1	0	0	0	1.22 ns	32.20 **	30.55 **	0.19 ns	1.16 ns

Table 2.13. (Continued)

Dependent Variable	Treatment Number[1] and Mean Values[2]									Dependent Variables and F Values[3]				
	1	2	3	4	5	6	7	8	9					
ground caliper (mm)	9.73	7.54	9.44	7.79	8.98	8.22	8.87	8.36	11.66					
height (cm)	35.8	34.9	37.3	36.5	33.3	33.0	33.7	37.5	41.3					
leader extension (cm)	11.4	10.5	12.8	12.1	9.2	9.1	9.7	13.1	17.9	ground	height	leader	top dry	root dry
top dry weight (g)	16.82	12.26	17.60	14.11	14.43	13.56	12.23	13.66	25.67	caliper		extension	weight	weight
root dry weight (g)	11.27	6.68	12.09	6.39	9.34	7.55	8.62	8.35	14.03					
Contrasts														
4 vs. 8	0	0	0	1	0	0	0	-1	0	4.07 ns	2.61 ns	1.19 ns	0.13 ns	5.21 *
Planting Time 1 vs. Planting Time 2														
1, 3, 5, 7 vs. 2, 4, 6, 8	1	-1	1	-1	1	-1	1	-1	0	52.66 **	2.18 ns	3.27 ns	9.12 **	43.46 **
1, 3, 5 vs. 2, 4, 6	1	-1	1	-1	1	-1	0	0	0	61.56 **	4.00 ns	1.57 ns	17.25 **	56.92 **
7 vs. 8	0	0	0	0	0	0	1	-1	0	0.75 ns	34.86 **	32.89 **	1.24 ns	0.01 ns

[1] 1 = FL-48-P1, 2 = FL-48-P2, 3 = FL-7-P1, 4 = FL-7-P2, 5 = SL-7-P1, 6 = SL-39-P2, 7 = SL-1-P1, 8 = SL-1-P2, 9 = undisturbed. See Table 2.1 for treatment code descriptions.

[2] Means have been adjusted for the covariate when applicable.

[3] ns = not significant at 0.05 level, * = significant at 0.05 level, ** = significant at 0.01 level.

Planting Time 2 (June 15)

First-year survival equaled 94 % for FL-7-P2 seedlings, 98 % for FL-48-P2 and SL-1-P2 seedlings, and 99 % for SL-39-P2 seedlings. There was a highly significant difference between planting times for top and root dry weight and ground caliper when all treatments were compared by a single linear contrast regardless of whether the freshly lifted seedlings (SL-1-P1 and SL-1-P2) were included in the single degree of freedom F test (Table 2.13). SL-1-P2 seedlings were clearly larger than any of the treatments outplanted on June 15. This was particularly apparent for height growth and leader extension which were significantly greater (α=0.01) for SL-1-P2 than SL-39-P2 and FL-48-P2 seedlings. Treatment FL-7-P2 exhibited a significantly greater height (α=0.05) and leader extension (α=0.01) after one growing season than treatment FL-48-P2. No significant differences were found to occur between any of the outplants for top dry weight.

Raith Trial

Periodic Ground Caliper and Leader Extension Increment

Planting Time 1 (May 8)

Ground caliper increment was greater for the fall lifted than the spring lifted seedlings during both growth periods (Figure 2.23). This was particularly apparent during the second growth period when periodic ground caliper increment increased for the fall lifted and decreased for the spring lifted seedlings. Periodic leader extension increments were greatest for all treatments during the first growth period. Leader extension was greatest for FL-48-P1 seedlings during the first growth period and FL-7-P1 seedlings during the second.

Planting Time 2 (June 9)

Ground caliper increments were smaller for all seedlings during the second growth period (Figure 2.24). Ground caliper increment was greatest for the spring lifted seedlings during the first growth period and the fall lifted seedlings during the second. It was very similar for the spring lifted seedlings during both growth periods and for the fall lifted seedlings during the second. Periodic leader extension increments were greater for all seedlings during the first growth period. FL-48-P2 seedlings had the greatest increments of leader extension during the first growth period and FL-7-P2 seedlings had the greatest increments during the second. Leader extension was minimal for SL-1-P2 seedlings during both growth periods.

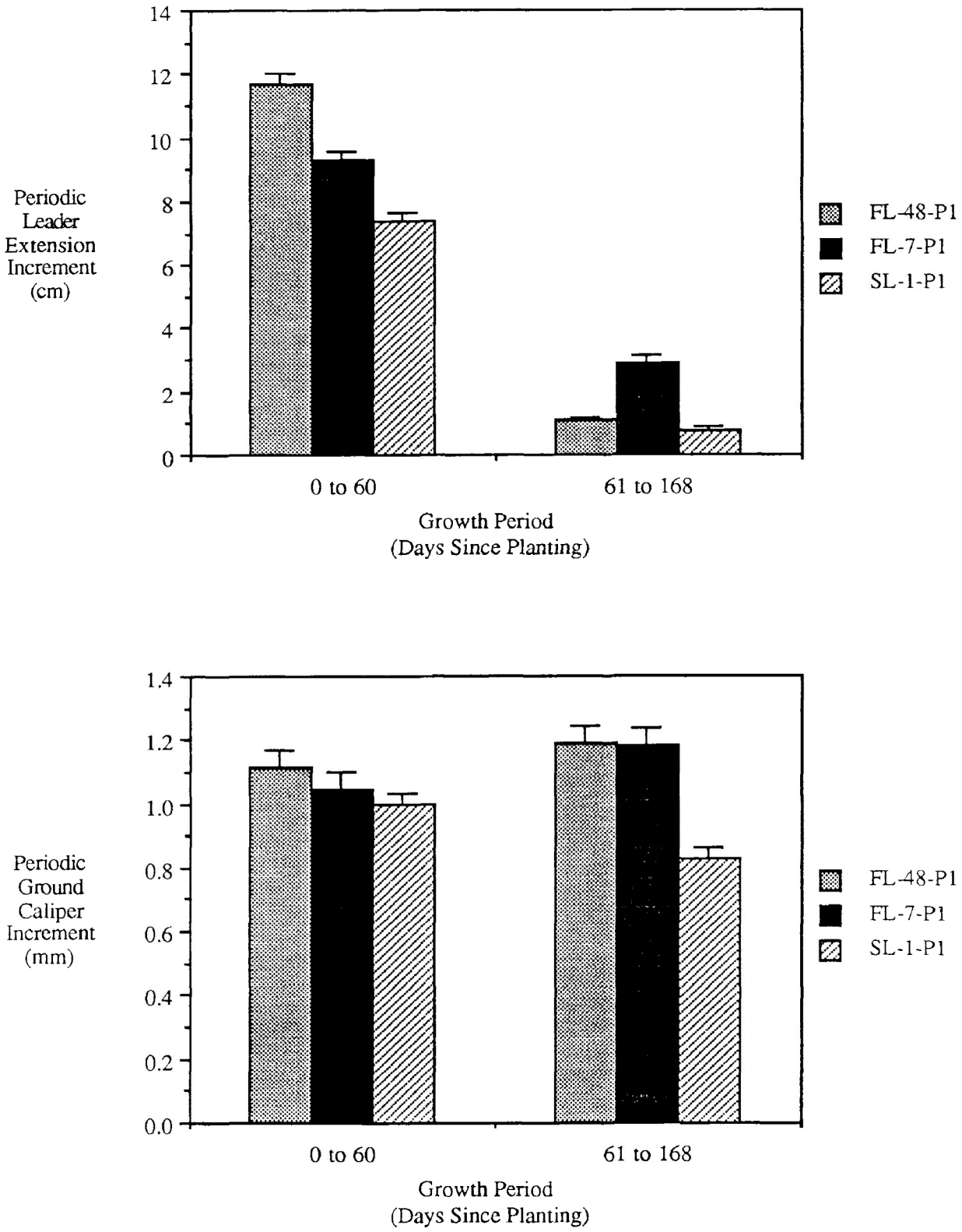

Figure 2.23. Periodic leader extension (above) and ground caliper (below) increment for the lifting-storage treatments monitored during Raith Trial: Planting Time 1. All treatments were measured immediately following outplanting (May 8, 1987), after 60 days (July 7), and at the end of the growing season (October 23). Vertical bars show standard error. See Table 2.2 for treatment code descriptions.

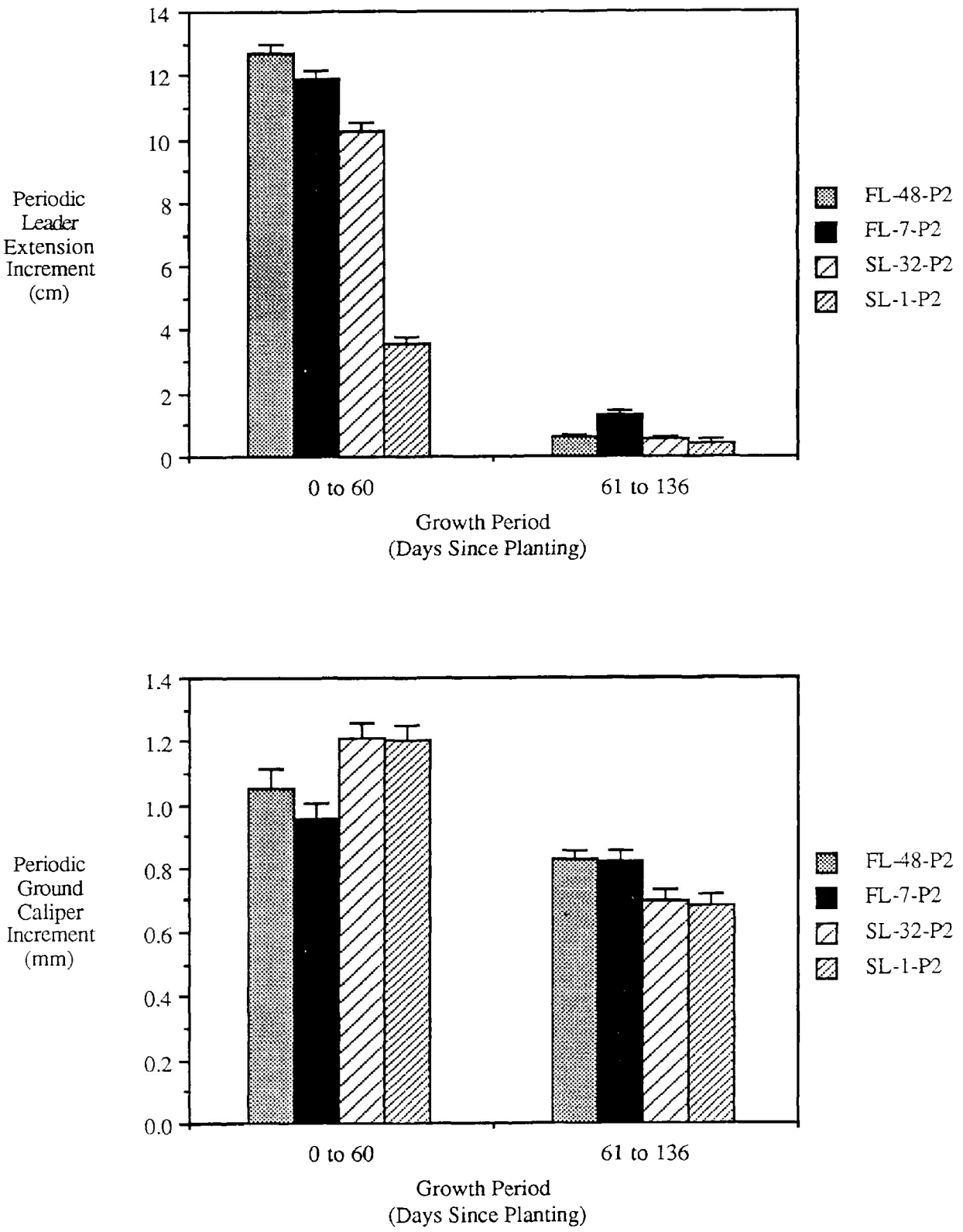

Figure 2.24. Periodic leader extension (above) and ground caliper (below) increment for the lifting-storage treatments monitored during Raith Trial: Planting Time 2. All treatments were measured immediately following outplanting (June 9, 1987), after 60 days (August 8), and at the end of the growing season (October 23). Vertical bars show standard error. See Table 2.2 for treatment code descriptions.

End of Season Measurements

Planting Time 1 (May 8)

First-year survival equaled 100 % for FL-48-P1 seedlings and 96 % for FL-7-P1 and SL-1-P1 seedlings. With the exception of top dry weight, the largest morphological attributes measured after one growing season for Planting Time 1 seedlings were recorded for treatment FL-48-P1 (Table 2.14). These values were not significantly greater than those measured for FL-7-P1 seedlings. However, highly significant differences occurred between both of the fall lifted treatments and SL-1-P1 seedlings for height, leader extension, and top dry weight.

Planting Time 2 (June 9)

First-year survival equaled 87 % for treatment SL-32-P2 and exceeded 99 % for all other Planting Time 2 seedlings. There was a highly significant difference between planting times for height and leader extension after the first growing season when all treatments were compared by a single linear contrast (Table 2.14); Planting Time 2 seedlings were taller and had extended longer leaders. When treatment SL-1-P2 was excluded from the linear contrast (thereby eliminating the influence of pre-lifting current growth), ground caliper and root dry weight were significantly larger for Planting Time 1 seedlings. No significant differences occurred between the fall lifted seedlings from Planting Time 2. However, there was a significant or highly significant difference between height, leader extension, and top and root dry weight for the spring lifted seedlings. Height and leader extension after one growing season were significantly greater (α=0.01) for the fall lifted than SL-32-P2 seedlings.

Table 2.14 Linear contrast information determined for ground caliper, height, leader extension, and top and root dry weight measured in late October, 1987, at the Raith outplanting site. The single degree of freedom F tests were based on an analysis of variance for leader extension and root dry weight and an analysis of covariance using 1986 height as a covariate for ground caliper, height and top dry weight.

Dependent Variable	Treatment Number[1] and Mean Values[2]							Dependent Variables and F Values[3]				
	1	2	3	4	5	6	7					
ground caliper (mm)	6.92	6.31	6.77	6.32	6.78	6.57	7.09					
height (cm)	37.0	37.4	36.3	37.4	31.2	34.1	37.1					
leader extension (cm)	12.7	13.0	12.3	13.3	8.1	10.7	13.1	ground	height	leader	top dry	root dry
top dry weight (g)	12.11	10.79	12.39	11.60	8.51	10.10	12.98	caliper		extension	weight	weight
root dry weight (g)	3.79	2.94	3.65	2.78	3.72	3.32	4.34					
Contrasts												
Planting Time 1 (May 8)												
Fall lifted seedlings												
1 vs. 3	1	0	-1	0	0	0	0	0.35 ns	1.03 ns	0.64 ns	0.10 ns	0.13 ns
Fall vs. spring lifted seedlings												
1 vs. 5	1	0	0	0	-1	0	0	0.42 ns	90.34 **	66.12 **	24.55 **	0.23 ns
3 vs. 5	0	0	1	0	-1	0	0	0.00 ns	59.94 **	48.59 **	25.24 **	0.00 ns
Planting Time 2 (June 9)												
Fall lifted seedlings												
2 vs. 4	0	1	0	-1	0	0	0	0.00 ns	0.00 ns	0.01 ns	0.91 ns	0.29 ns
Spring lifted seedlings												
6 vs. 7	0	0	0	0	0	1	-1	4.01 ns	19.24 **	13.36 **	11.34 **	5.54 *
Fall vs. spring lifted seedlings												
2 vs. 6	0	1	0	0	0	-1	0	1.35 ns	19.52 **	16.97 **	0.43 ns	1.08 ns
2 vs. 7	0	1	0	0	0	0	-1	9.48 **	0.10 ns	0.22 ns	6.46 *	12.46 **
4 vs. 6	0	0	0	1	0	-1	0	1.07 ns	21.95 **	17.67 **	3.15 ns	2.05 ns
4 vs. 7	0	0	0	1	0	0	-1	9.93 **	0.16 ns	0.32 ns	2.69 ns	16.22 **

Table 2.14 (Continued)

Dependent Variable	Treatment Number[1] and Mean Values[2]							Dependent Variables and F Values[3]				
	1	2	3	4	5	6	7					
ground caliper (mm)	6.92	6.31	6.77	6.32	6.78	6.57	7.09					
height (cm)	37.0	37.4	36.3	37.4	31.2	34.1	37.1					
leader extension (cm)	12.7	13.0	12.3	13.3	8.1	10.7	13.1					
top dry weight (g)	12.11	10.79	12.39	11.60	8.51	10.10	12.98	ground caliper	height	leader extension	top dry weight	root dry weight
root dry weight (g)	3.79	2.94	3.65	2.78	3.72	3.32	4.34					
Contrasts												
Planting Time 1 vs. Planting Time 2												
1, 3, 5, vs. 2, 4, 6, 7	4	-3	4	-3	4	-3	-3	3.97 ns	22.71 **	20.17 **	0.73 ns	3.85 ns
1, 3, 5 vs. 2, 4, 6	1	-1	1	-1	1	-1	0	8.21 **	15.02 **	13.52 **	0.01 ns	8.40 **
5 vs. 7	0	0	0	0	1	0	-1	2.15 ns	95.80 **	72.08 **	37.94 **	3.76 ns

[1] 1 = FL-48-P1, 2 = FL-48-P2, 3 = FL-7-P1, 4 = FL-7-P2, 5 = SL-1-P1, 6 = SL-32-P2 , 7 = SL-1-P2. See Table 2.2 for treatment code descriptions.

[2] Means have been adjusted for the covariate when applicable.

[3] ns = not significant at 0.05 level, * = significant at 0.05 level, ** = significant at 0.01 level.

DISCUSSION

For successful establishment, an outplant must attain a favourable internal water status by controlling water loss from the needle surface while exploiting additional soil water reserves through an expanding root system. This will promote rapid early root and shoot growth which in turn, will reduce weed competition and the impact of other biotic and/or environmental stresses (McCreary and Duryea 1985). There is a growing realization that consistent reforestation success is contingent on a thorough understanding of the impact of all nursery cultural and handling techniques on seedling physiology (Duryea and Brown 1984, Duryea and Landis 1984, Duryea 1985). Furthermore, an increased understanding of these effects will lead to improved reforestation programs and ultimately increase future forest yields. Fall lifting and overwinter frozen storage have gained widespread usage, but their effect on early physiological and morphological response has not been extensively researched. Moreover, no field trials have compared the effects of varied storage methods on plant water relations for Ontario's boreal conifers. The intent of the following discussion is to address the hypothesis that the date of lifting and the temperature and duration of storage affects seedling physiology and thereby influences the physiological and morphological response following outplanting. Physiological response variables examined include g_s, E_t, Ψ_{xylem}, and early root growth. Morphological response variables examined include height, ground caliper and leader extension increment, and seedling top and root dry weight.

ENVIRONMENTAL CONDITIONS AND SEEDLING PHYSIOLOGICAL RESPONSE

Nursery Trial - Planting Time 1 (May 14)

Water Relations Response

Owing to greater microclimatic variation, differences in g_s and E_t were less well defined under field than controlled conditions (Chapter 1) making interpretation of the results considerably more difficult. In spite of the increased variability, it is clear that the selected lifting-storage treatments influenced seedling water relations during early establishment. Most importantly, the gaseous exchange patterns recorded for the fall and spring lifted seedlings indicate that inherent response differed between groups. The generally greater g_s and E_t rates exhibited by the fall lifted seedlings suggests that they exercised poor stomatal control over transpirational losses during the critical establishment period. Since the efflux of water vapour is closely associated with the influx of CO_2 (Salisbury and Ross 1985), this response difference may have increased the photosynthetic capacity and favoured early growth for the fall

lifted seedlings. However, the inability to regulate transpirational losses would place the fall lifted seedlings at an increased risk to desiccation under conditions of soil or atmospheric drought. Response differences were most apparent as light intensity, temperature, and the evaporative demand changed diurnally. However, treatment differences were also evident from first measurement response determined over a 22 day post-planting period that was frequently characterized by conditions of low atmospheric stress.

The g_s and E_t rates of the present study were occasionally higher than those reported for coniferous seedlings during several previous investigations (Hinckley *et al.* 1978, Blake and Sutton 1987, Grossnickle and Blake 1987a,b). These differences can be attributed partly to the numerous environmental and/or plant factors that potentially affect such comparisons (Hinckley *et al.* 1978, Squire and Black 1981). Moreover, the different types of porometers used in the various studies have been shown to yield different results from identical samples (Landsberg *et al.* 1975) and studies have been conducted under controlled, greenhouse, and field conditions (Hinckley *et al.* 1978). Finally, results have been based on both total and projected leaf surface area; depending on needle morphology, this alone would result in at least a two-fold difference in reported values.

The g_s and E_t responses were less similar under field than controlled conditions (Chapter 1) illustrating that they are not subject to common control processes. Rather, g_s is considered to regulate E_t (Jarvis and Morison 1981). They are often positively correlated because both increase in response to increasing temperatures and light intensities. However, g_s commonly decreases as E_t increases in response to increasing vapour pressure deficits at the leaf-air interface.

Since edaphic, atmospheric, and plant factors vary temporally, water relations parameters can not be directly compared between sample days. For example, a decreased Ψ_{xylem} from one day to the next may have been caused by a decreased Ψ_{soil} or an increased vapour pressure gradient at the leaf-air interface during the second day. However, treatment response hierarchies indicate trends in time. The variation that occurred between replicates frequently indicated that additional observations were required to estimate mean g_s, E_t, and Ψ_{xylem} within reasonable confidence intervals (Freese 1962). As previously discussed, plant water relations sampling is frequently limited by the number of measurements it is feasible to make over a predetermined time interval without regard for variation between the measurements (Jarvis 1981). This discussion will therefore be primarily concerned with differences, similarities, and trends apparent through a visual inspection of the provided figures.

First Measurement Patterns (1 to 22 Days After Planting)

The lack of a clear association between gaseous exchange and any of the simultaneously recorded atmospheric variables is not surprising since g_s and E_t (and Ψ_{xylem}) are affected by numerous other

environmental and plant factors (Figures 2.1 and 2.2). Moreover, the interactions among controlling factors affect seedling water status in complex ways. Thus, it is difficult to determine the influence of any single cause (Burrows and Milthorpe 1976, Jarvis 1976, Hinckley *et al.* 1978, Squire and Black 1981). Furthermore, the field environment as perceived by seedlings is rarely constant for more than a few minutes and changes in one variable are frequently confounded by changes in another (Squire and Black 1981, Livingston and Black 1987). Thus, the available data are insufficient to identify treatment response differences to the measured atmospheric conditions.

The gaseous exchange patterns recorded for the fall and spring lifted seedlings generally agree with those measured under controlled conditions (Chapter 1) by indicating that early response differed between groups. The commonly greater g_s and E_t rates recorded for the fall lifted seedlings, particularly apparent after Day 10, suggest that they exercised poor stomatal control over transpirational losses. Gaseous exchange differences were not reflected by Ψ_{xylem} differences because Ψ_{xylem} was recorded near dawn, prior to transpirational losses (Hinckley *et al.* 1978).

In contrast with previous studies (Baldwin and Barney 1976, Hallman *et al.* 1978, Sands 1984, Örlander 1986), the undisturbed seedlings did not consistently exhibit the greatest g_s and E_t rates or the highest Ψ_{xylem} values. These differences may be attributed to different sample times; the first measurement values of the present study were recorded before transpirational losses limited g_s or lowered Ψ_{xylem}. The parameters of the studies cited above were recorded during more stressful atmospheric conditions, presumably, after internal water deficits reduced g_s, E_t, and Ψ_{xylem} for the outplants. The similar Ψ_{xylem} values indicate that internal water status improved overnight (e.g. via hydraulic recharge) for all treatments regardless of differences in water vapour loss or water absorbing capacity. The higher Ψ_{xylem} recorded for the FL-48-P1 seedlings may indicate greater root development (Nambiar *et al.* 1979).

The generally greater g_s and E_t rates recorded for the fall lifted, in comparison with the spring lifted seedlings can not be explained by the available data. As discussed in Chapter 1, endogenous ABA concentrations may have been greater for the fall lifted seedlings following overwinter frozen storage (Blake 1983). This should have reduced stomatal response in comparison with the spring lifted seedlings (Jones and Mansfield 1970, Davies *et al.* 1981, Mansfield and Davies 1985). It is also possible that the high rates of first measurement g_s and E_t measured for the fall lifted seedlings are, in part, a consequence of incomplete stomatal closure during darkness (Grossnickle and Blake 1985) or that cold storage reduced the photosynthetic capacity (McCracken 1978) and indirectly affected stomatal response.

The increased g_s rates recorded for the fall lifted seedlings over the 22 day post-planting period agree with the results of Chapter 1 and several previous investigations. For example, year-old needles of cold stored jack pine (Grossnickle and Blake 1985, Grossnickle 1988b) and white (Grossnickle and Blake 1985) and black spruce (Grossnickle 1987) seedlings showed increased g_s rates following potting under

controlled conditions. When Blake (1983) compared the water relations response (measured within 2 hours of midday) of fall lifted, overwinter frozen stored and spring lifted, 2+0 white spruce seedlings under controlled conditions, he found current but not year-old needles of fall lifted seedlings to exhibit higher g_s rates about 30 days after potting. Since the present study did not determine gaseous exchange rates separately for current and year-old foliage and was conducted under field conditions, it is difficult to compare stomatal behaviour between studies.

As discussed in Chapter 1, increases in g_s with time out of cold storage have been attributed to a reduced SPAC resistance, primarily at the soil-root interface, and a higher Ψ_{plant} contingent on increased root development (Grossnickle and Blake 1985, Grossnickle 1987, 1988b). It is probable that the increased rates observed here occurred for similar reasons. Indeed, the fall lifted seedlings rapidly grew new white roots and Ψ_{plant} increased over the 22 day post-planting period (as indicated by the increased Ψ_{xylem} values). Moreover, the $\Psi_{xylem} : E_t$ relationships (Figure 2.9) indicate that the effective resistance of the water transfer pathway had decreased (i.e. the R_{SPAC} coefficient [β_1] became less negative) for the fall lifted seedlings 22 days after planting (Elfving *et al.* 1972). Since the spring lifted seedlings also developed new roots and showed increased Ψ_{xylem} since planting, it is likely that their relatively stable g_s rates reflect more effective stomatal control.

Diurnal Patterns

May 15, 1987 (1 day after planting)

The g_s rates were greater for the undisturbed than outplanted seedlings (Figure 2.4). This response difference likely occurred because the fall lifted seedlings were dormant, or nearly so, and not physiologically attuned to those factors that normally promote stomatal opening. On the other hand, the spring lifted seedlings had broken dormancy prior to lifting but were subjected to various stresses between lifting and planting (e.g. bending and breaking of plant parts and drying of roots). This would impair vitality and possibly, their ability to regulate gaseous exchange in a normal way during establishment. It is also possible that the outplants experienced water stress due to their smaller root systems (i.e. larger shoot : root ratios) and poor root-soil contact (Sands 1984). Moreover, rhizosphere disturbances associated with planting (i.e. soil compaction and the introduction of air spaces) further increase the SPAC resistance (Sands 1984, Kaufmann and Fiscus 1985). Indeed, the $\Psi_{xylem} : E_t$ relationships indicate that the SPAC resistance was greater for the outplanted than the undisturbed seedlings (Elfving *et al.* 1972). Under such conditions, g_s rates may have been limited by available turgor following planting. However, the diurnal patterns of Ψ_{xylem} did not differ greatly between treatments suggesting that all seedlings experienced similar levels of water stress. It is possible that the undisturbed seedlings exhibited a lower Ψ_{xylem} for stomatal closure (i.e. a lower osmotic potential at the turgor loss point [$\Psi_{\pi(TLP)}$]) than the outplanted seedlings. However, this is unlikely since treatment FL-7-P1 and the spring lifted,

stored seedlings were shown to have lower $\Psi_{\pi(TLP)}$ than the freshly lifted seedlings at this time (Chapter 1, Table 1.3) and the freshly lifted seedlings were at a similar physiological stage to the undisturbed seedlings. Therefore, it is probable that too few Ψ_{xylem} observations were made (this was occasionally supported by high standard errors) or that Ψ_{xylem} is a less sensitive indicator of seedling water relations than g_s and E_t.

The greater g_s rates recorded for the undisturbed than outplanted seedlings indicates that stomatal closure limited photosynthesis during early establishment regardless of lifting-storage method. This response is noteworthy because it strongly suggests that seedling growth and respiration immediately following outplanting were at the expense of reserve, rather that currently assimilated carbohydrates. It thereby supports Ronco's (1973) suggestion that carbohydrate concentrations must not fall below a critical threshold level during storage if survival and seedling vigour are to be assured. Marshall (1985) clearly illustrated the importance of carbohydrate reserves during the post-planting period when discussing the reserve concentrations of two hypothetical seedlings during the lifting-storage-planting sequence. The first seedling had greater reserves when lifted and was able to withstand respirational losses while in storage and following outplanting until photosynthesis began. The second seedling, lifted with a lower reserve carbohydrate content, was able to survive the storage period but died after outplanting before photosynthesis could meet the demands of respiration and growth.

The similar gaseous exchange patterns observed for the fall and spring lifted seedlings under controlled conditions and over the 22 day first measurement period were not apparent from the diurnal response one day after planting. The 48 day conditioning period at above freezing temperatures increased g_s, E_t, and Ψ_{xylem} and reduced the SPAC resistance for the fall lifted seedlings (i.e. FL-48-P1 seedlings). While previous studies support low g_s rates and high SPAC resistances after removal from frozen storage (Grossnickle and Blake 1985, Grossnickle 1987, 1988b), the physiological effects of above freezing temperature conditioning periods have not been well quantified. Presumably, they would more effectively satisfy the chilling requirement for dormancy release and increase stomatal responsiveness immediately following planting. Except for a transient increase in g_s and E_t for the freshly lifted seedlings, both spring lifted treatments showed similar response patterns. This increase mimicked that exhibited by the undisturbed seedlings and may have occurred because both treatments were in a similar physiological condition and responded equally to environmental factors that promote stomatal opening. As discussed, g_s and E_t probably declined for the freshly lifted seedlings with available turgor.

June 5, 1987 (22 days after planting)

A more distinct separation occurred between g_s and E_t patterns 22 days after planting (Figure 2.6). The wider divergence in g_s was largely due to increased rates for the fall lifted seedlings. The wider divergence in E_t was a consequence of a greater relative increase for the fall lifted seedlings since rates

increased for all seedlings with the greater evaporative demand. At this time, the fall and spring lifted seedlings formed two distinct groups supporting the results of Chapter 1 and those at first measurement. They thereby provide additional evidence that the nursery lifting-storage practices have predisposed each group to respond differently during establishment.

The increased g_S rates recorded for the fall lifted seedlings with time out of cold storage agree with the results of Chapter 1 and the first measurement response patterns and presumably occurred for the reasons mentioned. The increased Ψ_{xylem} values indicate that internal water relations had improved since planting for all seedlings. These increases can be attributed to lower resistances to waterflow at the soil-root interface (due to increased root development) and an increased hydraulic conductivity through the surrounding soil (due to rain and soil compaction around the root systems). The higher Ψ_{xylem} values recorded near dawn indicate that the availability of water for growth was greater as each seedling began its transpirational day. The higher values recorded at the end of the day indicate that seedling water status improved more rapidly as the evaporative demand diminished. The higher evening values recorded for the fall than spring lifted seedlings, in spite of their greater E_t rates, may be due to greater root development and water absorption.

The different SPAC resistances that occurred between treatments are not easily explained because the R_{SPAC} coefficient of the Ohm's law representations accounts for all component resistances of the soil, root, xylem, and leaf. The total plant resistance is further complicated by sink/source relationships that occur throughout the water transfer pathway (Hinckley *et al.* 1978, Kaufmann and Fiscus 1985). The decreased SPAC resistances for the fall lifted seedlings are likely attributable to greater g_S rates (i.e. a lower stomatal resistance, the inverse of g_S) and reduced resistances at the soil-root interface. The greater resistance for the spring lifted, stored seedlings may be due to their lower g_S rates. However, g_S was similar for the freshly lifted and undisturbed seedlings 22 days after planting and as noted above, it is likely that resistances at the soil-root interface decreased for all seedlings. The advanced phenological condition of the spring lifted and undisturbed seedlings (Table 2.7) may account for the increased SPAC resistances since rapidly expanding shoots may allocate greater water reserves away from E_t and towards growth (Boyer 1974, Fiscus *et al.* 1983). Indeed, the Ψ_{xylem} : E_t relationships for the spring lifted and undisturbed seedlings are more sigmoidal than linear indicating that growth partitioning occurred at higher Ψ_{xylem} (Fiscus *et al.* 1983).

July 4, 1987 (51 days after planting)

The greater similarity between the outplanted and undisturbed seedlings 51 days after planting (Figure 2.8) suggests that water relations had improved for the outplants by this time and they were therefore better established than on the two previous diurnal sample days. Presumably, internal water reserves improved with an increased water absorption capacity. This is further evidenced by the rapid

recovery towards first measurement Ψ_{xylem} values as the evaporative demand diminished towards nightfall in spite of the high diurnal E_t rates and low afternoon Ψ_{xylem}. Greater gaseous exchange rates were recorded for the spring than the fall lifted seedlings. The increased g_s rates would benefit the spring lifted seedlings by increasing their photosynthetic capacity and growth after the risk of desiccation had passed (i.e. after they were established). In addition to the increased g_s rates for the spring lifted seedlings, the greater E_t rates recorded for all seedlings can be attributed to a greater evaporative demand.

The resistance to waterflow through the SPAC had decreased since June 5 for the spring lifted seedlings only, presumably in response to both a increased g_s and a reduced resistance at the soil-root interface. In contrast, the increased SPAC resistances for the fall lifted and undisturbed seedlings may reflect the decreased g_s. The coefficients of determination (r^2) indicate that the Ohm's law analogy described the $\Psi_{xylem} : E_t$ relationships better on July 4 than on the two previous diurnal sample days. Thus, on July 4, the soil-to-leaf resistances were more constant (i.e. the R_{SPAC} coefficient was less variable over the range of E_t) and Ψ_{xylem} decreased more linearly as E_t increased (Elfving *et al.* 1972). The similar y-intercepts indicate that a similar Ψ_{soil} was perceived by all seedlings at the start of the transpirational day (Kaufmann and Hall 1974, Kaufmann and Fiscus 1985).

Root Growth Response

New root development was strongly influenced by lifting-storage treatment (Table 2.9, Figure 2.10a). The greater indices recorded for the fall lifted seedlings indicate that they extended new roots and re-established intimate root-soil contact more effectively than the spring lifted seedlings. Since rapid early root growth is essential for the resumption of normal water relations and consequent establishment (Sands 1984), the root growth indices suggest that the fall lifted seedlings established themselves better than the spring lifted seedlings following field planting.

The lifting date and the temperature and duration of storage are believed to affect early root growth through interactions with bud dormancy status and carbohydrate availability (Ritchie and Dunlap 1980). The possible affects of these interactions on RGC determined under non-limiting conditions for similar lifting-storage treatments (the date of lifting or the duration of storage differed temporally by 7 days) were discussed in Chapter 1. Presumably, these interactions affected early root growth under nursery conditions in a similar way. It was also noted that winter injury had a detrimental effect on RGC for the spring lifted seedlings.

Early root growth differed under field and controlled conditions (Chapter 1, Table 1.4 and Figure 1.7a). This is not surprising since a relationship between early root growth measured under field and non-limiting conditions has not been extensively proven (Ritchie 1985, Burdett 1987, Sutton 1987). These differences cannot be explained by the available data. In particular, aside from the possibility of within

treatment variation, the increased root growth for field planted FL-7-P1 and the spring lifted, stored seedlings cannot be explained. Indeed, the literature suggests that new root development should have decreased for all treatments in response to the environmental constraints imposed by the planting site, especially soil water and temperature limitations. For example, RGC was negligible for white spruce seedlings when Ψ_{soil} was held at -0.15 MPa (Day and MacGillivray 1975) and RGC for Douglas-fir (*Pseudotsuga menseizeii* [Mirb.] Franco) seedlings held at -0.2 MPa was only one-third that of control seedlings held near field capacity (Ritchie 1985). Thus, new root development should have been retarded by soil water deficits that presumably occurred (due to the lack of snow cover and spring rainfall) prior to May 16 (Day 2). Hereafter, soil water shortages may have been precluded by adequate rainfall. This is supported by the first measurement Ψ_{xylem} values which indicate that the Ψ_{soil} perceived by the seedlings at the start of each transpirational day gradually increased as new roots developed. As well, average air temperature (9.5 ° C) determined over the 14 day experimental period suggests that cold soil temperatures should have limited root growth following field planting. Indeed, optimum soil temperatures for root development of several temperate zone species reportedly range from 18 ° C to 25 ° C (Ritchie and Dunlap 1980) and soil temperatures averaging 10 ° C and 15 ° C limited root growth for jack pine (Grossnickle and Blake 1985) and Douglas-fir (Stone *et al.* 1962) seedlings, respectively.

Nursery Trial - Planting Time 2 (June 15)

Water Relations Response

Early water relations clearly differed between treatments lending additional support to the hypothesis that the lifting date and the temperature and duration of storage influence seedling physiology during establishment. Moreover, the salient results of Planting Time 2 generally concur with those of Planting Time 1 and those measured under controlled conditions (Chapter 1) providing further evidence that the response patterns were inherent to the selected lifting-storage methods. Most importantly, the g_s and E_t response patterns indicate that the fall lifted seedlings maximized CO_2 influx at the expense of water vapour efflux and, presumably, a more favourable internal water balance during the critical establishment period. Further, their initially high SPAC resistances indicate that water absorption did not balance transpirational losses. These results suggest that the fall lifted seedlings are less likely to become established than the spring lifted seedlings following outplanting onto droughty soils were water absorption would be further limited.

As previously discussed (Chapter 1), the differences that occurred between planting times for the fall and spring lifted, stored seedlings can be partly attributed to further physiological changes and/or pathological deterioration due to the extended storage periods. The freshly lifted and undisturbed seedlings were not subjected to extensive storage but were more phenologically advanced during Planting Time 2. This effect would certainly influence seedling physiology (Lavender 1981, 1988) and presumably, g_s, E_t,

and Ψ_{xylem}. However, these effects do not appear to have been quantified during the period of rapid shoot elongation. In addition, environmental conditions varied between planting times and within treatment variation likely attributed to further differences since samples were necessarily small due to limited sampling time and equipment constraints.

First Measurement Patterns (1 to 21 Days After Planting)

Fluctuations in first measurement g_s and E_t most closely followed fluctuations in RH (Figures 2.11 and 2.12). However, in accordance with Planting Time 1, and for the previously noted reasons, a clear association was not evident for any of the selected atmospheric variables. The greater rates exhibited by the fall lifted seedings agree with Planting Time 1, but were less apparent, and did not clearly increase following Planting Time 2, presumably because the more stressful environment did not promote wider pore apertures. In contrast with Planting Time 1, the 48 day conditioning period at above freezing temperatures clearly reduced g_s and E_t rates for the fall lifted seedlings. This may also be due to environmental differences that occurred between trials. On the other hand, extended sub-freezing temperature storage may have caused further damage to the stomatal mechanism and resulted in greater gaseous exchange rates for the FL-7-P2 seedlings.

The undisturbed seedlings had well established root systems during both planting times and new root development increased or was constant between planting times (Table 2.9, Figure 2.10). Thus, the clearly higher Ψ_{xylem} values recorded for the undisturbed seedlings over the 21 day period following Planting Time 2 suggest that Ψ_{soil} limited nighttime absorption for the outplants. Lower Ψ_{soil} is supported by less rainfall over the 21 day post-planting period. This indicates that root losses associated with outplanting can be expected to cause varied levels of water stress depending on the field environment and thereby emphasizes the importance of minimizing such losses during all lifting-storage-planting phases, especially if planting is to be done during hot dry periods. Ψ_{xylem} increased for the outplants as they developed new roots. Since Ψ_{soil} did not vary greatly prior to Day 16, the day to day fluctuations in Ψ_{xylem} probably reflect varied evaporative demands, which lead to varied transpirational debts, that were satisfied to different degrees overnight.

Diurnal Patterns

June 16, 1987 (1 day after planting)

The g_s rates were minimal for all outplants by mid-morning indicating that stomatal closure limited E_t and, presumably, photosynthesis at this time (Figure 2.14). This result supports the results of Planting Time 1 and presumably occurred for similar reasons. As discussed, the response differences that occurred between the outplanted and undisturbed seedlings emphasizes the importance of reserve

carbohydrates for respiration and growth during early establishment. The higher Ψ_{xylem} values recorded for the undisturbed in comparison with the outplanted seedlings suggests that they were able to offset their greater transpirational losses and maintain a more favourable internal water balance by accessing additional water reserves through well established root systems. In contrast, the outplants became water stressed and maintained generally lower Ψ_{xylem} (particularly during the evening) through stomatal closure since their more limited root systems and poor root-soil contact hindered water absorption. Their greater resistance to water uptake is reflected by more negative R_{SPAC} coefficients in the $\Psi_{xylem} : E_t$ relationships (Figure 2.19). However, the low coefficients of determination (r^2) indicate that waterflow was not modeled particularly well by the Ohm's law analogy at this time.

July 8, 1987 (23 days after planting)

A more distinct separation occurred between g_s and E_t response patterns 23 days after planting (Figure 2.16). The wider divergence in g_s rates was largely due to increased rates for the fall lifted seedlings. The wider divergence in E_t rates was a consequence of a greater relative increase for the fall lifted treatments since diurnal E_t rates increased for all treatments with the greater evaporative demand. At this time, the fall and spring lifted seedlings formed two distinct groups supporting the results of Chapter 1, Planting Time 1, and the first measurement response patterns of Planting Time 2 thereby providing additional evidence that the nursery lifting-storage practices have predisposed each group to respond differently during establishment.

The increased g_s rates recorded for the fall lifted seedlings with time out of cold storage support the results of Chapter 1, Planting Time 1, and the first measurement response patterns of Planting Time 2 and presumably occurred for the forementioned reasons. The increased Ψ_{xylem} values indicate that internal water relations had improved since planting for all seedlings. These increases occurred because the hydraulic conductivity through the surrounding soil increased (due to rainfall) and because the seedlings were more efficient at water absorption (due to increased root development). The higher values recorded near dawn indicate that the availability of water for growth was greater as each seedling began its transpirational (and photosynthetic) day. This is supported by the higher β_1 coefficients of the $\Psi_{xylem} : E_t$ relationships. The higher Ψ_{xylem} values recorded at the end of the day indicate that seedling water status improved more rapidly in response to the reduced transpirational demand at this time. While Ψ_{xylem} was less sensitive to the previously noted g_s and E_t response differences, the commonly higher values recorded for the fall, in comparison with the spring lifted seedlings, may be due to their greater root development.

The decreased SPAC resistances for the stored seedlings are likely attributable to greater g_s rates and reduced resistances at the soil-root interface coincident with new root development and increased soil water availability. The greater decreases for the fall lifted seedlings reflect their greater root development.

The increased SPAC resistances for the freshly lifted and undisturbed seedlings may be due to differences in water partitioning between E_t and growth (Fiscus *et al.* 1983) or they may simply reflect varied atmospheric and plant factors.

August 13, 1987 (59 days after planting)

The greater similarity between the outplanted and undisturbed seedlings for g_s and E_t rates 59 days after planting (Figure 2.18) suggests that the outplants were well established at this time. The higher Ψ_{xylem} values recorded for the undisturbed seedlings indicate that they continued to maintain the most favourable internal water relations. In previous studies, Scots (*Pinus sylvestris* L.) (Örlander 1986), ponderosa (*P. ponderosa* Laws.) and lodgepole pine outplants (Baldwin and Barney 1976) required two or more growing seasons to normalize water uptake and increase Ψ_{xylem} to levels of well established, naturally occurring seedlings. The greater gaseous exchange rates recorded for the spring lifted seedlings 51 days following Planting Time 1 (July 4) were not apparent for the corresponding treatments 59 days following Planting Time 2 (August 13). It is possible that the more moderate atmospheric conditions that prevailed on August 13 did not limit stomatal opening for the fall lifted seedlings at this time.

Stomatal conductance and Ψ_{xylem} were considerably greater on August 13 than on the two previous diurnal sampling days. These differences reflect better establishment for the outplants and reduced environmental stress for all treatments. The higher Ψ_{xylem} values, particularly at first measurement, can be attributed to increased root area (Nambiar *et al.* 1979) and a high Ψ_{soil} (48.2 mm of rain fell during the previous 48 hours). Under such conditions of non-limiting soil water, light and the absolute humidity difference between the needle and the air (AHD) are believed to be the primary factors that regulate pore width (Kaufmann 1982). Since the VPD (which approximates the AHD when leaf and air temperature are equal) was relatively low on August 13, and Ψ_{xylem} relatively high, it is likely that the stomatal opening was not limited to a great degree by available turgor. In spite of the higher g_s rates for all treatments, E_t rates increased for the spring lifted treatments only clearly reflecting the lower VPD on August 13. The greater E_t rates were reflected by a reduced SPAC resistance while the SPAC resistance increased for the fall lifted and undisturbed seedlings. This clearly represents a resistance to waterflow at the leaf-air interface that is not plant related.

Root Growth Response

New root growth was strongly influenced by lifting-storage treatment (Table 2.9, Figure 2.10b). The greater root development that occurred for the fall lifted seedlings indicate that they extended new roots, re-established intimate root-soil contact, and established themselves better than the spring lifted seedlings. Thus, the spring lifted treatments, particularly SL-1-P2, had a comparatively limited ability to replace water losses from the needle surface. The similarities and differences that occurred between

planting times cannot be fully explained because they are subject to numerous interdependent and interrelated factors (discussed in Chapter 1) not specifically addressed during the present study.

Previous studies with both coniferous and deciduous forest tree seedlings showed root growth to vary widely following storage depending on lifting date, storage conditions, and the duration of storage (Ritchie and Dunlap 1980). As previously noted, these variations suggested that the lifting-storage method affects RGC through interactions with bud dormancy and carbohydrate reserves (Ritchie and Dunlap 1980). Although carbohydrate reserves were presumably lower for the fall lifted seedlings during Planting Time 2, new root development increased dramatically. A similar result occurred under non-limiting conditions (Chapter 1, Table 1.4 and Figure 1.7b). Perhaps, carbohydrate levels were sufficient for root development during both planting times and the extended storage period promoted a more uniform achievement of the chilling requirement which in turn increased RGC. It is also possible that the longer daylength and warmer temperatures characterizing Planting Time 2 increased the production of current photosynthate which is considered to be the primary carbon source for new root development (Etter and Carlson 1973, Ritchie 1982, van den Driessche 1987). In addition, warmer soil temperatures promote root growth by increasing metabolic activity and root cell turgidity through increased water absorption (because of increased membrane permeability and decreased water viscosity) (Lopushinsky and Kaufmann 1984). Since increased water absorption increases Ψ_{xylem} and therefore g_s, photosynthesis is further enhanced (Andersen *et al.* 1986). The greater indices recorded for the spring lifted, stored seedlings can presumably be attributed to increased current photosynthate production since it is unlikely that RGC would increase during storage for non-dormant seedlings. The lower indices recorded for the freshly lifted seedlings can presumably be related to differences in root growth periodicity that occurred between planting times.

Early root growth differed under field and controlled conditions (Chapter 1, Table 1.4 and Figure 1.7b). As previously noted, a relationship between early root growth measured under field and non-limiting conditions has not been extensively proven (Ritchie 1985, Burdett 1987, Sutton 1987). The lower indices for the fall and freshly lifted seedlings may be due to lower available soil water (Day and MacGillivray 1975) or greater evaporative stress resulting in a shorter transpirational (and photosynthetic) day. Aside from the possibility of within treatment variation, the greater indices for the spring lifted, stored seedlings remains largely unexplained.

SEEDLING MORPHOLOGICAL RESPONSE

Nursery Trial

Planting Time 1 (May 14)

Survival rates exceeded 99 % for all treatments after one growing season. The undisturbed seedlings generally showed greater growth increments (Figure 2.20) and were clearly larger than the outplants after one growing season (Table 2.13) indicating that all lifting-storage treatments reduced growth. The smaller reductions for the fall than spring lifted seedlings suggests that the fall lifted seedlings became better established. This may have occurred because the spring lifted seedlings were physiologically active at the time of lifting (as evidenced by advanced phenology and/or new white roots) and therefore, more susceptible to damage than the dormant, fall lifted seedlings during the lifting-storage-planting sequence (Sutton 1984). Thus, to establish themselves, the fall lifted seedlings had only to renew growth processes while the spring lifted seedlings, especially those that were freshly lifted, had to recover from stresses imposed during handling while continuing physiological processes essential for growth. Moreover, if the seedlings were spring lifted after carbohydrate reserves had been invested in renewed growth, but prior to significant current photosynthate accumulations, it is likely that carbohydrate reserves were limited during establishment. It is also possible that growth-regulating compounds no longer favoured root initiation for the spring lifted seedlings since relative concentrations of plant growth regulators change as seedlings begin active growth (Lavender 1988). Thus, their ability to re-initiate and replace new roots that had been damaged during the lifting-storage-planting sequence may have been greatly impaired.

Minimum ground caliper increment occurred during the period of maximum leader extension (Days 22 to 42) because the cambial region is a comparatively weak carbohydrate sink that competes poorly with the strong sinks of developing shoots (Kramer and Kozlowski 1979). With this period as the exception, ground caliper increments generally increased over the growing season, presumably in response to increased photosynthate production (due to an expanding needle area and more favourable conditions for photosynthesis) and a weakening of sink strengths in the developing shoots. Dry weight increases for black spruce nursery stock have been shown to closely follow degree day accumulations providing soil water and nutrient availability do not limit growth (Armson and Sadreika 1974, McClain 1982). Seedling dry weights often correlate well with root collar diameter (Armson and Sadreika 1974) and ground caliper growth progressions closely followed degree day accumulations during the present study (Figure 2.21). The differences that occurred between the undisturbed and planted seedlings probably reflect more limited water absorption for the outplants due to their more limited root systems. The sigmoidal relationship for the spring lifted seedlings suggests that soil water and nutrient availability limited diameter growth towards the end of the growing season (Armson and Sadreika 1974), possibly because of a more limited

root system in comparison with the fall lifted seedlings. This is supported by the significantly greater root dry weights recorded for the fall than spring lifted treatments after one growing season.

It is evident from the periodic leader extension increments that the fall lifted seedlings, particularly treatment FL-7-P1, exhibited a delayed phenological response. Overwinter frozen storage also delayed bud burst for numerous other coniferous seedlings (Jorgensen and Stanek 1962, Nyland 1974, Blake 1983, Ritchie 1984b, Ritchie *et al.* 1985). As discussed in Chapter 1, this delay is apparently due to sub-optimal conditions for dormancy release that operate during cold dark storage. While a delay in bud flushing may be beneficial in reducing the effects of late frosts (Jorgensen and Stanek 1962, Nyland 1974) or transpirational losses (through a reduced needle area) during the critical establishment period (i.e. prior to root development), such may also render new growth more susceptible to desiccation during the warmer, drier periods that occur during late spring and summer (Nyland 1974). Regardless of the delayed bud burst, the fall lifted seedlings showed significantly greater first year height growth and leader extension than the spring lifted seedlings. This may be attributable to differences in internal water reserves since shoot elongation did not begin for the fall lifted seedlings until new roots had developed and water absorption was able to offset growth and transpirational demands.

Planting Time 2 (June 15)

Survival rates were slightly lower for Planting Time 2 seedlings; the poorest rate, though still quite acceptable at 94 %, occurred for the FL-7-P2 seedlings. Of the selected morphological attributes determined after one growing season, only leader extension and height differed significantly between the fall and spring lifted, stored seedlings. In contrast, the largest attributes were commonly recorded for the freshly lifted seedlings. However, a sizable portion of this growth occurred prior to lifting (Table 2.3).

The delayed bud burst observed for the fall lifted seedlings during Planting Time 1 was less pronounced during Planting Time 2 (Figure 2.22). It is likely that the warmer post-planting conditions advanced the phenological development for all stored seedlings. Ground caliper growth progressions closely followed degree day accumulations and the relationship was similar for all lifting-storage treatments. Moreover, the ground caliper increment : accumulated degree growing days relationship was similar for both planting times further indicating that temperature plays a key role in determining growth. After one growing season, morphological response attributes differed significantly between planting dates for ground caliper and top and root dry weight and reflect the additional (one month) growing period for Planting Time 1 seedlings. Since leader extension occurs over a relatively short period for spruce seedlings (i.e. spruce seedlings have fully preformed shoots in the winter buds [fixed growth]), sufficient growing time followed both planting dates for it to be completed.

Raith Trial

Planting Time 1 (May 8) and 2 (June 9)

The relatively low, survival rate of 87 % recorded for the spring lifted, stored seedlings is presumably site related since survival equaled 99 % for similar seedlings outplanted the following week at the TBFN. Morphological response differences were less pronounced following planting in the more variable Raith, than nursery environment (Table 2.14, Figures 2.23 and 2.24). This was particularly apparent for the fall lifted treatments which did not differ significantly for either planting time. The freshly lifted seedlings of Planting Time 2 were clearly the largest after one growing season. As previously discussed, a large percentage of this growth occurred prior to lifting. The greater leader extension increments recorded for the fall lifted seedlings during the 60 day period following Planting Time 2 presumably reflect a more favourable growing environment. In particular, soil and air temperatures were warmer and photoperiods longer. The reduced ground caliper increments over the same period might be attributable to increased sink strengths for the more rapidly expanding shoots.

The results of both the nursery and the Raith trials indicate that fall lifted, frozen stored, spring lifted, cool stored, and freshly lifted $1^1/_2 + 1^1/_2$ black spruce transplants can be successfully established on fresh, loamy soils of glaciolacustrine and ground moraine origin during the spring planting season (early May to mid-June). This concurs with experimentation by McClain (1981, 1983) during which fall lifted, overwinter frozen stored ($-2 \pm 1\,^\circ$ C) and spring lifted, cool stored ($+2 \pm 1\,^\circ$ C) $1^1/_2 + 1^1/_2$ and 3+0 black spruce seedlings survived and grew well following outplanting onto typical mixedwood sites at biweekly intervals beginning in mid-May through to the end of July. Planting of freshly lifted, rising $1^1/_2 + 1^1/_2$ and 3+0 black spruce seedlings beyond this date showed acceptable survival and growth after four growing seasons (McClain 1981). In another study aimed at extending the planting season, Sutton (1982b) planted spring lifted, frozen stored (temperature not provided) 3+0 black spruce seedlings on a variety of outwash and till sites at two week intervals beginning in July through to mid-October in each of three consecutive years. In spite of variations in planting stock, and adverse storage, climatic and site conditions, Sutton's results were remarkably consistent and showed reasonably good survival and growth following the first two (July) sequential plantings. Thereafter, survival and growth declined rapidly.

CONCLUSIONS

The central hypothesis under test in this study was that the date of lifting and the temperature and duration of storage affects seedling physiology and thereby influences the physiological and morphological response following outplanting. The results support this hypothesis. In particular, they showed the selected lifting-storage treatments to affect early plant water relations through interactions with both early root development and stomatal function.

Establishment mechanisms differed between the fall and spring lifted seedlings. The former exhibited prolific root growth but ineffectively controlled transpirational losses during early establishment. This response likely favoured growth under the conditions of the present study but could be detrimental following field planting onto droughty sites, or if water absorption were limited by cold soil temperatures or flooding. The latter more effectively reduced transpirational losses, at the expense of CO_2 uptake and presumably growth, immediately following outplanting. In particular, root growth, which has been shown to depend on current photosynthate (Etter and Carlson 1973, Ritchie 1982, van den Driessche 1987), may have been limited. This was supported by lower root growth indices for the spring lifted treatments. Due to their poor root development, the spring lifted seedlings would probably have been less successfully established during times of seasonal water stress.

In comparison with the undisturbed seedlings, all lifting-storage treatments reduced growth. The fall lifted seedlings showed generally larger morphological attributes after one growing season than the freshly lifted seedlings following Planting Time 1, and the spring lifted, stored seedlings following both planting times. The extended conditioning period at above freezing temperatures variably affected growth for the fall lifted seedlings. Regardless of the manner in which the selected lifting-storage treatments influenced early physiological response, survival and growth determined after one growing season indicated that fall lifted, frozen stored, spring lifted, cool stored, and freshly lifted $1^1/_2 + 1^1/_2$ black spruce transplants can be successfully established on fresh, loamy soils of glaciolacustrine and ground moraine origin during the spring planting season (early May to mid-June).

CHAPTER 3

ESTABLISHMENT AND EARLY GROWTH OF BLACK SPRUCE (*Picea mariana* [Mill.] B.S.P.) IN RELATION TO SELECTED NURSERY LIFTING AND STORAGE PRACTICES. 3. PHYSIOLOGICAL AND MORPHOLOGICAL RESPONSE DURING ESTABLISHMENT. SUMMARY, CONCLUSIONS, AND IMPLICATIONS FOR FOREST MANAGEMENT.

SUMMARY, CONCLUSIONS, AND IMPLICATIONS FOR FOREST MANAGEMENT

The importance of Ontario's forest industry cannot be overstated. In economic terms, forestry contributes significantly to provincial revenues and is a major employer. It is sociologically important by contributing to the vitality and stability of several communities, particularly in the north (Smyth *et al.* 1989), and frequently benefits other sectors including mining, fish and wildlife, and recreation. To ensure its long term health, it is imperative that new forests are established and grow rapidly until maturity. In the face of dwindling forest management funding, it has been proposed that regeneration efforts be concentrated on those areas that will yield maximum financial returns (i.e. 'prime sites') and that more cost-effective regeneration methods be employed (Teskey 1986, Greenwood 1987).

Forest regeneration by planting continues to be the mainstay of the regeneration program in Ontario because it most effectively minimizes future tending and can concentrate genetically superior stock on high quality sites. Indeed, it has recently been recommended as the best method of increasing the yield and quality of a desired species within a specified time (Galloway and Squires 1988). Maximum financial returns can only be realized if newly planted seedlings become successfully established and rapidly begin normal growth processes. To ensure survival and rapid early growth, outplants must be physiologically prepared to respond to the planting site environment. Most importantly, a newly planted seedling must achieve and maintain a favourable internal water balance during the establishment phase.

A seedling's physiological preparedness is subject to numerous biological, physical, and environmental stresses that influence the seedling's development between the time of cone collection and outplanting. The stress events that occur during each substandard phase of transplanting, handling, storage, shipping, etc. are presumed to be cumulative; damage occurring in one phase of the nursery operation is added to damage that occurred prior to that phase, or has yet to occur in a following phase (Navratil 1973, DeYoe 1988). Thus, even mild stress, if persistent, will eventually injure the seedling by reducing its ability to recuperate from further stress events (Timmis 1980). It follows that stock must be flawlessly handled during all phases of the regeneration process to minimize the incidence of stress and thereby, maximize seedling fitness and outplanting performance potential (Edgren 1980).

This thesis investigated the early water relations and growth response of fall and spring lifted $1^1/_2 + 1^1/_2$ black spruce (*Picea mariana* [Mill.] B.S.P.) transplants in a series of controlled environment, nursery, and field trials. Prior to planting in early May and mid-June, seedlings were: (1) fall lifted (October 29, 1986), overwinter stored at $-2 \pm 1^\circ$ C and conditioned at $+2 \pm 1^\circ$ C for 7 or 48 days, (2)

spring lifted (May 6, 1987), stored at +2 ± 1 ° C until removed, and (3) spring lifted, stored at +2 ± 1 °C for 1 day (i.e. freshly lifted). The central hypothesis under test was that the date of lifting and the temperature and duration of storage affects seedling physiology and thereby influences the physiological and morphological response following outplanting. The results indicate that this hypothesis should be accepted. In particular, they showed the selected lifting-storage treatments to affect early plant water relations through interactions with both early root development and stomatal function.

Regardless of potting/planting time and growing environment, the fall lifted seedlings exhibited prolific root growth but ineffectively controlled transpirational losses during early establishment. This response likely favoured growth under the conditions of the present study but could be detrimental following field planting onto drought prone sites, or if water absorption was otherwise limited (e.g. cold soil temperatures). Water relations response was variably affected but not greatly influenced by the extended conditioning period. The spring lifted seedlings more effectively reduced transpirational losses, at the expense of carbon dioxide (CO_2) uptake and presumably growth, immediately following outplanting. In particular, root growth, which has been shown to depend on current photosynthate (Etter and Carlson 1973, Ritchie 1982, van den Driessche 1987), may have been limited. This was supported by lower root growth indices for the spring lifted treatments. Due to their poor root development, the spring lifted seedlings would probably have been less successfully established during times of seasonal water stress.

Under the conditions of the present study, the fall lifted seedlings showed generally larger morphological attributes after one growing season than the freshly lifted seedlings following the May plantings and the spring lifted, stored seedlings following both planting times. While the extended conditioning period at above freezing temperatures variably affected growth for the fall lifted seedlings, only height and leader extension differed significantly after one growing season. Regardless of the manner in which the selected lifting-storage treatments influenced early physiological response, survival and growth determined after one growing season indicated that fall lifted, frozen stored, spring lifted, cool stored, and freshly lifted $1^1/_2 + 1^1/_2$ black spruce transplants can be successfully established on fresh, loamy soils of glaciolacustrine and ground moraine origin during the spring planting season (early May to mid-June).

The findings of this study have very serious implications for forest management. The results clearly indicate that commonly applied nursery lifting and storage practices predispose seedlings to respond variously to the outplanting environment. Forest renewal can maximize cost-effectiveness only if these response differences are understood. The results further emphasize the need to ascertain the vitiating effects of all handling practices on seedling physiology. Failure to do so may allow continuance of handling practices that incur unnecessary reductions of performance potential. Anything less than maximum undermines the 'prime site' program and represents an opportunity cost to forestry companies.

These costs will be incurred through increased tending in the short term, and, more importantly, through reduced yields and longer rotation periods in the long term. The present study should be extended to include additional field trials on a variety of sites over a number of years. In this way, the inference would be broadened to include a range of soil water regimes, weather conditions, site preparation techniques and the various interactions. Since not all of the effects of lifting-storage practice on post-planting performance are apparent after one growing season (Burdett 1983), survival and growth response should be determined during a second year, or later assessment. Finally, additional research should be conducted to investigate modifications to the frozen storage environment that would promote more favourable stomatal response during early establishment. This is especially pertinent since overwinter frozen storage is becoming more widely used provincially. In particular, the effects of light, warming periods, and fluctuating temperatures on early seedling physiology should be investigated.

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APPENDICES

APPENDIX I

DETERMINATION OF FOLIAGE AREA USING THE DELTA T AREA METER

To obtain an absolute value of the average stomatal conductance (g_s) or transpiration (E_t) rate for each seedling measured with the model CS-102 whole seedling porometer, the projected needle area (i.e. the area that is silhouetted when measured photometrically) of the evaporating needle surface must be known. It is relatively simple to destructively determine the projected needle area (PNA) at a given point in time using a Rhizometer (Morrison and Armson 1968) or one of the commercially available microprocessor area meters. However, it is difficult to non-destructively determine PNA during a test period because it changes as pre-test needles are lost and current needles develop.

The general approach taken was to measure all foliage (both pre-test and newly developed) at the end of each trial using an area meter. New foliage development was estimated for the potting trials from regression equations developed to predict the PNA of new foliage from new branch length which was monitored for each trial. New foliage development was estimated for the nursery trials using ratios relating PNA determined at the end of each trial to new branch length (NBL) which was monitored during each trial. Old needle loss was determined at the end of each trial by counting bare sterigmata and multiplying this value by the average area of a single needle. Seedlings were assumed to have all previous seasons foliage at the start of each trial and old needle loss was assumed to be linear over each trial.

FOLIAGE AREA MEASUREMENT

The equipment used to measure PNA consisted of a Delta T Devices Ltd. microprocessor area meter, Ikegami Model ITC-510 black and white high resolution (850 horizontal line) video camera, 15 mm lens, camera stand, light box, and a black and white video monitor. The camera was positioned so its focal plane was 30 cm above the light box surface creating a measurement window of 13 cm vertical by 14 cm horizontal.

PNA was determined on excised needles that were randomly scattered (time limitations prevented needles to be arranged at right angles to camera scan for maximum accuracy) in approximately 8 cm^2 samples on the back-lighted box in view of the camera. The area meter scanned each horizontal camera line and summed the line segments traversed by the needles. Calibration was made using the silhouette area of fine copper wire (0.0635 mm diameter) cut to simulate a PNA of 8 cm^2 and permanently mounted between two sheets of acetate forming a template. The template was placed in an identical position within the measurement window each time the area meter was calibrated.

Seedlings to be measured for PNA were severed at the root collar. The tops were bagged separately, air dried at room temperature for 5 days, and placed in a forced air convection oven at 70 °C for 24 hours to facilitate the removal of needles. The average shrinkage factor was determined separately for one-year-old or older and current (but cutinized) foliage from each lifting-storage treatment on randomly chosen 50 needle samples. Each sample was measured for fresh PNA and remeasured after the above drying treatment. The number of samples needed to estimate the average shrinkage factor ±10 % at the 95 % confidence level was determined using a two stage survey and the following formula (Freese, 1962):

$$n = \frac{t^2 \times s^2}{E^2} \qquad (I.1)$$

where:

n = the number of 50 needle samples required
t = student's t value with n-1 degrees of freedom
s = the standard deviation based on 5 preliminary samples from stage 1
E = allowable error or the average shrinkage factor × 0.1

FOLIAGE AREA ESTIMATION

The following step by step procedure outlines the methods used to estimate PNA for each trial.

1. New Branch Development

   i. Prior to potting in the controlled environment chamber or outplanting at the Thunder Bay Forest Nursery, a white latex paint ring was painted on the main stem of each seedling immediately below the 1986 terminal whorl.
   ii. NBL above the paint ring was measured and recorded in 1-cm classes on the day of potting and weekly thereafter (potting trials), and concurrent with diurnal sampling of water relations response (nursery trials).
   iii. At the end of each trial, trees were excavated, taken to the lab, and NBL above (NBL_{above}) and below (NBL_{below}) the paint ring was measured and recorded in 1-cm classes.

2. Old Needle Area Determination

i. The number of sterigmata without needles were counted on all old branches (i.e. ≥1 year old) at the end of each trial.

ii. Fifty needle samples were randomly chosen from each lifting-storage treatment and measured for fresh area. Each sample was then subjected to the above drying treatment and re-measured. The number of samples needed to estimate the average shrinkage factor ± 10 % at 95 % confidence was determined using a two stage survey and equation (I.1). The average shrinkage factor was then calculated for old foliage for each lifting-storage treatment.

iii. All old branches were bagged with remaining needles and subjected to the above drying treatment.

iv. Sufficient 50 needle samples were taken to determine the average 50 needle area ± 10 % at the 95 % confidence for each lifting-storage treatment using a two stage survey and equation (I.1). The average area of a single needle was calculated for each seedling on the basis of the 50 needle samples as follows:

$$\text{average area of a single needle} = \text{average 50 needle sample area} \div 50 \qquad \text{(I.2)}$$

v. The remaining old foliage was measured for PNA. The sum of all measured old foliage for each seedling was corrected for shrinkage. This value represented old foliage area remaining at the end of the trial.

$$\text{old foliage area} = (\text{dry area of 50 needle sample to determine shrinkage} + \text{dry area of 50 needle samples to determine average needle area} + \text{dry area of remaining old needles}) \times \text{average shrinkage factor determined for old foliage} \qquad \text{(I.3)}$$

vi. It was assumed that each seedling was completely foliated at the beginning of the trial. Therefore, old foliage lost over the trial was calculated as follows:

$$\text{area of lost old foliage} = \text{number of sterigmata counted in 2i above} \times \text{average shrinkage factor determined for old foliage (2ii above)} \times \text{average area of a single needle (2iv above)} \qquad \text{(I.4)}$$

vii. Old foliage area at the beginning of the trial was taken as the sum of the old foliage area measured at the end of the trial (2v above) and the area of lost old foliage (2vi above).

3. Old Needle Area Loss

i. Old foliage area loss was assumed to be linear over each trial.

4. New Needle Area Determination

Controlled Environment: Potting Time 1 (May 21)

Because of time constraints, it was not possible to destructively sample new foliage from the first potting trial. Consequently, new foliage area had to be predicted for each developing bud or shoot (new branch) by the following simple linear regression equation developed for succulent (not cutinized) branches taken from the second potting trial:

$$PNA = (-\ 0.82843 + 1.59201 \times \sqrt{\text{new branch length}^2}) \qquad (I.5)$$

Equation (I.5) had a high coefficient of determination ($r^2 = 0.84$) and met all the assumptions of simple linear regression indicating that it fit the data set very well. PNA's predicted for each new branch measured above and below the paint ring were summed for each seedling and used to estimate the PNA at the end of the trial. The ratio relating new foliage area above the paint ring to new foliage area below the paint ring ($PNA_{above} : PNA_{below}$) was determined for each seedling. PNA's predicted for each new branch measured above the paint ring at the beginning of the trial and twice (weekly) during the trial were summed for each seedling and used to estimate PNA above the paint ring at these times. The ratio $PNA_{above} : PNA_{below}$ was used to estimate new foliage below the paint ring at the beginning of the trial and twice (weekly) during the trial. New foliage estimates above and below the paint ring were summed to estimate total new foliage development. New foliage development was assumed to be linear between each estimation.

Controlled Environment: Potting Time 2 (June 24)

The following procedure was performed separately both above and below the paint ring to determine new foliage area at the end of the trial for all well-watered seedlings over the entire trial.

i. Each tree was severed at the paint ring.
ii. All succulent foliage was measured for fresh needle area at the end of the trial. Foliage area measurements were recorded in 1-cm classes by branch length. Succulent tips of hardened branches were removed and also measured for fresh foliage area.
iii. Fifty needle samples of hardened (cutinized), current foliage were randomly pulled and the above procedure was used to determine an average shrinkage factor for each tree.
iv. All remaining new branches were bagged with remaining needles and dried to facilitate needle removal. Following removal, all remaining needles were measured for PNA .

Equation (I.5) and the procedure used to predict new foliage development for the first potting trial was used to predict new foliage development for well-watered treatments FL-48-P2, FL-7-P2,

and SL-48-P2 at the beginning of the trial and twice (weekly) during the trial. The following simple linear regression developed for hardened branches taken from the well-watered treatments and the procedure used to predict new foliage development for the first potting trial were used to predict new foliage development for each developing bud or shoot (new branch) measured for well-watered treatment SL-1-P2:

$$PNA = (-\ 0.63705 + 1.27664 \times \sqrt{\text{new branch length}^2}) \qquad (I.6)$$

Equation (I.6) had a very high coefficient of determination ($r^2 = 0.97$) and met all the assumptions of simple linear regression indicating that it fit the data set very well.

It was not possible to measure new foliage area at the end of the trial for the water stressed treatments because it was too brittle to handle. Furthermore, much of the new foliage had not developed cutin and was so desiccated it could no longer be detected by the area meter. Consequently, new foliage area had to be predicted from branch length regressions developed using data collected from the well-watered treatments.

Equation (I.5) and the procedure used to predict new foliage development for the first potting trial were used to predict new foliage development for water stressed treatments FL-48-P2, FL-7-P2, and SL-48-P2 at the beginning and end of the trial of the trial and twice (weekly) during the trial. Equation (I.6) and the procedure used to predict new foliage development for the first potting trial were used to predict new foliage development for water stressed treatment SL-1-P2 at the beginning and end of the trial and twice (weekly) during the trial. Both of these equations overestimated needle area for the non-watered treatments towards the end of the trial because they were based on healthy branches and did not account for needle desiccation and loss. This was of little consequence since the water stressed treatments were transpiring minimally at this time.

Field Environment: Nursery Trial - Planting Time 1 (May 14) and 2 (June 15)

Equations (I.5) and (I.6) effectively predicted the foliage area of succulent and hardened shoots respectively. Unfortunately, both equations proved less useful for predicting foliage area of developing shoots that were intermediate between these two stages. Consequently, a different approach had to be taken to estimate new foliage development for the nursery trials whose seedlings traversed these stages of development over the extended experimental period. The following procedure was performed separately both above and below the paint ring to determine new foliage area for each seedling at the end of each trial.

i. Each tree was severed at the paint ring.

ii. The total NBL was measured.

iii. All succulent foliage was measured for fresh needle area at the end of the trial. Succulent tips of hardened branches were removed and also measured for fresh foliage area.

iv. Fifty needle samples of hardened, current foliage were randomly pulled and the above procedure was used to determine an average shrinkage factor for each tree.

v. All remaining new branches were bagged with remaining needles and dried to facilitate needle removal. Following removal, all remaining needles were measured for PNA .

The ratios $PNA_{above} : PNA_{below}$ and $NBL_{above} : PNA_{above}$ were determined at the end of each trial. The ratio $NBL_{above} : PNA_{above}$ and the NBL's measured above the paint ring concurrent with each diurnal sample of water relations response (1 ii above) were used to estimate foliage development above the paint ring at these times. The ratio $PNA_{above} : PNA_{below}$ was then used to estimate foliage development below the paint ring at these times. New foliage estimates above and below the paint ring were summed to estimate total new foliage development. New foliage development was assumed to be linear between each estimation.

APPENDIX II

ROOT GROWTH CODING SYSTEM

Class[1]	Description
0	no new root growth
1	some new roots, none over 1 cm long
2	1 - 3 new roots over 1 cm long
3	4 - 10 new roots over 1 cm long
4	11 - 30 new roots over 1 cm long
5	31 - 50 new roots over 1 cm long
6	51 - 70 new roots over 1 cm long
7	more than 70 new roots over 1 cm long

[1] After Burdett (1979).

APPENDIX III

MEAN RATES OF STOMATAL CONDUCTANCE AND TRANSPIRATION, ASSOCIATED SAMPLE SIZES, STANDARD ERRORS, AND MULTIPLE RANGE TEST STATISTICS DETERMINED FOR POTTING TIMES 1 AND 2

Table III.1. Stomatal conductance and transpiration rates (n, $\bar{x}$, S.E.) for $1^1/_2 + 1^1/_2$ black spruce transplants measured in a controlled environment chamber at Lakehead University during Potting Time 1 (May 21). Half the potted seedlings were watered to the drip point every second day (well-watered = WW) while the other half were watered in the same way for 3 days and then allowed to dry (water stressed = WS). Means within a sample time without a common letter are significantly different ($\alpha = 0.05$).

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance		Transpiration	
			Mean ($cm \cdot sec^{-1}$)	standard error ($cm \cdot sec^{-1}$)	Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
First Light						
1	FL-48-P1-WW	3	0.227bc	0.041	0.088ab	0.012
1	FL-7-P1-WW	3	0.264bc	0.043	0.104ab	0.013
1	SL-14-P1-WW	4	0.368abc	0.057	0.124ab	0.020
1	SL-1-P1-WW	3	0.525ab	0.059	0.170a	0.013
1	FL-48-P1-WS	4	0.164c	0.046	0.057b	0.013
1	FL-7-P1-WS	4	0.166c	0.031	0.065b	0.011
1	SL-14-P1-WS	3	0.458abc	0.122	0.179a	0.047
1	SL-1-P1-WS	4	0.608a	0.104	0.170a	0.015
3	FL-48-P1-WW	3	0.218	0.066	0.126	0.027
3	FL-7-P1-WW	3	0.169	0.014	0.097	0.012
3	SL-14-P1-WW	4	0.163	0.027	0.098	0.015
3	SL-1-P1-WW	3	0.138	0.008	0.084	0.004
3	FL-48-P1-WS	4	0.184	0.061	0.107	0.033
3	FL-7-P1-WS	4	0.204	0.042	0.121	0.022
3	SL-14-P1-WS	3	0.223	0.070	0.139	0.042
3	SL-1-P1-WS	4	0.128	0.015	0.077	0.011
4	FL-48-P1-WW	3	0.458	0.177	0.130	0.038
4	FL-7-P1-WW	3	0.329	0.050	0.095	0.017
4	SL-14-P1-WW	4	0.267	0.035	0.081	0.015
4	SL-1-P1-WW	3	0.226	0.028	0.074	0.017
4	FL-48-P1-WS	4	0.420	0.121	0.135	0.039
4	FL-7-P1-WS	4	0.345	0.090	0.092	0.021
4	SL-14-P1-WS	3	0.349	0.127	0.097	0.042
4	SL-1-P1-WS	4	0.241	0.032	0.072	0.011
5	FL-48-P1-WW	3	0.373	0.103	0.153	0.024
5	FL-7-P1-WW	3	0.286	0.021	0.112	0.016
5	SL-14-P1-WW	4	0.199	0.017	0.076	0.016
5	SL-1-P1-WW	3	0.176	0.023	0.073	0.010
5	FL-48-P1-WS	4	0.302	0.088	0.113	0.020
5	FL-7-P1-WS	4	0.300	0.066	0.112	0.022
5	SL-14-P1-WS	3	0.257	0.069	0.113	0.039
5	SL-1-P1-WS	4	0.175	0.015	0.073	0.009
6	FL-48-P1-WW	3	0.335	0.122	0.144	0.055
6	FL-7-P1-WW	3	0.264	0.032	0.109	0.010
6	SL-14-P1-WW	4	0.165	0.018	0.074	0.007
6	SL-1-P1-WW	3	0.115	0.014	0.045	0.007
6	FL-48-P1-WS	4	0.253	0.073	0.111	0.038
6	FL-7-P1-WS	4	0.264	0.048	0.126	0.028
6	SL-14-P1-WS	3	0.208	0.068	0.089	0.029
6	SL-1-P1-WS	4	0.134	0.014	0.058	0.008
7	FL-48-P1-WW	3	0.376	0.128	0.140	0.028

Table III.1. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance		Transpiration	
			Mean ($cm \cdot sec^{-1}$)	standard error ($cm \cdot sec^{-1}$)	Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
7	FL-7-P1-WW	3	0.315	0.030	0.104	0.022
7	SL-14-P1-WW	4	0.155	0.016	0.053	0.005
7	SL-1-P1-WW	3	0.116	0.007	0.041	0.008
7	FL-48-P1-WS	4	0.292	0.097	0.113	0.028
7	FL-7-P1-WS	4	0.285	0.073	0.094	0.017
7	SL-14-P1-WS	3	0.182	0.062	0.065	0.026
7	SL-1-P1-WS	4	0.124	0.007	0.046	0.005
8	FL-48-P1-WW	3	0.370	0.125	0.126a	0.029
8	FL-7-P1-WW	3	0.347	0.051	0.112ab	0.015
8	SL-14-P1-WW	4	0.139	0.022	0.049b	0.013
8	SL-1-P1-WW	3	0.118	0.013	0.042b	0.006
8	FL-48-P1-WS	4	0.276	0.114	0.081ab	0.019
8	FL-7-P1-WS	4	0.276	0.061	0.085ab	0.010
8	SL-14-P1-WS	3	0.172	0.037	0.064ab	0.016
8	SL-1-P1-WS	4	0.103	0.001	0.038b	0.002
10	FL-48-P1-WW	3	0.379a	0.139	0.154a	0.055
10	FL-7-P1-WW	3	0.403a	0.077	0.148a	0.023
10	SL-14-P1-WW	4	0.123b	0.021	0.045b	0.010
10	SL-1-P1-WW	3	0.103b	0.012	0.041b	0.004
10	FL-48-P1-WS	4	0.122b	0.018	0.055b	0.010
10	FL-7-P1-WS	4	0.160b	0.028	0.065b	0.009
10	SL-14-P1-WS	3	0.075b	0.017	0.030b	0.008
10	SL-1-P1-WS	4	0.076b	0.005	0.033b	0.004
11	FL-48-P1-WW	3	0.463a	0.158	0.143a	0.031
11	FL-7-P1-WW	3	0.548a	0.083	0.164a	0.036
11	SL-14-P1-WW	4	0.176b	0.032	0.041b	0.011
11	SL-1-P1-WW	3	0.142b	0.033	0.038b	0.013
11	FL-48-P1-WS	4	0.113b	0.010	0.033b	0.008
11	FL-7-P1-WS	4	0.190b	0.042	0.053b	0.011
11	SL-14-P1-WS	3	0.107b	0.015	0.040b	0.011
11	SL-1-P1-WS	4	0.091b	0.003	0.030b	0.002
12	FL-48-P1-WW	3	0.408a	0.150	0.146a	0.031
12	FL-7-P1-WW	3	0.451a	0.078	0.178a	0.063
12	SL-14-P1-WW	4	0.124b	0.024	0.049b	0.014
12	SL-1-P1-WW	3	0.067b	0.032	0.033b	0.016
12	FL-48-P1-WS	4	0.094b	0.013	0.043b	0.008
12	FL-7-P1-WS	4	0.078b	0.014	0.031b	0.004
12	SL-14-P1-WS	3	0.063b	0.018	0.028b	0.011
12	SL-1-P1-WS	4	0.055b	0.005	0.023b	0.001
13	FL-48-P1-WW	3	0.283a	0.094	0.141a	0.042
13	FL-7-P1-WW	3	0.335a	0.091	0.161a	0.048
13	SL-14-P1-WW	4	0.097b	0.023	0.046b	0.011
13	SL-1-P1-WW	3	0.086b	0.011	0.042b	0.003
13	FL-48-P1-WS	4	0.054b	0.004	0.028b	0.003
13	FL-7-P1-WS	4	0.049b	0.004	0.026b	0.003
13	SL-14-P1-WS	3	0.045b	0.008	0.023b	0.005
13	SL-1-P1-WS	4	0.048b	0.002	0.027b	0.002

Table III.1. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance Mean ($cm \cdot sec^{-1}$)	Stomatal Conductance standard error ($cm \cdot sec^{-1}$)	Transpiration Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	Transpiration standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
14	FL-48-P1-WW	3	0.337a	0.113	0.132a	0.043
14	FL-7-P1-WW	3	0.480a	0.108	0.181a	0.036
14	SL-14-P1-WW	4	0.128b	0.025	0.047b	0.011
14	SL-1-P1-WW	3	0.123b	0.018	0.042b	0.002
14	FL-48-P1-WS	4	0.078b	0.013	0.034b	0.008
14	FL-7-P1-WS	4	0.078b	0.008	0.032b	0.005
14	SL-14-P1-WS	3	0.080b	0.013	0.033b	0.009
14	SL-1-P1-WS	4	0.064b	0.002	0.029b	0.001
16	FL-48-P1-WW	3	0.279a	0.051	0.140a	0.016
16	FL-7-P1-WW	3	0.378a	0.115	0.164a	0.064
16	SL-14-P1-WW	4	0.117b	0.032	0.052b	0.016
16	SL-1-P1-WW	3	0.126b	0.011	0.058b	0.009
16	FL-48-P1-WS	4	0.046b	0.013	0.025b	0.010
16	FL-7-P1-WS	4	0.047b	0.012	0.023b	0.007
16	SL-14-P1-WS	3	0.059b	0.004	0.029b	0.002
16	SL-1-P1-WS	4	0.046b	0.006	0.024b	0.004
17	FL-48-P1-WW	3	0.255b	0.050	0.113b	0.017
17	FL-7-P1-WW	3	0.408a	0.117	0.180a	0.067
17	SL-14-P1-WW	4	0.119bc	0.024	0.046b	0.007
17	SL-1-P1-WW	3	0.105bc	0.008	0.038b	0.004
17	FL-48-P1-WS	4	0.077c	0.024	0.037b	0.012
17	FL-7-P1-WS	4	0.067c	0.023	0.031b	0.009
17	SL-14-P1-WS	3	0.036c	0.005	0.016b	0.003
17	SL-1-P1-WS	4	0.053c	0.006	0.027b	0.004
18	FL-48-P1-WW	3	0.257	0.053	0.107a	0.003
18	FL-7-P1-WW	3	0.238	0.078	0.084ab	0.021
18	SL-14-P1-WW	4	0.068	0.012	0.028c	0.002
18	SL-1-P1-WW	3	0.155	0.041	0.057bc	0.015
19	FL-48-P1-WW	3	0.173a	0.011	0.076a	0.001
19	FL-7-P1-WW	3	0.197a	0.019	0.080a	0.010
19	SL-14-P1-WW	4	0.082b	0.013	0.033b	0.003
19	SL-1-P1-WW	3	0.087b	0.014	0.037b	0.009
20	FL-48-P1-WW	3	0.203ab	0.024	0.070ab	0.001
20	FL-7-P1-WW	3	0.275a	0.040	0.090a	0.019
20	SL-14-P1-WW	4	0.118b	0.016	0.040b	0.009
20	SL-1-P1-WW	3	0.156b	0.021	0.059ab	0.012
21	FL-48-P1-WW	3	0.202	0.014	0.067ab	0.011
21	FL-7-P1-WW	3	0.284	0.050	0.084a	0.018
21	SL-14-P1-WW	4	0.140	0.030	0.038c	0.007
21	SL-1-P1-WW	3	0.165	0.018	0.053bc	0.013
Daytime						
3	FL-48-P1-WW	3	0.276	0.091	0.342	0.102
3	FL-7-P1-WW	3	0.232	0.030	0.280	0.039

Table III.1. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance Mean ($cm \cdot sec^{-1}$)	Stomatal Conductance standard error ($cm \cdot sec^{-1}$)	Transpiration Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	Transpiration standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
3	SL-14-P1-WW	4	0.283	0.057	0.329	0.065
3	SL-1-P1-WW	3	0.220	0.047	0.266	0.042
3	FL-48-P1-WS	4	0.232	0.055	0.291	0.063
3	FL-7-P1-WS	4	0.204	0.039	0.248	0.043
3	SL-14-P1-WS	3	0.333	0.117	0.406	0.142
3	SL-1-P1-WS	4	0.246	0.040	0.298	0.041
4	FL-48-P1-WW	3	0.331	0.116	0.371	0.130
4	FL-7-P1-WW	3	0.276	0.035	0.298	0.034
4	SL-14-P1-WW	4	0.340	0.056	0.349	0.064
4	SL-1-P1-WW	3	0.251	0.059	0.250	0.034
4	FL-48-P1-WS	4	0.266	0.081	0.292	0.085
4	FL-7-P1-WS	4	0.258	0.059	0.275	0.057
4	SL-14-P1-WS	3	0.231	0.053	0.258	0.062
4	SL-1-P1-WS	4	0.281	0.046	0.300	0.045
5	FL-48-P1-WW	3	0.319	0.110	0.376	0.118
5	FL-7-P1-WW	3	0.260	0.031	0.297	0.029
5	SL-14-P1-WW	4	0.273	0.043	0.305	0.039
5	SL-1-P1-WW	3	0.203	0.046	0.233	0.039
5	FL-48-P1-WS	4	0.248	0.077	0.295	0.081
5	FL-7-P1-WS	4	0.226	0.045	0.269	0.050
5	SL-14-P1-WS	3	0.309	0.107	0.359	0.125
5	SL-1-P1-WS	4	0.233	0.029	0.275	0.034
6	FL-48-P1-WW	3	0.296	0.113	0.343	0.124
6	FL-7-P1-WW	3	0.241	0.037	0.268	0.039
6	SL-14-P1-WW	4	0.259	0.037	0.272	0.032
6	SL-1-P1-WW	3	0.169	0.029	0.186	0.017
6	FL-48-P1-WS	4	0.265	0.079	0.305	0.078
6	FL-7-P1-WS	4	0.236	0.055	0.259	0.049
6	SL-14-P1-WS	3	0.284	0.085	0.336	0.104
6	SL-1-P1-WS	4	0.204	0.027	0.236	0.034
7	FL-48-P1-WW	3	0.332	0.164	0.325	0.132
7	FL-7-P1-WW	3	0.284	0.041	0.294	0.051
7	SL-14-P1-WW	4	0.298	0.057	0.273	0.039
7	SL-1-P1-WW	3	0.189	0.049	0.181	0.021
7	FL-48-P1-WS	4	0.233	0.085	0.224	0.060
7	FL-7-P1-WS	4	0.257	0.075	0.260	0.060
7	SL-14-P1-WS	3	0.281	0.084	0.279	0.090
7	SL-1-P1-WS	4	0.150	0.010	0.159	0.013
8	FL-48-P1-WW	3	0.315	0.095	0.351	0.084
8	FL-7-P1-WW	3	0.326	0.055	0.351	0.066
8	SL-14-P1-WW	4	0.273	0.043	0.271	0.030
8	SL-1-P1-WW	3	0.192	0.042	0.194	0.026
8	FL-48-P1-WS	4	0.255	0.097	0.274	0.086
8	FL-7-P1-WS	4	0.255	0.077	0.262	0.062
8	SL-14-P1-WS	3	0.198	0.041	0.219	0.051
8	SL-1-P1-WS	4	0.121	0.008	0.138	0.012

Table III.1. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance Mean ($cm \cdot sec^{-1}$)	Stomatal Conductance standard error ($cm \cdot sec^{-1}$)	Transpiration Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	Transpiration standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
10	FL-48-P1-WW	3	0.302ab	0.126	0.382ab	0.139
10	FL-7-P1-WW	3	0.390a	0.073	0.457a	0.094
10	SL-14-P1-WW	4	0.228ab	0.070	0.225b	0.062
10	SL-1-P1-WW	3	0.150ab	0.055	0.167b	0.051
10	FL-48-P1-WS	4	0.128ab	0.015	0.166b	0.013
10	FL-7-P1-WS	4	0.157ab	0.047	0.190b	0.049
10	SL-14-P1-WS	3	0.100b	0.016	0.127b	0.023
10	SL-1-P1-WS	4	0.075b	0.007	0.095b	0.010
11	FL-48-P1-WW	3	0.393a	0.132	0.431a	0.113
11	FL-7-P1-WW	3	0.404a	0.056	0.446a	0.080
11	SL-14-P1-WW	4	0.277ab	0.053	0.270ab	0.050
11	SL-1-P1-WW	3	0.181b	0.037	0.194b	0.021
11	FL-48-P1-WS	4	0.102b	0.012	0.124b	0.012
11	FL-7-P1-WS	4	0.116b	0.025	0.132b	0.024
11	SL-14-P1-WS	3	0.071b	0.011	0.088b	0.015
11	SL-1-P1-WS	4	0.061b	0.010	0.074b	0.011
12	FL-48-P1-WW	3	0.358ab	0.129	0.451a	0.142
12	FL-7-P1-WW	3	0.421a	0.090	0.500a	0.107
12	SL-14-P1-WW	4	0.283abc	0.056	0.310ab	0.053
12	SL-1-P1-WW	3	0.184bc	0.040	0.215b	0.027
12	FL-48-P1-WS	4	0.069c	0.006	0.096b	0.010
12	FL-7-P1-WS	4	0.076c	0.012	0.101b	0.014
12	SL-14-P1-WS	3	0.050c	0.008	0.070b	0.012
12	SL-1-P1-WS	4	0.045c	0.003	0.061b	0.007
13	FL-48-P1-WW	3	0.371ab	0.117	0.498a	0.142
13	FL-7-P1-WW	3	0.426a	0.070	0.540a	0.090
13	SL-14-P1-WW	4	0.297ab	0.055	0.333ab	0.064
13	SL-1-P1-WW	3	0.207bc	0.061	0.243bc	0.045
13	FL-48-P1-WS	4	0.066c	0.010	0.092bc	0.014
13	FL-7-P1-WS	4	0.076c	0.011	0.103bc	0.011
13	SL-14-P1-WS	3	0.065c	0.013	0.093bc	0.022
13	SL-1-P1-WS	4	0.041c	0.007	0.057c	0.010
14	FL-48-P1-WW	3	0.384ab	0.115	0.514a	0.126
14	FL-7-P1-WW	3	0.451a	0.081	0.580a	0.123
14	SL-14-P1-WW	4	0.286ab	0.059	0.328b	0.063
14	SL-1-P1-WW	3	0.222bc	0.053	0.278b	0.039
14	FL-48-P1-WS	4	0.070c	0.013	0.101b	0.017
14	FL-7-P1-WS	4	0.068c	0.017	0.094b	0.016
14	SL-14-P1-WS	3	0.056c	0.010	0.085b	0.017
14	SL-1-P1-WS	4	0.040c	0.004	0.060b	0.006
16	FL-48-P1-WW	3	0.399a	0.102	0.564a	0.119
16	FL-7-P1-WW	3	0.423a	0.032	0.565a	0.045
16	SL-14-P1-WW	4	0.274b	0.041	0.339b	0.048
16	SL-1-P1-WW	3	0.247b	0.021	0.323b	0.003
16	FL-48-P1-WS	4	0.066c	0.009	0.108c	0.019
16	FL-7-P1-WS	4	0.038c	0.008	0.056c	0.011
16	SL-14-P1-WS	3	0.053c	0.002	0.086c	0.003

Table III.1. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance Mean ($cm \cdot sec^{-1}$)	Stomatal Conductance standard error ($cm \cdot sec^{-1}$)	Transpiration Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	Transpiration standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
16	SL-1-P1-WS	4	0.030c	0.003	0.049c	0.005
17	FL-48-P1-WW	3	0.374a	0.058	0.508a	0.058
17	FL-7-P1-WW	3	0.420a	0.050	0.545a	0.072
17	SL-14-P1-WW	4	0.280ab	0.078	0.325b	0.080
17	SL-1-P1-WW	3	0.195bc	0.034	0.272b	0.048
17	FL-48-P1-WS	4	0.057c	0.010	0.088c	0.017
17	FL-7-P1-WS	4	0.052c	0.009	0.076c	0.010
17	SL-14-P1-WS	3	0.042c	0.011	0.067c	0.020
17	SL-1-P1-WS	4	0.034c	0.005	0.054c	0.010
18	FL-48-P1-WW	3	0.380a	0.024	0.492a	0.022
18	FL-7-P1-WW	3	0.347ab	0.072	0.422ab	0.077
18	SL-14-P1-WW	4	0.208b	0.059	0.248b	0.062
18	SL-1-P1-WW	3	0.217b	0.050	0.285b	0.066
19	FL-48-P1-WW	3	0.361	0.058	0.420	0.033
19	FL-7-P1-WW	3	0.368	0.069	0.379	0.061
19	SL-14-P1-WW	4	0.247	0.051	0.251	0.044
19	SL-1-P1-WW	3	0.266	0.052	0.266	0.051
20	FL-48-P1-WW	3	0.407	0.027	0.449	0.014
20	FL-7-P1-WW	3	0.445	0.059	0.439	0.070
20	SL-14-P1-WW	4	0.311	0.065	0.282	0.054
20	SL-1-P1-WW	3	0.304	0.057	0.301	0.055
21	FL-48-P1-WW	3	0.383	0.051	0.421	0.027
21	FL-7-P1-WW	3	0.431	0.024	0.448	0.044
21	SL-14-P1-WW	4	0.330	0.050	0.326	0.046
21	SL-1-P1-WW	3	0.314	0.037	0.320	0.053

[1] See Table 1.1 for treatment code descriptions.

Table III.2. Stomatal conductance and transpiration rates (n, $\bar{x}$, S.E.) for $1^1/_2 + 1^1/_2$ black spruce transplants measured in a controlled environment chamber at Lakehead University during Potting Time 2 (June 24). Half the potted seedlings were watered to the drip point every second day (well-watered = WW) while the other half were watered in the same way for 3 days and then allowed to dry (water stressed = WS). Means within a sample time without a common letter are significantly different ($\alpha = 0.05$).

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance		Transpiration	
			Mean ($cm \cdot sec^{-1}$)	standard error ($cm \cdot sec^{-1}$)	Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
First Light						
1	FL-48-P2-WW	4	0.913	0.263	0.427	0.129
1	FL-7-P2-WW	4	0.510	0.060	0.250	0.032
1	SL-48-P2-WW	4	0.806	0.069	0.386	0.044
1	SL-1-P2-WW	3	0.618	0.101	0.243	0.063
1	FL-48-P2-WS	4	1.019	0.426	0.320	0.094
1	FL-7-P2-WS	4	0.747	0.135	0.316	0.040
1	SL-48-P2-WS	4	1.009	0.292	0.428	0.098
1	SL-1-P2-WS	4	1.037	0.383	0.255	0.097
3	FL-48-P2-WW	4	0.480a	0.091	0.250a	0.045
3	FL-7-P2-WW	4	0.314ab	0.072	0.165ab	0.031
3	SL-48-P2-WW	4	0.298ab	0.031	0.166ab	0.013
3	SL-1-P2-WW	3	0.133b	0.016	0.072b	0.009
3	FL-48-P2-WS	4	0.285ab	0.033	0.152ab	0.025
3	FL-7-P2-WS	4	0.321ab	0.034	0.189a	0.021
3	SL-48-P2-WS	4	0.298ab	0.068	0.154ab	0.032
3	SL-1-P2-WS	4	0.217b	0.022	0.078b	0.024
4	FL-48-P2-WW	4	0.255a	0.044	0.161a	0.030
4	FL-7-P2-WW	4	0.148abc	0.021	0.093bc	0.015
4	SL-48-P2-WW	4	0.146abc	0.020	0.091bc	0.010
4	SL-1-P2-WW	3	0.053c	0.007	0.033c	0.007
4	FL-48-P2-WS	4	0.129bc	0.029	0.086bc	0.022
4	FL-7-P2-WS	4	0.219ab	0.025	0.132ab	0.017
4	SL-48-P2-WS	4	0.172abc	0.044	0.111ab	0.024
4	SL-1-P2-WS	4	0.054c	0.010	0.034c	0.007
5	FL-48-P2-WW	4	0.303ab	0.066	0.181ab	0.041
5	FL-7-P2-WW	4	0.186bc	0.029	0.116bcd	0.019
5	SL-48-P2-WW	4	0.197bc	0.025	0.127abcd	0.022
5	SL-1-P2-WW	3	0.089c	0.018	0.046cd	0.007
5	FL-48-P2-WS	4	0.167bc	0.040	0.101bcd	0.016
5	FL-7-P2-WS	4	0.335a	0.032	0.212a	0.015
5	SL-48-P2-WS	4	0.216abc	0.032	0.138abc	0.018
5	SL-1-P2-WS	4	0.070c	0.010	0.039d	0.006
7	FL-48-P2-WW	4	0.509a	0.097	0.234ab	0.023
7	FL-7-P2-WW	4	0.269ab	0.041	0.139bc	0.023
7	SL-48-P2-WW	4	0.260ab	0.086	0.125bc	0.037
7	SL-1-P2-WW	3	0.117b	0.010	0.054c	0.003
7	FL-48-P2-WS	4	0.364ab	0.195	0.131bc	0.046
7	FL-7-P2-WS	4	0.577a	0.157	0.279a	0.073
7	SL-48-P2-WS	4	0.124b	0.036	0.063c	0.020
7	SL-1-P2-WS	4	0.139b	0.087	0.048c	0.025
8	FL-48-P2-WW	4	0.350a	0.060	0.165a	0.041

Table III.2. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance Mean ($cm \cdot sec^{-1}$)	Stomatal Conductance standard error ($cm \cdot sec^{-1}$)	Transpiration Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	Transpiration standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
8	FL-7-P2-WW	4	0.214b	0.036	0.110ab	0.025
8	SL-48-P2-WW	4	0.142bc	0.021	0.067bc	0.007
8	SL-1-P2-WW	3	0.051c	0.001	0.022c	0.001
8	FL-48-P2-WS	4	0.152bc	0.031	0.070bc	0.024
8	FL-7-P2-WS	4	0.353a	0.022	0.161a	0.020
8	SL-48-P2-WS	4	0.113bc	0.017	0.054bc	0.016
8	SL-1-P2-WS	4	0.041c	0.004	0.019c	0.004
9	FL-48-P2-WW	4	0.470a	0.079	0.213a	0.042
9	FL-7-P2-WW	4	0.297b	0.052	0.141b	0.028
9	SL-48-P2-WW	4	0.156c	0.008	0.068c	0.004
9	SL-1-P2-WW	3	0.064c	0.006	0.029c	0.008
9	FL-48-P2-WS	4	0.152c	0.021	0.069c	0.012
9	FL-7-P2-WS	4	0.315b	0.029	0.141b	0.011
9	SL-48-P2-WS	4	0.107c	0.010	0.051c	0.010
9	SL-1-P2-WS	4	0.040c	0.003	0.018c	0.003
11	FL-48-P2-WW	4	0.453a	0.035	0.221a	0.022
11	FL-7-P2-WW	4	0.264ab	0.043	0.141ab	0.026
11	SL-48-P2-WW	4	0.173b	0.048	0.088b	0.019
11	SL-1-P2-WW	3	0.071b	0.011	0.033b	0.005
11	FL-48-P2-WS	4	0.118b	0.020	0.061b	0.015
11	FL-7-P2-WS	4	0.284ab	0.152	0.144ab	0.069
11	SL-48-P2-WS	4	0.050b	0.016	0.029b	0.011
11	SL-1-P2-WS	4	0.049b	0.013	0.022b	0.002
12	FL-48-P2-WW	4	0.348a	0.063	0.187a	0.035
12	FL-7-P2-WW	4	0.270a	0.045	0.156a	0.029
12	SL-48-P2-WW	4	0.123b	0.009	0.065b	0.005
12	SL-1-P2-WW	3	0.059b	0.007	0.030b	0.005
12	FL-48-P2-WS	4	0.079b	0.011	0.039b	0.009
12	FL-7-P2-WS	4	0.144b	0.015	0.082b	0.008
12	SL-48-P2-WS	4	0.061b	0.008	0.031b	0.009
12	SL-1-P2-WS	4	0.029b	0.002	0.014b	0.002
15	FL-48-P2-WW	4	0.267a	0.049	0.176a	0.036
15	FL-7-P2-WW	4	0.235a	0.031	0.158a	0.018
15	SL-48-P2-WW	4	0.118b	0.016	0.077b	0.015
15	SL-1-P2-WW	3	0.058b	0.012	0.036b	0.008
15	FL-48-P2-WS	4	0.067b	0.010	0.048b	0.008
15	FL-7-P2-WS	4	0.105b	0.009	0.075b	0.006
15	SL-48-P2-WS	4	0.049b	0.005	0.036b	0.006
15	SL-1-P2-WS	4	0.026b	0.003	0.019b	0.002
16	FL-48-P2-WW	4	0.210a	0.033	0.123a	0.026
16	FL-7-P2-WW	4	0.192a	0.021	0.119ab	0.019
16	SL-48-P2-WW	4	0.111bc	0.012	0.063abc	0.005
16	SL-1-P2-WW	3	0.075bc	0.022	0.048bc	0.018
16	FL-48-P2-WS	4	0.089bc	0.031	0.062abc	0.028
16	FL-7-P2-WS	4	0.126b	0.031	0.080abc	0.023
16	SL-48-P2-WS	4	0.054bc	0.007	0.035c	0.008
16	SL-1-P2-WS	4	0.026c	0.001	0.017c	0.002

Table III.2. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance Mean ($cm \cdot sec^{-1}$)	Stomatal Conductance standard error ($cm \cdot sec^{-1}$)	Transpiration Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	Transpiration standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
17	FL-48-P2-WW	4	0.175a	0.023	0.103a	0.019
17	FL-7-P2-WW	4	0.166ab	0.021	0.102a	0.015
17	SL-48-P2-WW	4	0.122abc	0.015	0.075ab	0.008
17	SL-1-P2-WW	3	0.077cd	0.027	0.051ab	0.021
17	FL-48-P2-WS	4	0.092bcd	0.031	0.066ab	0.028
17	FL-7-P2-WS	4	0.115abc	0.028	0.071ab	0.019
17	SL-48-P2-WS	4	0.058cd	0.003	0.041ab	0.006
17	SL-1-P2-WS	4	0.026d	0.001	0.017b	0.002
18	FL-48-P2-WW	4	0.148a	0.021	0.098a	0.021
18	FL-7-P2-WW	4	0.142a	0.013	0.100a	0.014
18	SL-48-P2-WW	4	0.124a	0.011	0.074ab	0.005
18	SL-1-P2-WW	3	0.080ab	0.030	0.043ab	0.017
18	FL-48-P2-WS	4	0.097ab	0.027	0.075ab	0.027
18	FL-7-P2-WS	4	0.129a	0.032	0.090a	0.027
18	SL-48-P2-WS	4	0.042b	0.003	0.029ab	0.006
18	SL-1-P2-WS	4	0.025b	0.003	0.018b	0.004
19	FL-48-P2-WW	4	0.103a	0.014	0.077a	0.013
19	FL-7-P2-WW	4	0.094a	0.009	0.072a	0.009
19	SL-48-P2-WW	4	0.091a	0.007	0.066a	0.003
19	SL-1-P2-WW	3	0.062ab	0.019	0.048ab	0.019
19	FL-48-P2-WS	4	0.060ab	0.009	0.049ab	0.011
19	FL-7-P2-WS	4	0.107a	0.020	0.089a	0.021
19	SL-48-P2-WS	4	0.030b	0.002	0.024b	0.005
19	SL-1-P2-WS	4	0.018b	0.002	0.015b	0.002
20	FL-48-P2-WW	4	0.079	0.009	0.062ab	0.010
20	FL-7-P2-WW	4	0.083	0.010	0.067ab	0.009
20	SL-48-P2-WW	4	0.088	0.003	0.068ab	0.003
20	SL-1-P2-WW	3	0.062	0.023	0.050ab	0.022
20	FL-48-P2-WS	4	0.055	0.015	0.045ab	0.015
20	FL-7-P2-WS	4	0.104	0.031	0.090a	0.030
20	SL-48-P2-WS	4	0.037	0.002	0.031b	0.005
20	SL-1-P2-WS	4	0.055	0.035	0.017b	0.004
21	FL-48-P2-WW	4	0.078ab	0.008	0.061abc	0.011
21	FL-7-P2-WW	4	0.073ab	0.008	0.060abc	0.007
21	SL-48-P2-WW	4	0.110a	0.010	0.081ab	0.006
21	SL-1-P2-WW	3	0.063ab	0.022	0.054abc	0.025
21	FL-48-P2-WS	4	0.061ab	0.019	0.054abc	0.021
21	FL-7-P2-WS	4	0.102a	0.033	0.091a	0.034
21	SL-48-P2-WS	4	0.025b	0.010	0.023bc	0.010
21	SL-1-P2-WS	4	0.011b	0.003	0.010c	0.004
Daytime						
1	FL-48-P2-WW	4	0.157ab	0.021	0.251ab	0.041
1	FL-7-P2-WW	4	0.110ab	0.007	0.181b	0.010
1	SL-48-P2-WW	4	0.218a	0.025	0.343a	0.032
1	SL-1-P2-WW	3	0.112ab	0.016	0.167b	0.025

Table III.2. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance Mean ($cm \cdot sec^{-1}$)	Stomatal Conductance standard error ($cm \cdot sec^{-1}$)	Transpiration Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	Transpiration standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
1	FL-48-P2-WS	4	0.096b	0.015	0.153b	0.028
1	FL-7-P2-WS	4	0.153ab	0.006	0.238ab	0.015
1	SL-48-P2-WS	4	0.214a	0.046	0.329a	0.069
1	SL-1-P2-WS	4	0.101b	0.017	0.142b	0.020
3	FL-48-P2-WW	4	0.274	0.034	0.453a	0.067
3	FL-7-P2-WW	4	0.158	0.020	0.270ab	0.035
3	SL-48-P2-WW	4	0.229	0.026	0.382ab	0.045
3	SL-1-P2-WW	3	0.125	0.037	0.181ab	0.049
3	FL-48-P2-WS	4	0.141	0.034	0.237ab	0.060
3	FL-7-P2-WS	4	0.232	0.016	0.385ab	0.031
3	SL-48-P2-WS	4	0.271	0.072	0.430ab	0.115
3	SL-1-P2-WS	4	0.108	0.025	0.160b	0.031
4	FL-48-P2-WW	4	0.266	0.029	0.458	0.058
4	FL-7-P2-WW	4	0.157	0.019	0.277	0.033
4	SL-48-P2-WW	4	0.220	0.034	0.389	0.065
4	SL-1-P2-WW	3	0.117	0.027	0.191	0.035
4	FL-48-P2-WS	4	0.140	0.032	0.245	0.056
4	FL-7-P2-WS	4	0.237	0.022	0.423	0.038
4	SL-48-P2-WS	4	0.262	0.077	0.467	0.123
4	SL-1-P2-WS	4	0.105	0.023	0.168	0.036
5	FL-48-P2-WW	4	0.318a	0.032	0.491a	0.067
5	FL-7-P2-WW	4	0.184ab	0.021	0.302ab	0.040
5	SL-48-P2-WW	4	0.227ab	0.036	0.341ab	0.050
5	SL-1-P2-WW	3	0.124b	0.030	0.183b	0.043
5	FL-48-P2-WS	4	0.156ab	0.046	0.242ab	0.075
5	FL-7-P2-WS	4	0.290ab	0.017	0.471a	0.043
5	SL-48-P2-WS	4	0.283ab	0.068	0.444ab	0.113
5	SL-1-P2-WS	4	0.123b	0.027	0.170b	0.034
7	FL-48-P2-WW	4	0.326a	0.032	0.484a	0.060
7	FL-7-P2-WW	4	0.199ab	0.026	0.305ab	0.039
7	SL-48-P2-WW	4	0.212ab	0.025	0.312ab	0.037
7	SL-1-P2-WW	3	0.107b	0.022	0.147b	0.029
7	FL-48-P2-WS	4	0.163b	0.044	0.223b	0.059
7	FL-7-P2-WS	4	0.319a	0.030	0.475a	0.057
7	SL-48-P2-WS	4	0.212ab	0.025	0.300ab	0.053
7	SL-1-P2-WS	4	0.088b	0.018	0.119b	0.018
8	FL-48-P2-WW	4	0.343a	0.042	0.521a	0.079
8	FL-7-P2-WW	4	0.214abc	0.039	0.346ab	0.055
8	SL-48-P2-WW	4	0.218abc	0.033	0.335ab	0.051
8	SL-1-P2-WW	3	0.098cd	0.014	0.135bc	0.016
8	FL-48-P2-WS	4	0.164bcd	0.043	0.246bc	0.063
8	FL-7-P2-WS	4	0.289ab	0.035	0.463a	0.051
8	SL-48-P2-WS	4	0.151bcd	0.023	0.230bc	0.028
8	SL-1-P2-WS	4	0.061d	0.013	0.086c	0.014
9	FL-48-P2-WW	4	0.425a	0.037	0.597a	0.046
9	FL-7-P2-WW	4	0.251bc	0.037	0.384b	0.056

Table III.2. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance Mean ($cm \cdot sec^{-1}$)	Stomatal Conductance standard error ($cm \cdot sec^{-1}$)	Transpiration Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	Transpiration standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
9	SL-48-P2-WW	4	0.237bcd	0.030	0.349bc	0.041
9	SL-1-P2-WW	3	0.110de	0.023	0.150de	0.030
9	FL-48-P2-WS	4	0.164bcde	0.031	0.257bcd	0.052
9	FL-7-P2-WS	4	0.267b	0.041	0.409b	0.056
9	SL-48-P2-WS	4	0.124cde	0.024	0.195cde	0.042
9	SL-1-P2-WS	4	0.048e	0.004	0.072e	0.007
11	FL-48-P2-WW	4	0.395a	0.053	0.578a	0.087
11	FL-7-P2-WW	4	0.259b	0.044	0.392b	0.070
11	SL-48-P2-WW	4	0.207bc	0.029	0.310bc	0.044
11	SL-1-P2-WW	3	0.091cd	0.022	0.126cd	0.033
11	FL-48-P2-WS	4	0.099cd	0.023	0.150cd	0.036
11	FL-7-P2-WS	4	0.132cd	0.023	0.208cd	0.038
11	SL-48-P2-WS	4	0.080cd	0.015	0.119cd	0.024
11	SL-1-P2-WS	4	0.028d	0.002	0.041d	0.003
12	FL-48-P2-WW	4	0.432a	0.060	0.599a	0.089
12	FL-7-P2-WW	4	0.287b	0.035	0.424b	0.045
12	SL-48-P2-WW	4	0.239b	0.041	0.341bc	0.056
12	SL-1-P2-WW	3	0.104c	0.025	0.146d	0.039
12	FL-48-P2-WS	4	0.088c	0.012	0.138d	0.020
12	FL-7-P2-WS	4	0.128c	0.016	0.202cd	0.026
12	SL-48-P2-WS	4	0.070c	0.012	0.107d	0.023
12	SL-1-P2-WS	4	0.031c	0.001	0.048d	0.003
13	FL-48-P2-WW	4	0.461a	0.055	0.673a	0.093
13	FL-7-P2-WW	4	0.298b	0.044	0.434b	0.061
13	SL-48-P2-WW	4	0.241b	0.047	0.341b	0.062
13	SL-1-P2-WW	3	0.114c	0.032	0.149c	0.040
13	FL-48-P2-WS	4	0.084c	0.013	0.131c	0.026
13	FL-7-P2-WS	4	0.119c	0.016	0.185c	0.026
13	SL-48-P2-WS	4	0.064c	0.006	0.102c	0.013
13	SL-1-P2-WS	4	0.028c	0.001	0.040c	0.002
15	FL-48-P2-WW	4	0.392a	0.047	0.627a	0.082
15	FL-7-P2-WW	4	0.264b	0.034	0.455b	0.061
15	SL-48-P2-WW	4	0.211b	0.037	0.340b	0.063
15	SL-1-P2-WW	3	0.114c	0.030	0.179c	0.045
15	FL-48-P2-WS	4	0.055c	0.010	0.101c	0.023
15	FL-7-P2-WS	4	0.075c	0.017	0.138c	0.034
15	SL-48-P2-WS	4	0.041c	0.008	0.080c	0.016
15	SL-1-P2-WS	4	0.020c	0.001	0.035c	0.002
16	FL-48-P2-WW	4	0.376a	0.026	0.607a	0.061
16	FL-7-P2-WW	4	0.250b	0.032	0.438b	0.066
16	SL-48-P2-WW	4	0.259b	0.053	0.427b	0.080
16	SL-1-P2-WW	3	0.125c	0.037	0.193c	0.056
16	FL-48-P2-WS	4	0.067c	0.021	0.122c	0.044
16	FL-7-P2-WS	4	0.096c	0.015	0.173c	0.027
16	SL-48-P2-WS	4	0.037c	0.004	0.066c	0.009
16	SL-1-P2-WS	4	0.019c	0.002	0.034c	0.005

Table III.2. (Continued)

Days Since Potting	Treatment Code[1]	Sample Size	Stomatal Conductance Mean ($cm \cdot sec^{-1}$)	Stomatal Conductance standard error ($cm \cdot sec^{-1}$)	Transpiration Mean ($mg \cdot cm^{-2} \cdot sec^{-1}$)	Transpiration standard error ($mg \cdot cm^{-2} \cdot sec^{-1}$)
17	FL-48-P2-WW	4	0.344a	0.014	0.562a	0.024
17	FL-7-P2-WW	4	0.254a	0.032	0.456a	0.067
17	SL-48-P2-WW	4	0.276a	0.051	0.440a	0.081
17	SL-1-P2-WW	3	0.128b	0.040	0.210b	0.066
17	FL-48-P2-WS	4	0.059b	0.022	0.116b	0.049
17	FL-7-P2-WS	4	0.113b	0.026	0.214b	0.054
17	SL-48-P2-WS	4	0.040b	0.003	0.072b	0.008
17	SL-1-P2-WS	4	0.018b	0.003	0.033b	0.006
18	FL-48-P2-WW	4	0.307a	0.019	0.499a	0.031
18	FL-7-P2-WW	4	0.214b	0.021	0.372a	0.048
18	SL-48-P2-WW	4	0.270ab	0.052	0.429a	0.076
18	SL-1-P2-WW	3	0.125c	0.040	0.216b	0.073
18	FL-48-P2-WS	4	0.067cd	0.015	0.127bc	0.033
18	FL-7-P2-WS	4	0.106cd	0.016	0.198b	0.033
18	SL-48-P2-WS	4	0.042cd	0.006	0.078bc	0.015
18	SL-1-P2-WS	4	0.016d	0.002	0.030c	0.005
19	FL-48-P2-WW	4	0.264a	0.008	0.435a	0.014
19	FL-7-P2-WW	4	0.179b	0.018	0.324a	0.033
19	SL-48-P2-WW	4	0.233ab	0.034	0.402a	0.047
19	SL-1-P2-WW	3	0.103c	0.027	0.166b	0.040
19	FL-48-P2-WS	4	0.068cd	0.021	0.137bc	0.051
19	FL-7-P2-WS	4	0.093c	0.015	0.186b	0.031
19	SL-48-P2-WS	4	0.031cd	0.004	0.060bc	0.010
19	SL-1-P2-WS	4	0.013d	0.001	0.026c	0.002
20	FL-48-P2-WW	4	0.263a	0.009	0.461a	0.014
20	FL-7-P2-WW	4	0.175b	0.015	0.330bc	0.027
20	SL-48-P2-WW	4	0.238a	0.023	0.412ab	0.035
20	SL-1-P2-WW	3	0.132bc	0.042	0.238cd	0.078
20	FL-48-P2-WS	4	0.065de	0.015	0.132de	0.035
20	FL-7-P2-WS	4	0.097cd	0.020	0.201d	0.045
20	SL-48-P2-WS	4	0.038de	0.002	0.078e	0.007
20	SL-1-P2-WS	4	0.017e	0.003	0.035e	0.006
21	FL-48-P2-WW	4	0.246a	0.014	0.400a	0.016
21	FL-7-P2-WW	4	0.176ab	0.032	0.307ab	0.061
21	SL-48-P2-WW	4	0.237a	0.019	0.407a	0.033
21	SL-1-P2-WW	3	0.127bc	0.033	0.209abc	0.058
21	FL-48-P2-WS	4	0.071cd	0.035	0.146bc	0.078
21	FL-7-P2-WS	4	0.104bcd	0.027	0.219abc	0.064
21	SL-48-P2-WS	4	0.031d	0.005	0.065c	0.012
21	SL-1-P2-WS	4	0.021d	0.003	0.042c	0.007

[1] See Table 1.1 for treatment code descriptions.

APPENDIX IV

SOIL WATER RETENTION CURVE CHARACTERIZING THE SOIL OF THE POTTING TRIALS

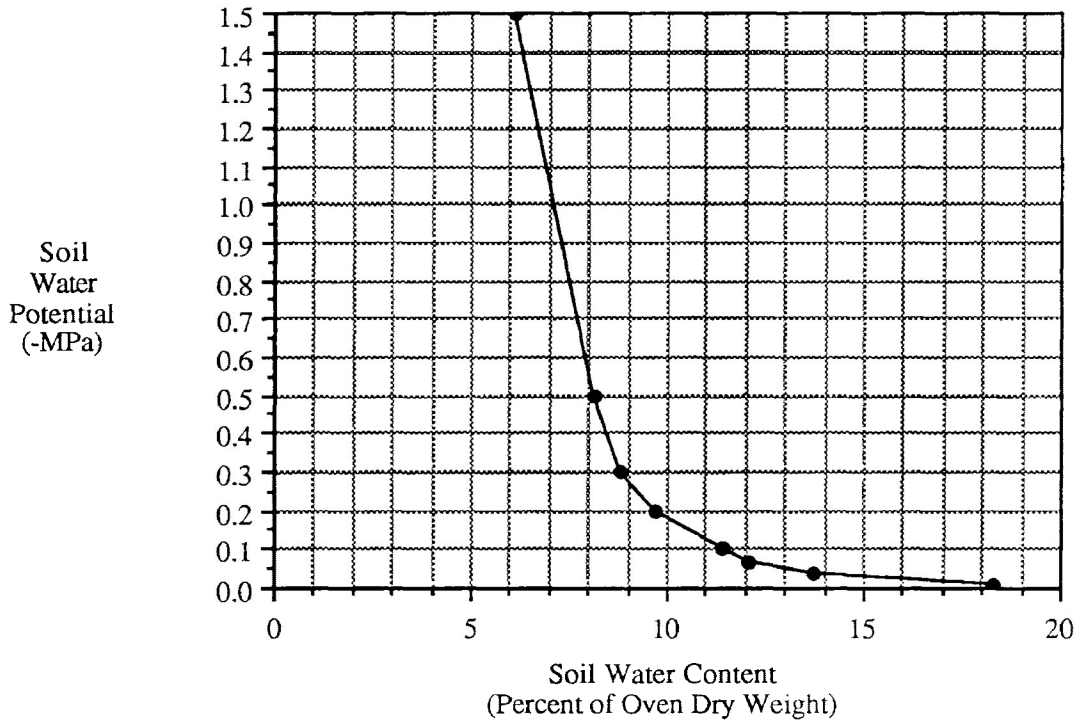

Figure IV.1. Soil water retention curve developed for the homogeneous soil mix taken from Compartment 13 at the Thunder Bay Forest Nursery and used during Potting Times 1 and 2.

APPENDIX V

AVERAGE SOIL WATER CONTENT EXPRESSED AS A PERCENTAGE BY WEIGHT OF TOTAL SOIL WATER HOLDING CAPACITY FOR THE WATER STRESSED SEEDLINGS OF POTTING TIMES 1 AND 2

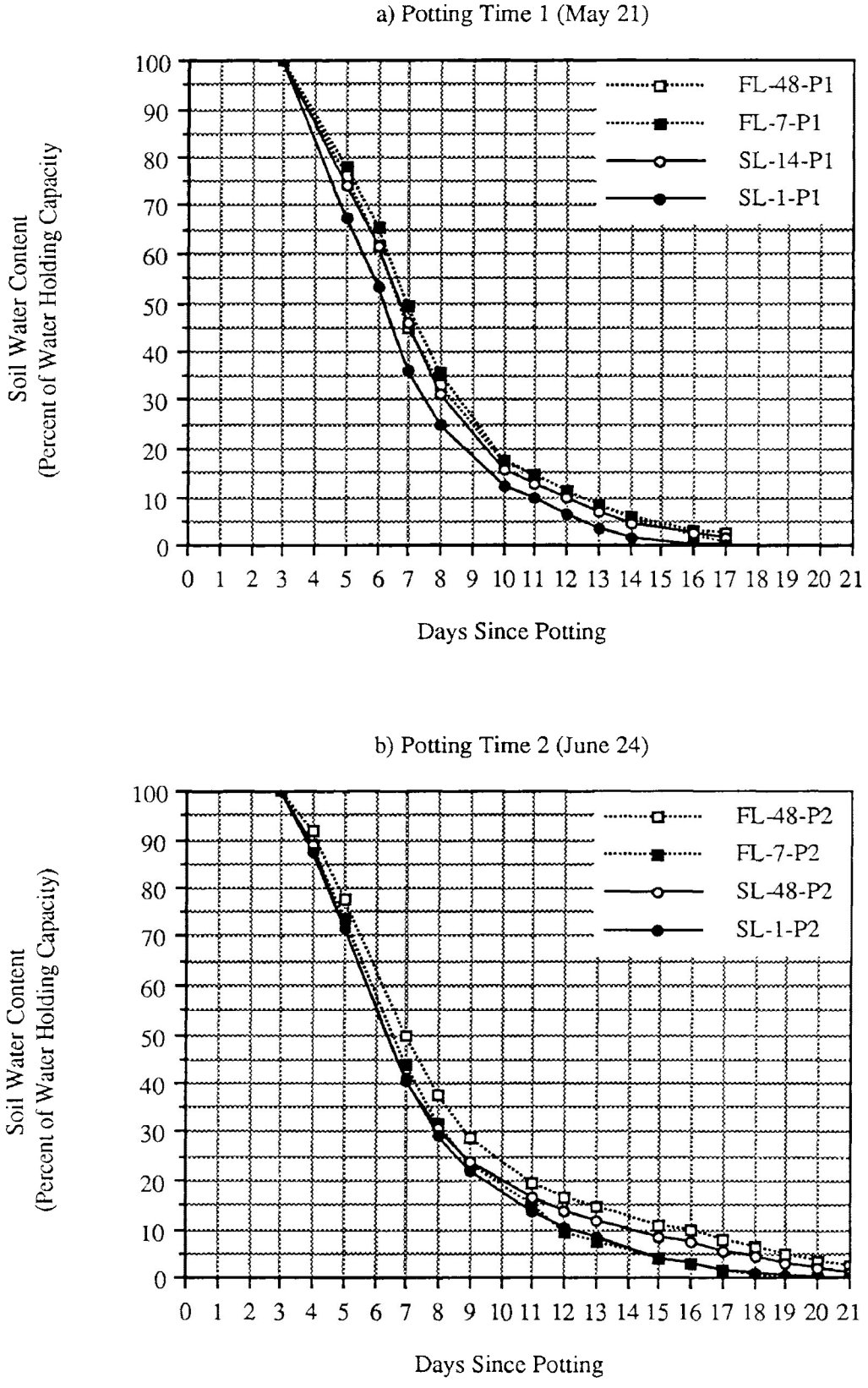

Figure V.1. Average soil water content determined gravimetrically and expressed as a percentage by weight of the total soil water holding capacity for the water stressed seedlings potted in a) Potting Time 1, and b) Potting Time 2. See Table 1.1 for treatment code descriptions.

APPENDIX VI

LOCATIONS AND EXPERIMENTAL DESIGNS FOR THE OUTPLANTING TRIALS

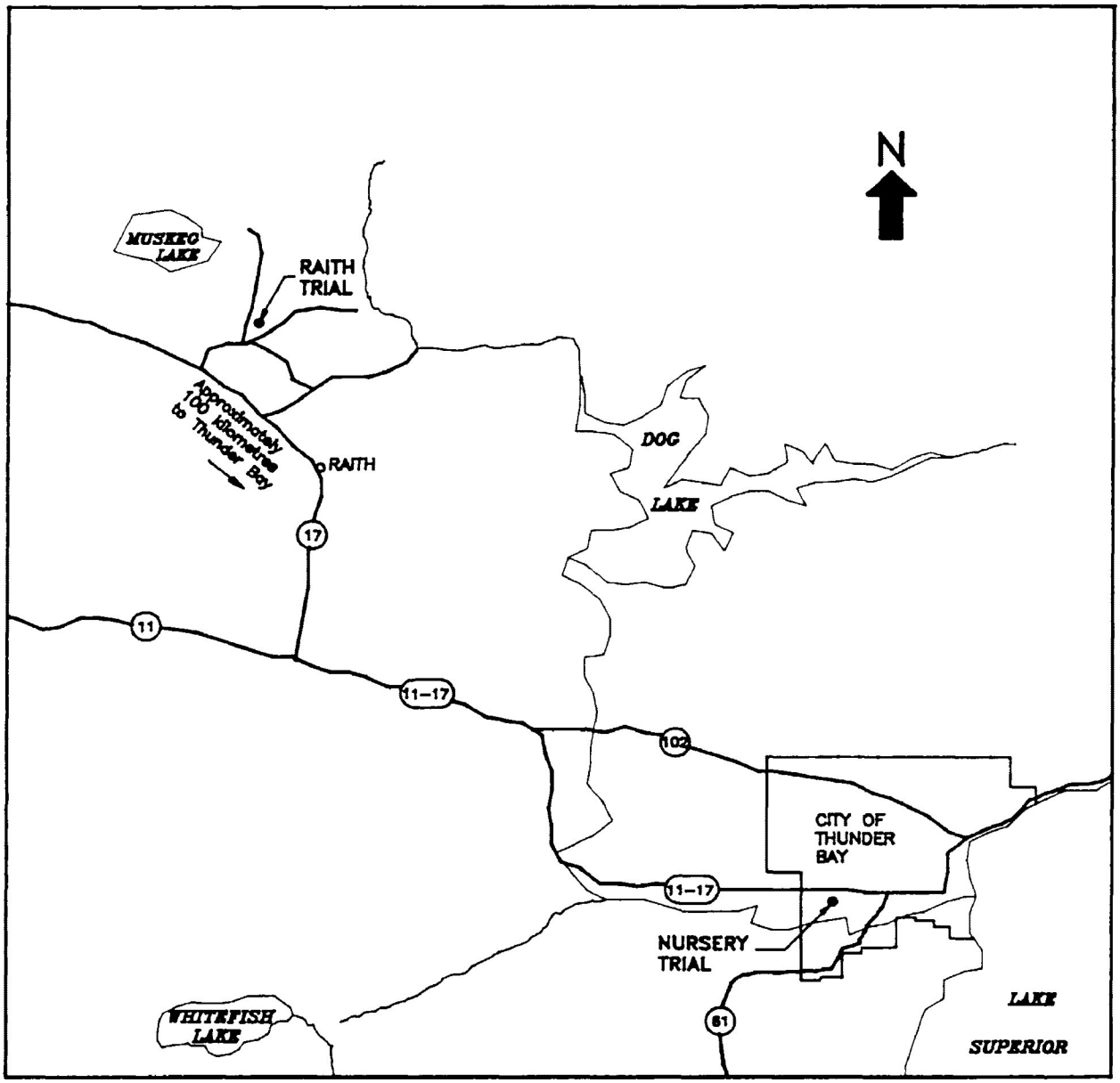

Figure VI.1. Schematic map indicating the location of the field trials.

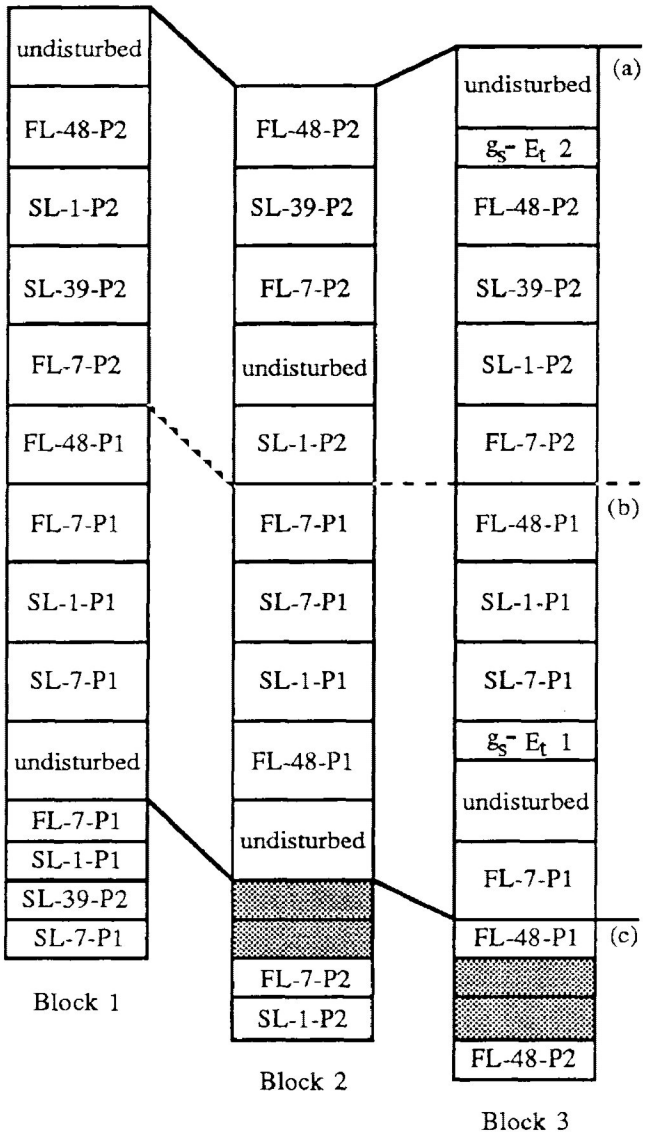

Figure VI.2. The experiments conducted at the Thunder Bay Forest Nursery to evaluate seedling physiological response. a) A randomized complete block design to monitor xylem pressure potential for Planting Time 2. The location of the stomatal conductance and transpiration experiment is indicated (g_s-E_t 2). b) A randomized complete block design to monitor xylem pressure potential for Planting Time 1. The location of the stomatal conductance and transpiration experiment is indicated (g_s-E_t 1). c) A completely randomized design to evaluate the root growth capacity of the outplants. See Table 2.1 for treatment code descriptions.

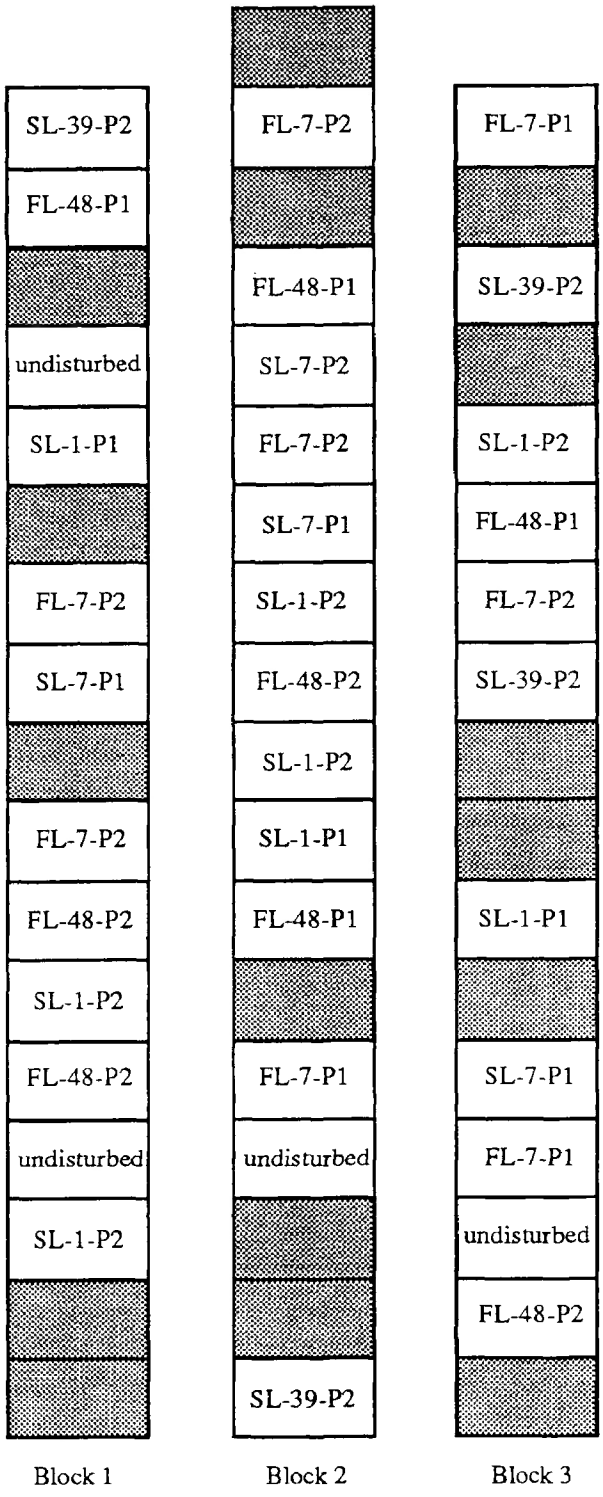

Figure VI.3. The randomized complete block design with unequal within block replication established at the Thunder Bay Forest Nursery to determine selected morphological response attributes of the outplanted and undisturbed seedlings. See Table 2.1 for treatment code descriptions.

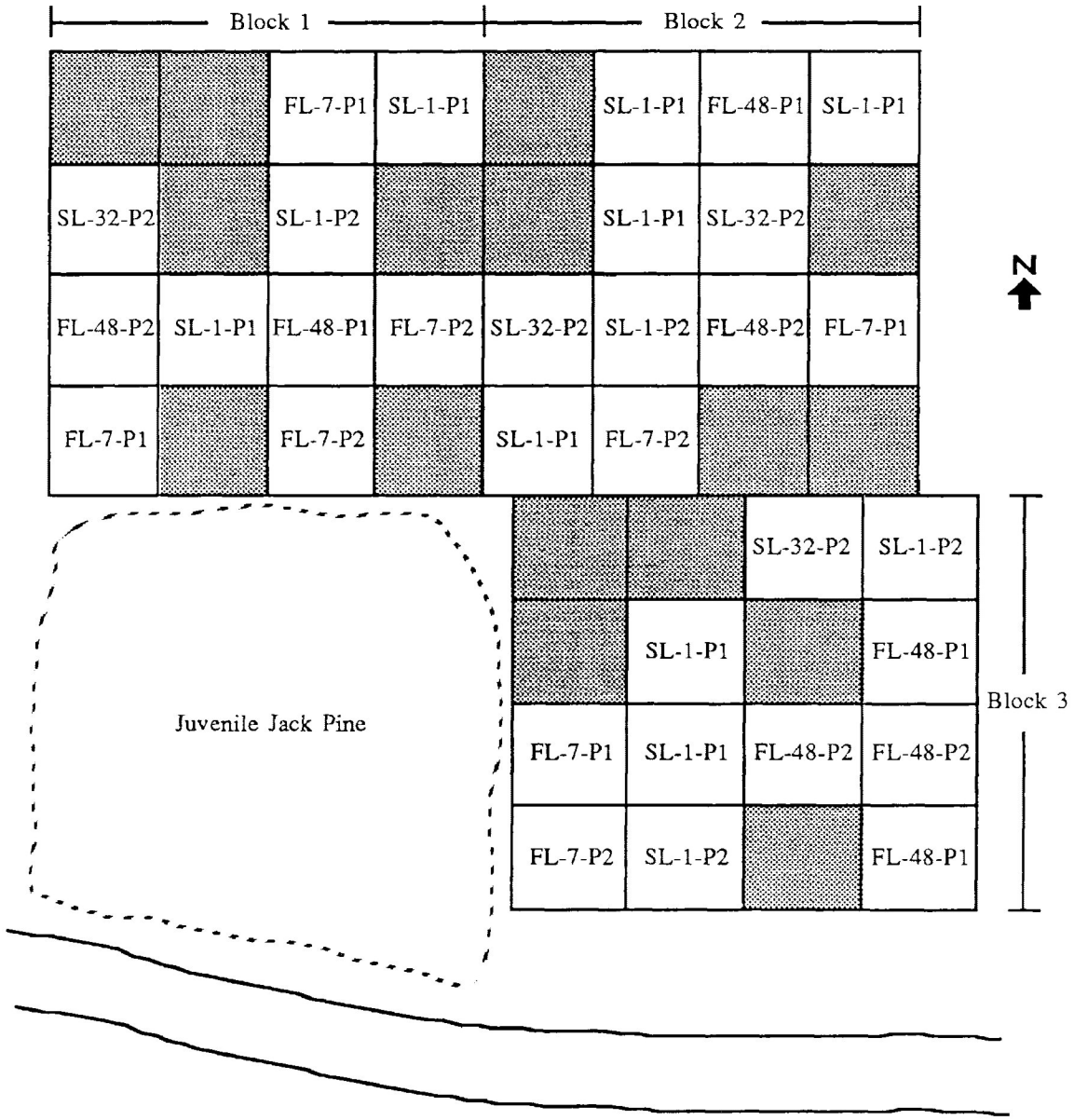

Figure VI.4. The randomized complete block design with unequal within block replication established at a regional outplanting site near Raith, Ontario to determine the selected morphological response attributes of the outplants. See Table 2.2 for treatment code descriptions.

APPENDIX VII

SOIL WATER RETENTION CURVES CHARACTERIZING THE SOILS OF THE OUTPLANTING TRIALS

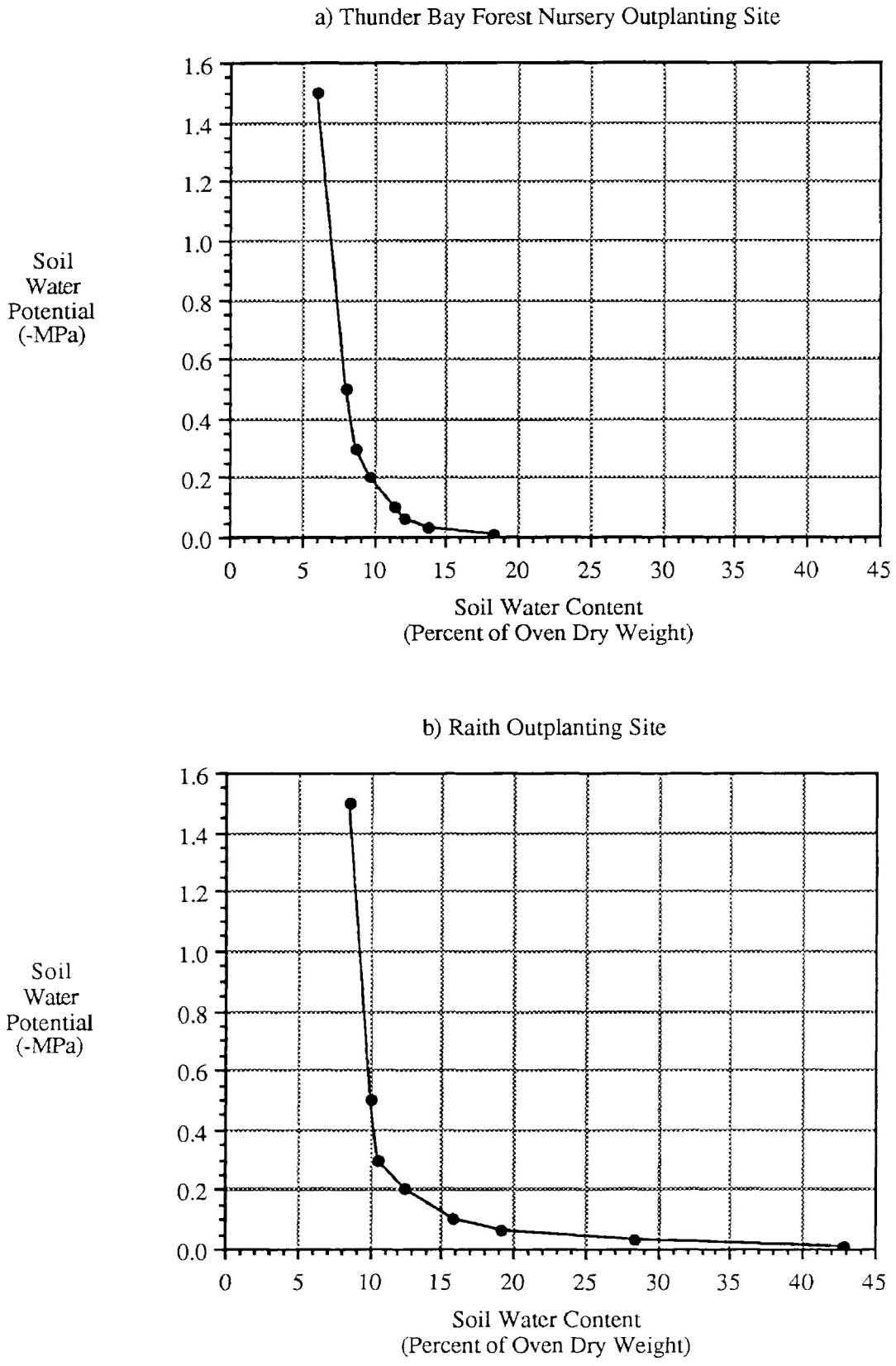

Figure VII.1. Soil water retention curves developed using a ceramic pressure plate extractor for: a) the Thunder Bay Forest Nursery outplanting site, and b) the Raith outplanting site.

APPENDIX VIII

SELECTED CLIMATIC DATA FOR THE THUNDER BAY FOREST NURSERY

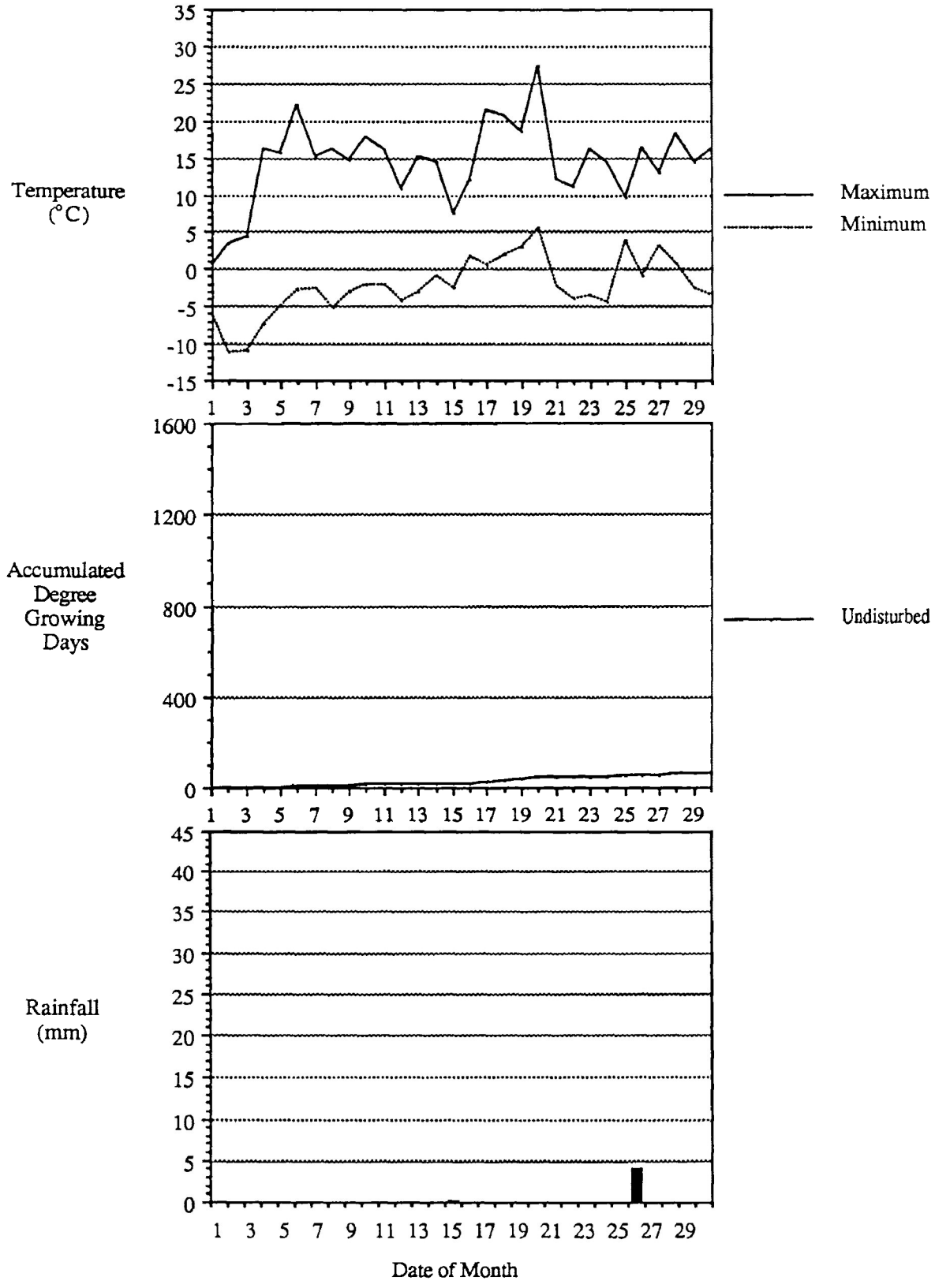

Figure VIII.1. Maximum and minimum daily temperatures, degree growing days (base 5 °C) accumulated since March 1, and daily rainfall for the Thunder Bay Forest Nursery during April, 1987 (Environment Canada 1987).

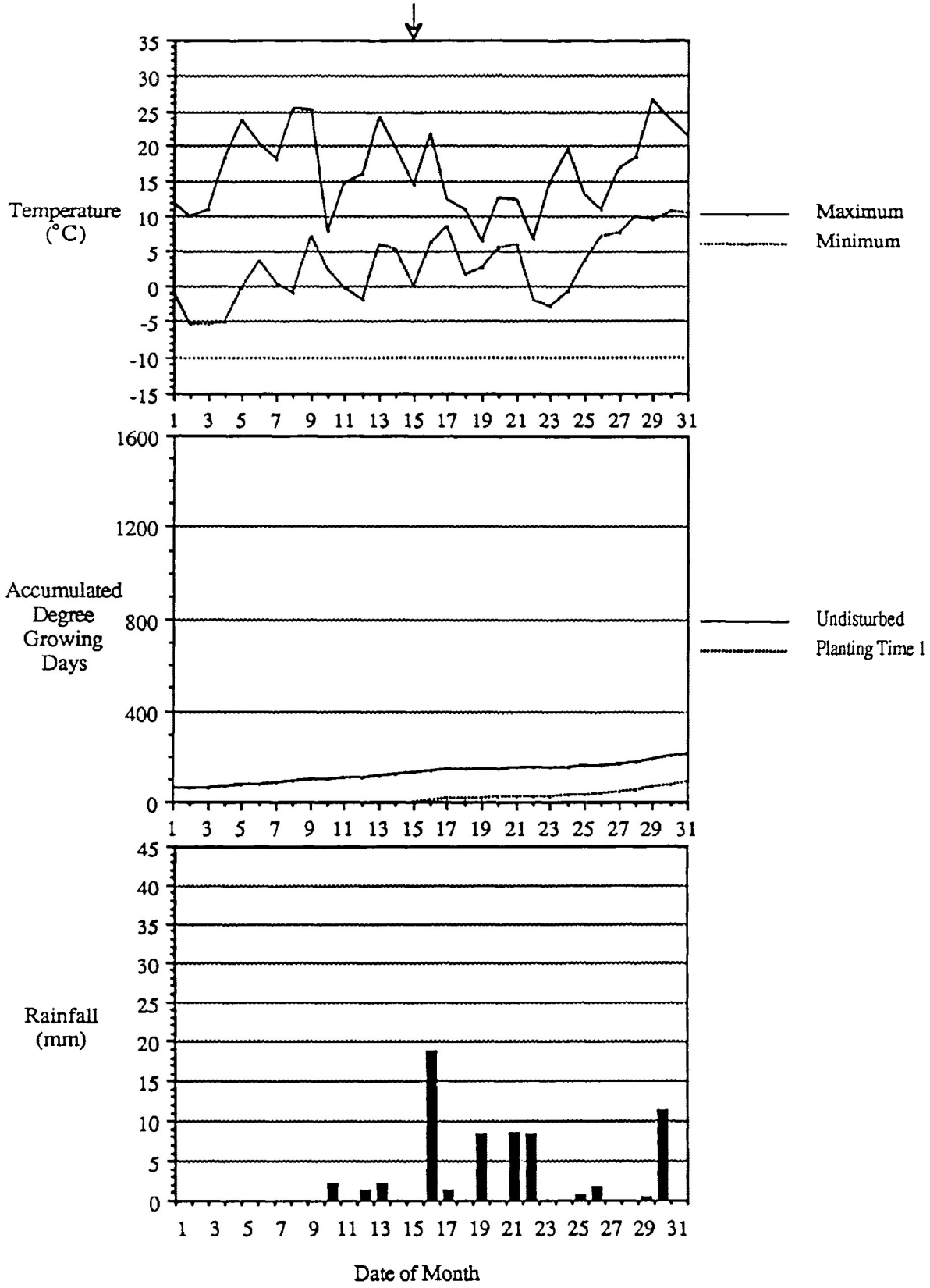

Figure VIII.2. Maximum and minimum daily temperatures, degree growing days (base 5 °C) accumulated since March 1 (undisturbed seedlings) and May 15 (Planting Time 1), and daily rainfall for the Thunder Bay Forest Nursery during May, 1987 (Environment Canada 1987). Arrow depicts date of diurnal sampling for stomatal conductance, transpiration and xylem pressure potential.

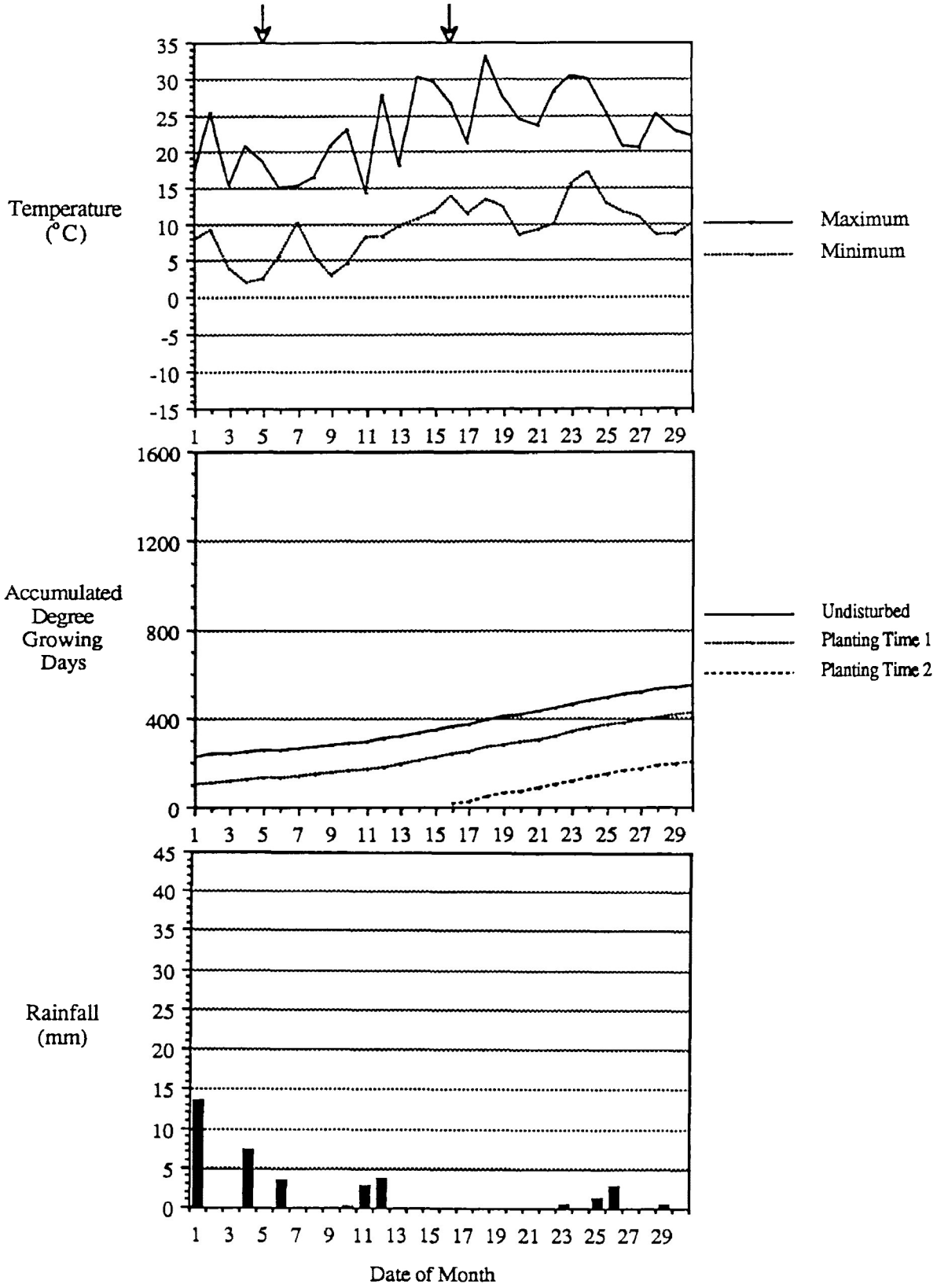

Figure VIII.3. Maximum and minimum daily temperatures, degree growing days (base 5 °C) accumulated since March 1 (undisturbed seedlings), May 15 (Planting Time 1) and June 16 (Planting Time 2), and daily rainfall for the Thunder Bay Forest Nursery during June, 1987 (Environment Canada 1987). Arrows depict dates of diurnal sampling for stomatal conductance, transpiration and xylem pressure potential.

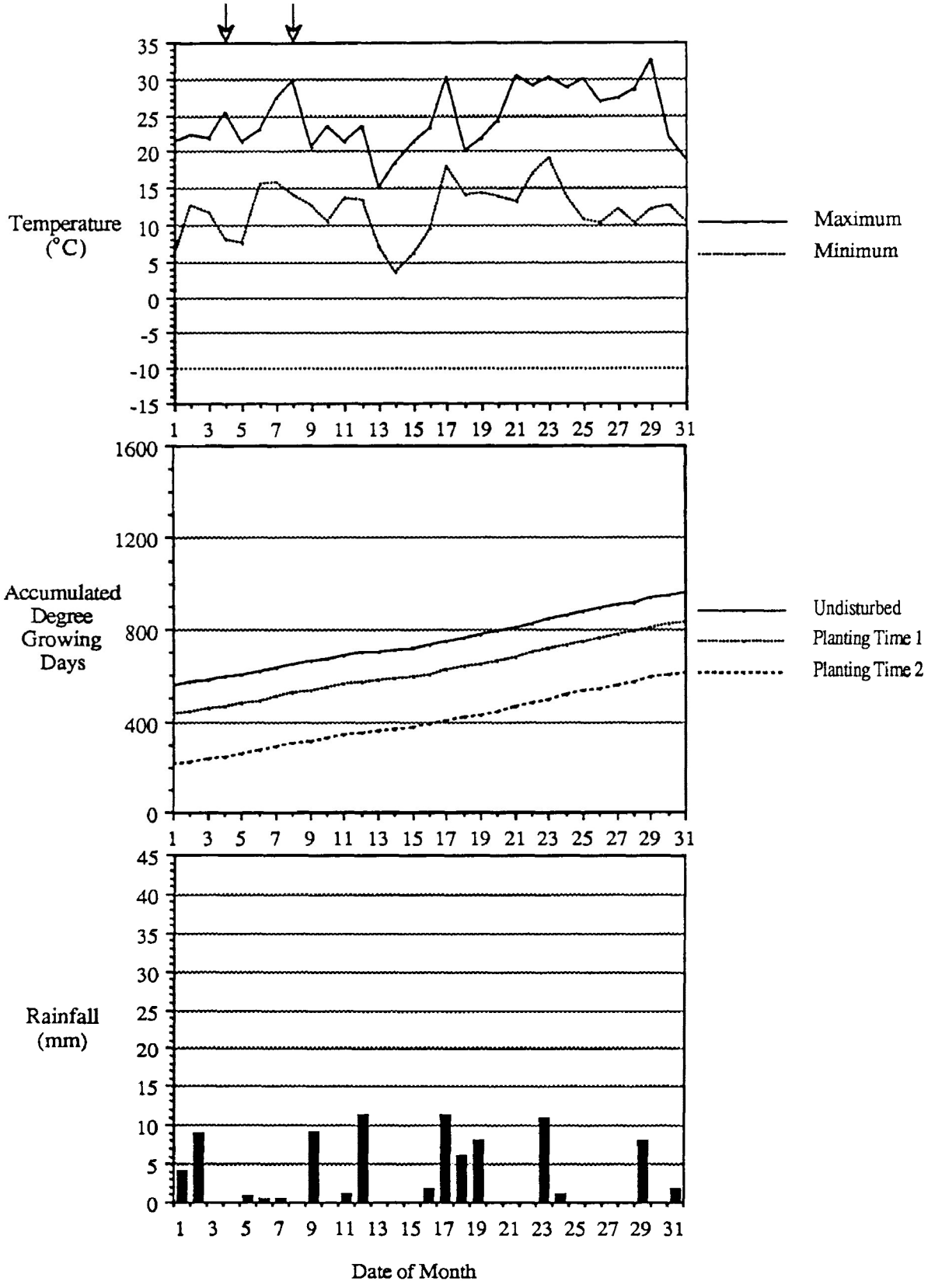

Figure VIII.4. Maximum and minimum daily temperatures, degree growing days (base 5°C) accumulated since March 1 (undisturbed seedlings), May 15 (Planting Time 1) and June 16 (Planting Time 2), and daily rainfall for the Thunder Bay Forest Nursery during July, 1987 (Environment Canada 1987). Arrows depict dates of diurnal sampling for stomatal conductance, transpiration and xylem pressure potential.

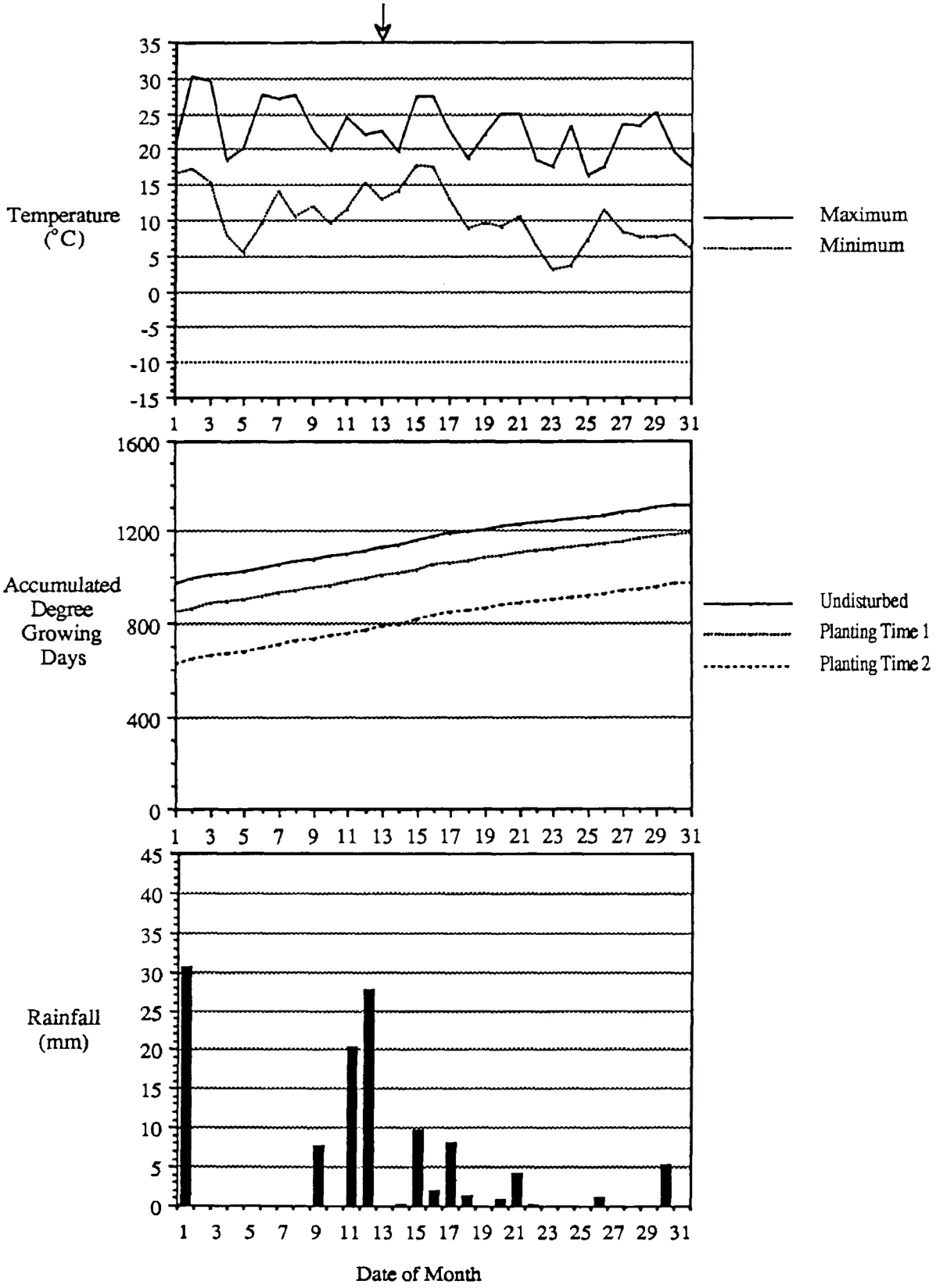

Figure VIII.5. Maximum and minimum daily temperatures, degree growing days (base 5°C) accumulated since March 1 (undisturbed seedlings), May 15 (Planting Time 1) and June 16 (Planting Time 2), and daily rainfall for the Thunder Bay Forest Nursery during August, 1987 (Environment Canada 1987). Arrow depicts date of diurnal sampling for stomatal conductance, transpiration and xylem pressure potential.

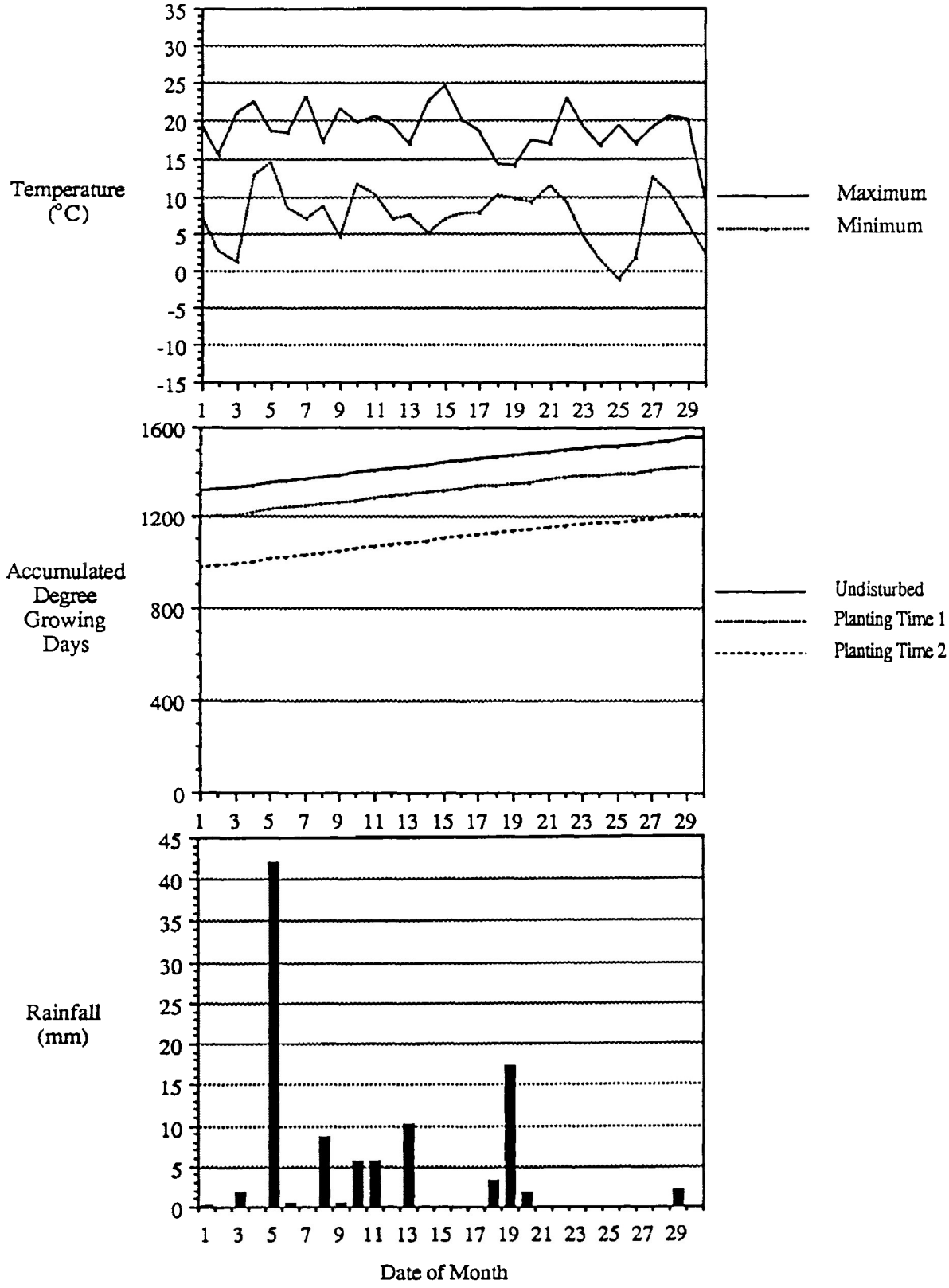

Figure VIII.6. Maximum and minimum daily temperatures, degree growing days (base 5°C) accumulated since March 1 (undisturbed seedlings), May 15 (Planting Time 1) and June 16 (Planting Time 2), and daily rainfall for the Thunder Bay Forest Nursery during September, 1987 (Environment Canada 1987).

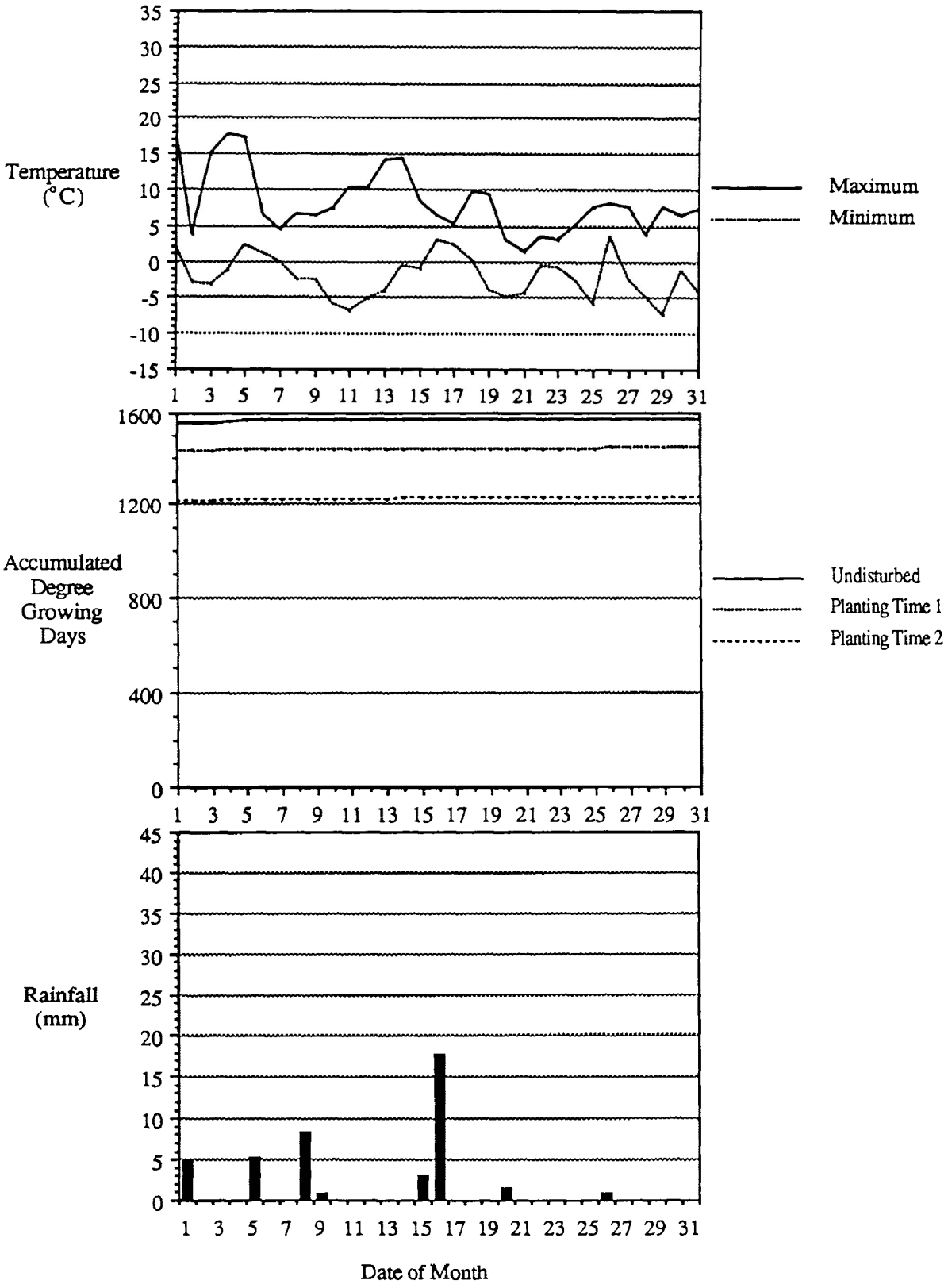

Figure VIII.7. Maximum and minimum daily temperatures, degree growing days (base 5 °C) accumulated since March 1 (undisturbed seedlings), May 15 (Planting Time 1) and June 16 (Planting Time 2), and daily rainfall for the Thunder Bay Forest Nursery during October, 1987 (Environment Canada 1987).

APPENDIX IX

SAMPLING DATES AND TIMES FOR RESPONSE VARIABLES MEASURED REPEATEDLY AT THE THUNDER BAY FOREST NURSERY

Table IX.1. Sampling dates and times for response variables measured repeatedly at the Thunder Bay Forest Nursery during Nursery Trial: Planting Time 1 (May 14, 1987).

Measurement Date	Days Since Planting	Sample Period (EDT)
Stomatal Conductance and Transpiration		
May 15	1	0915 - 2145
May 16	2	0815 - 1215
May 18	4	0815 - 1245
May 23	9	0930 - 2200
May 24	10	0900 - 1230
May 25	11	0800 - 1230
May 30	16	0930 - 1230
May 31	17	0900 - 1230
June 2	19	0930 - 1230
June 3	20	0800 - 1230
June 5	22	0930 - 2200
June 26	43	0600 - 1200
July 4	51	0930 - 2230
July 20	67	0945 - 1245
Xylem Pressure Potential		
May 15	1	0615 - 2115
May 16	2	0615 - 0715
May 17	3	0615 - 0715
May 18	4	0815 - 1115
May 19	5	0615 - 0715
May 20	6	0610 - 0710
May 21	7	0620 - 0720
May 23	9	0730 - 2210
May 24	10	0715 - 0815
May 25	11	0610 - 0710
May 27	13	0610 - 0710
May 28	14	0610 - 0710
May 30	16	0700 - 1400
May 31	17	0630 - 0730
June 1	18	0610 - 0710
June 3	20	0610 - 0710
June 4	21	0625 - 0725
June 5	22	0615 - 2200
June 26	43	0545 - 1305
July 4	51	0550 - 2210
July 20	67	0610 - 1405
Ground Caliper and Leader Extension Increment		
May 14	0	not applicable
June 4	21	not applicable
June 25	42	not applicable
July 16	63	not applicable
August 6	84	not applicable
October 21	160	not applicable

Table IX.2. Sampling dates and times for response variables measured repeatedly at the Thunder Bay Forest Nursery during Nursery Trial: Planting Time 2 (June 15, 1987).

Measurement Date	Days Since Planting	Sample Period (EDT)
Stomatal Conductance and Transpiration		
June 16	1	0600 - 2200
June 17	2	0800 - 1230
June 18	3	0600 - 1230
June 19	4	0900 - 1230
June 20	5	0900 - 1230
June 21	6	0830 - 1230
June 22	7	0800 - 1230
June 24	9	0600 - 2230
June 28	13	0800 - 1230
June 29	14	0800 - 1230
June 30	15	0730 - 2230
July 1	16	0930 - 1230
July 5	20	1000 - 1230
July 6	21	0900 - 1230
July 8	23	0900 - 2230
July 28	43	0915 - 1245
August 13	59	1130 - 2100
Xylem Pressure Potential		
June 16	1	0545 - 2245
June 17	2	0500 - 0600
June 18	3	0535 - 0635
June 19	4	0530 - 0630
June 20	5	0545 - 0645
June 21	6	0550 - 0650
June 22	7	0545 - 0645
June 23	8	0545 - 0645
June 24	9	0540 - 2220
June 25	10	0600 - 0700
June 27	12	0630 - 0730
June 28	13	0600 - 0700
June 29	14	0550 - 0650
June 30	15	0600 - 2200
July 1	16	0615 - 0715
July 2	17	0545 - 0645
July 3	18	0615 - 0715
July 5	20	0605 - 0705
July 8	23	0615 - 2200
July 28	43	0645 - 1320
August 13	59	0700 - 2100

Table IX.2. (Continued)

Measurement Date	Days Since Planting	Sample Period (EDT)
Ground Caliper and Leader Extension Increment		
June 15	0	not applicable
July 6	21	not applicable
July 27	42	not applicable
August 17	63	not applicable
September 7	84	not applicable
October 21	128	not applicable