Extension of the planting period of Norway spruce container seedlings: risks related to the drought – growth stage dynamics and handling practices

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Academic dissertation

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Istutus

Routa kun vaan maasta sulaa,
Eemelill' ei töistä pulaa
aukkoja on metsäss' monta,
puiden kasvuun verratonta,
hyötyisiksi nämä saapi,
taimet nuoret istuttaapi.
Kuopat syvät maahan kaivaa,
eukko niihin taimet painaa,
ruokamultaa juuriin käyttää,
sitten vasta kuopan täyttää,
hyvin pinnan tasoittaapi,
taimet lujaan puristaapi.
Eemeli myös aina muistaa,
korissa voi juuret kuivaa,
siksi täytyy sammalilla,
juuret peittää tuorehilla.

A. Liuksiala (1935)

ABSTRACT

Helenius, P. 2005. Extension of the planting period of Norway spruce container seedlings: risks related to the drought – growth stage dynamics and handling practices. Dissertationes Forestales 3. 46 p.

The first aim of this study was to investigate the possibility of extending the planting period of *Picea abies* container seedlings from May to June and July without the risk of excessive mortality and growth restrictions due to drought. The second aim was to investigate risks related to thawing practices of frozen-stored seedlings.

To achieve the first aim, 1.5-yr-old actively growing seedlings were exposed to different preplanting drying and postplanting drought periods. Seedlings kept dormant (sensu shoots not elongating) by prolonged frozen storage were also exposed to postplanting drought periods. To achieve the second aim, 1-yr-old frozen-stored seedlings were exposed to different thawing durations and temperatures before planting in mid-June.

Height growth and root egress of actively growing seedlings planted in late June–early July decreased when exposed to postplanting drought as affected by the soil water content at planting and atmospheric evaporative demand during drought periods. Survival and growth under drought were also decreased by preplanting drying of root plugs and seedlings. However, mortality of actively growing, well-watered seedlings was negligible when exposed to drought periods not longer than 2 to 3 weeks.

Prolonged frozen storage until late June had no observable negative effect on needle carbohydrate concentration and subsequent seedling outplanting performance. Contrary to actively growing seedlings, drought periods had no effect on root egress and chlorophyll fluorescence, and only moderate effect on xylem water potential of dormant seedlings. However, actively growing seedlings showed much greater root egress than dormant seedlings, except when exposed to very long (≥ 3 weeks) drought periods after planting.

Frozen-planting may adversely affect seedling performance at soil temperatures prevailing in Fennoscandia in spring or early summer, especially when soil is dry. Thawing over 4 to 8 days at 9–12 °C ensures complete thawing of the root plugs and unaffected field performance of frozen-stored seedlings.

Keywords: Frozen storage, *Picea abies*, Planting stress, Root growth, Soil water content, Survival

PREFACE

This study was carried out at the Suonenjoki Research Station of the Finnish Forest Research Institute during years 1999–2005. The study was supported by the Metsämiesten Säätiö Foundation and the Niemi Säätiö Foundation, both of which I gratefully acknowledge. In addition, I am grateful for the excellent working facilities provided by the Suonenjoki Research Station.

I wish to express my sincere thanks to Dr. Jaana Luoranen, Dr. Risto Rikala and Professor Pasi Puttonen for supervising my work. I also thank Dr. Heikki Smolander, Head of the Research Station for contributing to financing my work. I wish to thank Dr. Juha Lappi, Dr. Risto Häkkinen and Dr. Kari Leinonen for statistical guidance. I am also grateful to Kari for cooperation in writing my first scientific paper. I thank Dr. Elina Vapaavuori and Dr. Seija Kaakinen for guidance in chlorophyll fluorescence measurements and Dr. Juha Heiskanen and Dr. Marja-Liisa Juntunen for valuable comments on the manuscript of this thesis and Mr. Marc Grookes for checking the English language. Professor Marja-Liisa Sutinen and Professor Robert D. Guy are acknowledged for their careful work in reviewing the manuscript of this thesis. I am also grateful to Professor Pentti K. Räsänen for introducing me in the first place to the fascinating field of artificial forest regeneration. I thank my colleagues and friends at Suonenjoki Research Station for their help and support. In particular I want to thank Ms. Ritva Pitkänen, Ms. Anna-Maija Väänänen, Ms. Eeva Vehviläinen, Ms. Raija Kuismin, Mr. Jukka Laitinen, Mr. Pekka Voipio and Mr. Pekka Savola. Thanks also to the ’’techno’’ boys for creating a stimulating and dynamic environment to finish this thesis.

Finally, I want to thank my family and friends for their support.

Suonenjoki, July 2005 *Pekka Helenius*

LIST OF ORIGINAL ARTICLES

This thesis is based mainly on the following articles, which are referred to in the text by their Roman numerals. Additional data, collected during the experiment described in article I, are also presented. The articles are reprinted with kind permission of the publishers.

I Helenius, P., Luoranen, J., Rikala, R. & Leinonen, K. 2002. Effect of drought on growth and mortality of actively growing Norway spruce container seedlings planted in summer. Scandinavian Journal of Forest Research 17: 218–224.

II Helenius, P., Luoranen, J. & Rikala, R. 2005. Effect of preplanting drought on survival, growth and xylem water potential of actively growing *Picea abies* container seedlings. Scandinavian Journal of Forest Research 20: 103–109.

III Helenius, P., Luoranen, J. & Rikala, R. 2005. Physiological and morphological responses of dormant and growing Norway spruce container seedlings to drought after planting. Annals of Forest Science 62: 201–207.

IV Helenius, P. 2005. Effect of thawing regime on growth and mortality of frozen-stored Norway spruce container seedlings planted in cold and warm soil. New Forests 29: 33–41.

V Helenius, P., Luoranen, J. & Rikala, R. 2004. Effect of thawing duration and temperature on field performance of frozen-stored Norway spruce container seedlings. Silva Fennica 38: 347–352.

Most of the experiments and analyses in articles I–V were carried out by P. Helenius. The experimental designs in articles I, II, III and V were planned by P. Helenius, R. Rikala and J. Luoranen in collaboration. In article I, statistical analyses were carried out by K. Leinonen and P. Helenius in collaboration, and in article II by J. Luoranen. P. Helenius was the main writer in all articles. J. Luoranen and R. Rikala participated in the writing of articles I, II, III and V, and K. Leinonen in the writing of article I.

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1 BACKGROUND

Norway spruce [*Picea abies* (L.) Karst.] is currently the most used tree species in reforestation planting in Finland. The number of Norway spruce seedlings annually delivered from Finnish nurseries has increased over 70% during the past 20 years (1983−2003). At the same time, the share of container seedlings in Norway spruce has increased over 80%-units (Västilä 2004) (Figure 1). A corresponding trend can be found in Sweden (Fridh 2003), and when it comes to the share of container seedlings, also in Norway (K. Kohmann, Norwegian Forest Research Institute, personal communication).

Along with the increase in container seedling production, new practices and technology, such as hardplastic containers (Rikala 2002), single seed sowing (Tervo 1999a), automated container filling, seeding and packing machinery (Heiskanen et al. 1996, Tervo 1999b, Rantala et al. 2003b), irrigation and fertilization systems (Juntunen and Rikala 2001, Rikala 2002) and short-day treatment (Rosvall-Åhnebrink 1982, Coursolle et al. 1997) have been adopted to the nursery culture.

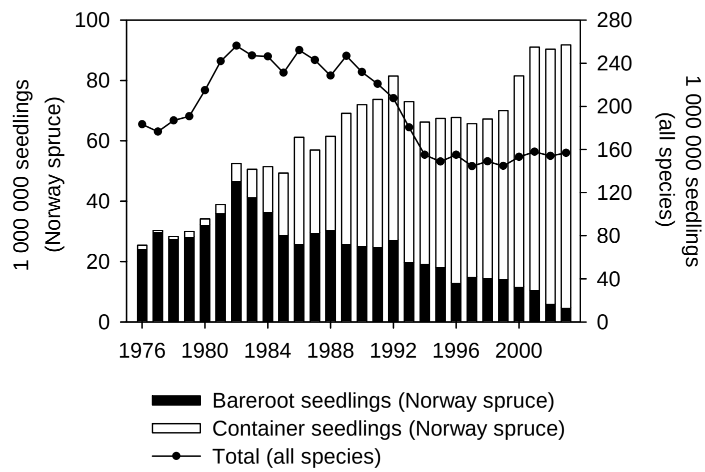

Figure 1. Annual number of Norway spruce seedlings and the number of all seedlings delivered for planting from Finnish nurseries between 1976 and 2002. Figure is based on Finnish Statistical Yearbook of Forestry (Anonymous 1977−1989, Västilä 2004). In addition to these numbers, Swedish nurseries currently produce and deliver about 12 million container seedlings, mostly Norway spruce, annually to Finland.

One of the latest practices in nurseries at northern latitudes is to lift and pack seedlings in cardboard boxes in autumn and store them in frozen storage over winter, usually at −1 to −5 ºC (see Camm et al. 1994 and McKay 1997). The intent in frozen storage is to avoid risks related to outdoor storage, such as winter desiccation, extreme temperatures, feeding by rodents, growth of snow mould and also uneven bud burst and frost damage in spring (Baig and Tranquillini 1980, Racey et al. 1985, Lindström and Nyström 1987, Colombo 1997, Grossnickle 2000, Paterson et al. 2001). In addition, frozen storage allows greater flexibility in seedling delivery from nurseries in spring and also helps to ease spring workloads. Currently it is estimated that 40 to 50% of the Norway spruce container seedlings delivered from the Finnish nurseries are frozen-stored, and it is expected that this number will increase in the near future (P. Helenius, unpublished questionnaire).

In Finland, frozen-stored seedlings are often delivered from the nurseries while in a frozen state, mainly for logistic reasons, and are thawed in the boxes during field storage prior to outplanting. Thawing rate is thus dependent on ambient weather conditions in a given year, and also on the date of delivery. Due to spring workloads in tree planting, the thawing and field storage period may extend up to 25 days, during which seedlings are commonly kept in the boxes (Rantala et al. 2003a). While darkness precludes any photosynthesis, seedling respiration rate and also growth rate of storage mould increases due to increased outdoor temperatures and the humid environment around the seedlings (Sutherland and Hunt 1990). Although daily mean outdoor air temperatures in central Finland remain below 15 °C until mid-June, the in-box temperature may rise excessively e.g. when the boxes are exposed to direct solar radiation. When prevailing long enough, these conditions reduce physiological quality and subsequent outplanting performance of seedlings (Kauppi 1984, Binder and Fielder 1995, Harper and O'Reilly 2000).

Whether overwintered in frozen storage or outdoors, seedlings are usually planted in southern and central Finland in May and early June, when they are still dormant, and there is available soil water. The planting period starts as soon as the soil is no longer frozen, and ends when seedlings start to grow and the soil is considered too dry for survival and growth. Consequently, the duration of the planting period is only 5 or 6 weeks. Such a short planting period can be seen, at least to some extent, as a relic of an era (1970s and early 1980s) when most of the seedlings were bare-root. In fact, one of the reasons why container seedlings were introduced in the first place was to extend the planting period (Huuri 1965, Low and Brown 1972, Stein et al. 1975). Despite considerable increase in container seedling production during the last 20 years (Figure 1), the planting period in Finland is still almost the same as in the early 1980s.

Theoretically it would be advantageous to extend the planting period to include also June and July from the plant physiological, logistical and also economical point of view. First, soil temperatures close to 15 °C in July (Figure 3) favour both root growth (Lopushinsky and Max 1990, Vapaavuori et al. 1992, Landhäusser et al. 2001) and water and nutrient uptake of spruce seedlings (Dighton and Harrison 1983, Grossnickle 1988, Marschner et al. 1991). Second, the potential of actively growing Norway spruce seedlings to root egress is high in July (Lyr and Hoffmann 1967, Nyström 1991, Luoranen et al. 2001, Figure 3) and, contrary to spring planting, soil temperature in July does not limit the expression of this high potential (Simpson and Ritchie 1997). Rapid extension of the roots from the root plug to the surrounding soil (root egress) is, in turn, a major determinant of establishment success of newly planted seedlings (Burdett 1979, Hines and Long 1986, Burdett 1990, Simpson 1990, Simpson et al. 1994). The effect of rapid root egress can be considered even more important to the establishment success when seedlings are exposed to severe environmental site conditions after planting such as low soil water and high evaporative demand (Simpson and Ritchie 1997). Third, during the last 20 years the number of workers employed in silvicultural work, e.g. in planting, has decreased over 40% in Finland (Elovirta 2004), and it is predicted that the decrease will continue in the near future (Työvoiman saatavuus… 2004). An extended planting period would thus enable planting all the seedlings with decreasing number of workers, improve job security for these workers and also ease spring workloads in nurseries. Fourth, an extended planting period is needed to make the best use of capital intensive planting machinery.

According to previous studies, a major impediment to the extension of the planting period is the risk of drought (Kinnunen et al. 1974, Valtanen et al. 1986, Nilsson and Örlander 1995). If the summer is warm and no irrigation is available during field storage, seedlings are easily exposed to drought even before planting. Drought stress may increase further after planting if the precipitation and capillary rise of water from deeper soil layers are insufficient to compensate for transpiration. As was demonstrated by Kauppi (1984), seedling injury (revealed by slow growth or increased mortality), is related to the accumulated strain, which is a function of a stress factor (e.g. high evaporative demand), stress resistance factor (e.g. seedling drought resistance) and site environment (e.g. soil water content), all varying in time. Unfortunately, when it comes to the extension of the planting period to June and July, the risk of high evaporative demand (both before and after planting) and low soil water coincide with low stress resistance of actively growing seedlings (Coutts 1981, Ritchie 1986, Deans 1990).

Since the stress resistance is closely related to the phenological stage of seedlings (Grossnickle 2000, McKay and Milner 2000, Colombo et al. 2003), theoretically it should be possible to decrease the risk of plantation failure due to drought in early summer by planting seedlings kept dormant by prolonged frozen storage instead of growing ones (cf. Ritchie et al. 1985, Mattson 1986, Ritchie and Landis 2004). Kohmann (1999) reported high survival when Norway spruce container seedlings were taken out of the cold storage a fortnight before planting in early July. Unfortunately, there is no information available about weather conditions during that experiment. Wang and Zwiazek (2001) showed that spring-lifted white spruce [*Picea glauca* (Moench) Voss] bare root seedlings could be successfully frozen-stored 7 weeks at −2 °C to facilitate late planting. Provided that dormant seedlings outperform growing seedlings under drought, successful extension of the planting period would only be a matter of scheduling the delivery of frozen-stored seedlings later than seedlings stored outdoors. Also short-day treatment has been used to induce dormancy and thus harden seedlings to enable them to withstand summer field site environmental conditions (cf. Vaartaja 1960, Grossnickle 2000). However, about two-thirds of the average accumulative temperature sum of the provenance (i.e. 600 to 700 d.d. in central Finland) is needed before short-day treatment can be successfully applied for Norway spruce (Koski and Sievänen 1985, Konttinen et al. 2000). In addition, short-day treatment should last at least two weeks to be effective (Konttinen et al. 2003). Thus, due to the late start of the growing season at northern latitudes, short-day treatment cannot be applied economically to produce hardened seedlings yet for plantings in June and early July.

In addition to drought, seedlings may also be exposed to mechanical stress (e.g. crushing, bending, abrasion, dropping etc.) during transport and handling (see McKay 1997). However, the present evidence suggests that these various forms of mechanical stress are not normally sufficient to adversely affect survival and growth of container-grown conifer seedlings (Simpson et al. 1994, Stjernberg 1997, Helenius et al. 2002).

2 RESEARCH FRAMEWORK

2.1 Drought and extension of the planting period

2.1.1 Water relations in plants

Sufficient water content of living tissues is essential for the normal functioning of plants. Water is an essential constituent of protoplasm and forms 80 to 90% of the fresh weight of actively growing tissue and approximately 50% of freshly cut wood. Water is also needed to maintain turgidity, cool down plants and transport ions, gases and molecules. Finally, water is important for photosynthesis (Kramer 1983, Larcher 1995, Kozlowski and Pallardy 1997). Water relations in plants are usually described in terms of water potential (Ψ), which is currently reported in megapascals (MPa). When water is lost from turgid leaf cells, for example as stomata open in the early morning and transpiration occurs, their Ψ decreases. This decrease causes flow of water from the xylem to the leaf cells and further from the root cells to xylem, and finally, from the soil to root cells (i.e. along a gradient of decreasing water potential) (Kozlowski et al. 1991). The driving force for this water movement through a plant is vapor pressure deficit in the air (i.e. the difference in Ψ from soil to air).

When there is available soil water, plant Ψ follows a diurnal pattern resulting from the changes in solar radiation. On hot, sunny days, water absorption by the roots usually lags behind the transpiration from the leaves because there is more resistance in water flow between soil and roots than between leaf and air, and Ψ decreases during the morning and early afternoon (Kozlowski et al. 1991). Transpiration is usually highest in the morning because stomata are wide open due to increased solar radiation, and Ψ has not yet decreased markedly. At low wind speeds, the rate of transpiration is usually further increased because of the decreased thickness of the layer of humid air (boundary layer) around the needles, whereas higher wind speeds tend to reduce transpiration by cooling the needles (Dixon and Grace 1984). In the evening and during the night these conditions are reversed, absorption exceeds transpiration, Ψ increases and usually equilibrates with that of root zone soil water potential before the sun rises again. This is why plant Ψ is often measured just before sunrise (i.e. predawn Ψ). However, as water is removed from the soil by transpiring plants and soil Ψ decreases, there is an accompanying increase in the resistance to water flow toward roots. Accordingly, the degree to which plant Ψ increases during the night (i.e. rate of rehydration) decreases gradually. Eventually, the water lost through transpiration is not replaced during the night and permanent wilting and death from desiccation occur.

2.1.2 Frequency of drought

In general, the term ''drought'' denotes a period without appreciable precipitation, during which the water content of the soil is reduced to such an extent that plants suffer from lack of water (McWilliam 1986, Larcher 1995, Kozlowski and Pallardy 1997). In addition, water in the soil, even if abundant, may not be readily available for plants if it is in a frozen state (Mayr et al. 2002, 2003b), or if low soil temperature restricts uptake of water by roots via increased viscosity (Grossnickle 1988). The degree to which the water content of the soil is reduced over a given period without precipitation is dependent on evaporation

(Grossnickle 2000), soil and growth medium properties (Groot and King 1993, Heiskanen 1999) and the amount of transpiring vegetation (Youngberg 1958, Jansson 1987, Newton and Comeau 1990, Nilsson and Örlander 1995). In southern and central Finland evaporation exceeds precipitation, i.e. climate is arid, in May, June and July (Solantie and Ekholm 1985). Despite aridity, soil water content remains relatively high in early May, because of the melted snow cover. Due to intense evaporation, soil water content begins to decrease during June, July and early August, accompanied with transient increases due to rain showers.

The risk of drought under conditions of intense evaporation on a given site can be roughly estimated by calculating the number of consecutive days between rain showers (i.e. duration of rainless periods) and the probability of these potential drought periods. In the following example, a threshold value of 1 mm rainfall was chosen to represent the end of a single rainless period. According to the non-linear regression curve fitted to the rainfall data collected at Suonenjoki Research Station in central Finland between 1975–2003, the probability of a one-week rainless period between 1 June and 31 August is 0.59 and a two-week rainless period 0.12 (Figure 2). A greater than four-week rainless period occurred only once during the entire 29-year observation period.

2.1.3 Responses of spruce seedlings to drought

Drought is an environmental factor that causes water stress for seedlings (Kozlowski and Pallardy 1997). In general, stress is defined as a significant deviation in some environmental factor, in this case in the availability of water, from optimal conditions for growth of seedlings (Margolis and Brand 1990). The negative response of the seedling to a stressful condition is called strain and it includes all the seedling properties which differ from the respective properties of a vigorous seedling (Kauppi 1984). The concepts of stress and strain are interdependent since it is the environment that applies stress but it is the strain response in the seedling that actually defines the stressfulness of an environmental condition (see Margolis and Brand 1990).

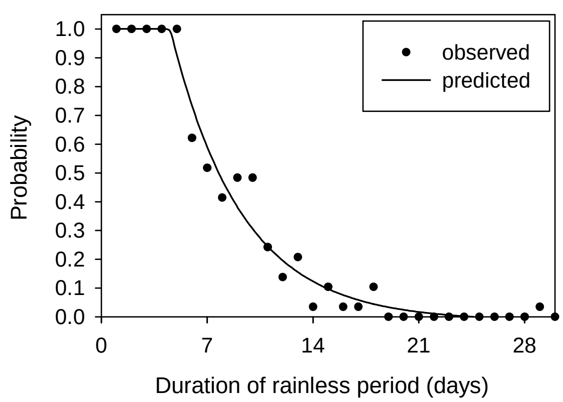

Figure 2. The observed and predicted probability of different rainless periods (1 to 30 days) between 1 June and 31 August (1975–2003) at Suonenjoki Research Station in central Finland. Rainless period refers to consecutive days with daily precipitation < 1 mm.

The development of strain and possible subsequent injury in the seedling under drought is not only due to the degree to which availability of water deviates from optimum; seedling internal factors are always involved (Kauppi 1984). Spruce like any other plant species has a specific way to maintain physiological activity and to survive when exposed to drought stress and is referred as drought resistance. Drought resistance can be divided into two main components: drought avoidance and drought tolerance (Levitt 1972). Drought avoidance is the postponement of desiccation. It can be achieved by reduction of water loss from the needles (i.e. cuticular development and stomatal control), reduction of the transpiring surface (i.e. premature shedding of needles and loss of minor branches), high water-conducting capacity of xylem or improved uptake of water from the soil (i.e. increased rooting) (Kozlowski et al. 1991, Kavanagh and Zaerr 1997, Grossnickle 2000, Riederer and Schreiber 2001, Mayr et al. 2003a). Drought tolerance is the capacity of the protoplasm of a seedling to undergo dehydration without irreversible injury and is determined by the maintenance of turgor (i.e. tissue elasticity and osmotic adjustment) or through desiccation tolerance (i.e. protoplasm and chloroplast tolerance to reduced water content) (Koppenaal et al. 1991, Larcher 1995, Grossnickle 2000). Most of these responses are dependent on the phenological stage of the seedlings (Grossnickle 2000, Grossnickle and Folk 2003).

2.1.4 Incidence of drought in nursery stock

When planting of forest tree seedlings is concerned, the risk of drought is more complex than in naturally regenerated seedlings of the same age. Prior to planting, nursery stock is often subjected to an unnatural environment, and external environmental factors (e.g. high air temperature, solar radiation, wind etc.) that usually pose no threat to naturally regenerated seedlings may be damaging to unacclimated nursery stock. The effect of preplanting drying on field performance of bare-rooted seedlings has been studied extensively with conifers (Huuri 1972, Örlander and Due 1986, Tabbush 1987, Rikala and Puttonen 1988, Deans et al. 1990, McKay and White 1997, McKay and Milner 2000, Brønnum 2005) and also broadleaves (Wilson and Clark 2000, Radoglou and Raftoyannis 2002), whereas less information is available on conifer container seedlings (Mitchell et al. 1972, Lähde 1978, Heiskanen and Rikala 2000).

Container seedlings are obviously less likely to be damaged when exposed to drying than bare-rooted seedlings because the root plug medium protects the roots from desiccation and serves as water storage (see McKay 1997, Mena-Petite et al. 2001, 2004). However, due to relative small volume of the root plugs (50–115 cm^3) used at Finnish nurseries for conifer seedlings (Rikala 2002), the water storage of the root plug is small even when saturated, and is rapidly depleted through transpiration from the shoot system and evaporation from the root plug medium. Rikala (1985) found that in greenhouse conditions evaporation from the root plug media easily exceeded transpiration by Scots pine (*Pinus sylvestris* L.) seedlings during their first growing season. Although evaporation from the root plug medium is mainly determined by the atmospheric conditions, it may also be affected by the properties of root plug medium (Mitchell et al. 1972) and container type where the seedlings are grown and delivered in (Lähde 1978, Heiskanen 1993a, Landis et al. 1990). For example hard plastic containers provided with separate, open-ended cells and air slits currently used at Finnish nurseries are poorly suited for transport and field storage purposes because of the risk of excessive evaporation from the bottom and sides. If the water content of the root plug decreases considerably, it may be difficult to rewet because of the water repellent properties and low hydraulic conductivity of dry organic material like low-humified peat used as a growing media in root plugs (Puustjärvi 1977, Landis 1989, Heiskanen 1993a). Moreover, when the root system is already severely desiccated, rewetting, even if technically successful, is not likely to mitigate the effect of desiccation on seedling survival and growth (Tabbush 1987, Balneaves and Menzies 1988).

Newly planted container seedlings may occasionally suffer from lack of water immediately after planting even in the absence of drought for several reasons. First, roots are initially confined to the planting hole and, compared to naturally established seedlings of the same age, have only limited access to the soil water reservoir (Burdett 1990, Margolis and Brand 1990). In addition, access to soil water may be further reduced by low hydraulic conductivity between the root plug medium and the surrounding soil (Heiskanen 1999, Heiskanen and Rikala 2003). Second, newly planted seedlings may lack completely or suffer from partial loss of new, unsuberized roots, which are efficient in water uptake (Chung and Kramer 1975, Sands et al. 1982), but are also sensitive to drying (Coutts 1981). Due to new roots often being confined to the surface of the root plug, they are easily exposed to drying and mechanical damage during transport, handling and field storage. In addition, newly planted seedlings may suffer from lack of water absorbing mycorrhizae (Dixon et al. 1980, Parke et al. 1983, Richter and Bruhn 1989, Kropp and Langlois 1990). Third, low soil temperature in spring and early summer may restrict the growth of roots into the surrounding soil (Söderström 1974, Tryon and Chapin 1983, Grossnickle and Blake 1985, Lopushinsky and Max 1990). Low soil temperature also increases the viscosity of water and thus increases its resistance to flow towards and across the roots (Running and Reid 1980, Goldstein et al. 1985, DeLucia 1986, Brand and Janas 1988). Fourth, peat-based root plug media tends to shrink when drying (Heiskanen 1993b). Shrinkage after planting may result in the formation of an air gap between the root plug and surrounding soil, thus restricting the growth of roots out of the root plug. It is likely that the effect of these factors on water availability will be emphasized when planting is indeed preceded or followed by a long dry period.

2.2 Thawing and planting practises of frozen-stored seedlings

2.2.1 Application of overwinter frozen storage

According to current knowledge, fall-lifted spruce seedlings can be successfully frozen-stored for up to 5 or 6 months, provided that seedlings have reached a sufficient stress resistance before storage (Ritchie et al. 1985, Colombo 1990, 1997, Stattin 1999, Perks et al. 2001), and that seedlings are protected against desiccation during storage (Lefevre et al. 1991, Odlum et al. 2001). Due to practical reasons, however, the normal frozen storage period for spring planted seedlings in central Finland may well exceed 6 months, let alone if planting period of frozen-stored seedlings is extended to June. There is some evidence that an extended frozen storage period may adversely affect physiological quality, e.g. decreased drought and freezing tolerance (Jiang et al. 1995), delayed photosynthetic recovery (Harper and Camm 1993, Jiang et al. 1995), and subsequent field performance of spruce seedlings (Camm and Harper 1991). Decreased drought and freezing tolerance is, at least partially, attributed to the respiratory consumption of reserve carbohydrates during storage (Ritchie 1982, Jiang et al. 1994). Considering the risk of low carbohydrate content in frozen-stored seedlings in spring, thawing should be organized to minimize further losses in carbohydrate content prior to outplanting (cf. Silim and Guy 1998).

2.2.2 Outplanting of frozen seedlings

Studies in North America have indicated that when seedlings are planted in warm soil (18−32 ºC) thawing of frozen-stored conifer seedlings might even be unnecessary, provided that frozen root plugs can be separated without mechanical damage to roots (Camm et al. 1995, Kooistra and Bakker 2002). In the study of Camm et al. (1995), differences in xylem water potential, net assimilation, stomatal conductance and chlorophyll fluorescence between frozen-planted and slowly thawed (9 days at 5−15 ºC) interior spruce seedlings [*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry] disappeared during the first 5 to 8 days after planting, and there appeared to be no lasting effects on growth when seedlings were planted frozen.

In southern and central Finland, soil temperature is relatively low (< 10 ºC) in May (Yli-Vakkuri 1960, Heikinheimo and Fougstedt 1992) when the traditional spring planting period usually starts (Figure 4). At that time, daytime air temperatures and solar radiation can already be rather high, increasing atmospheric evaporative demand. This, together with low soil temperature and frozen root plugs can have a more negative effect on the water balance of frozen-planted seedlings than in warm soil. To avoid extensive frost damage in autumn, frozen-stored seedlings should in any case be planted before mid-June (Luoranen et al. 2001, Hänninen et al. 2002). By that time, soil temperature may rise to over 15 ºC on cultivated clearcuts (Ritari and Lähde 1978, Kubin and Kemppainen 1994), which might enable safe planting of frozen seedlings. Unfortunately, soil scarification methods (e.g. mounding/spot mounding) that increase soil temperature, and are currently widely used for spruce in Finland (about 27% of the total annual site preparation area; Västilä 2004), also increase the risk of drought (Örlander 1986, Freij and Örlander 1987, Bassman 1989, Örlander et al. 1998, Hallsby and Örlander 2004). Before frozen-planting can be recommended on a large scale, more information about the effect of frozen root plugs on seedling performance, especially under different edaphic conditions, is needed (cf. Kooistra and Bakker 2002).

2.2.3 Thawing methods

Container seedlings are occasionally frozen-stored over winter in bundles (i.e. only root plugs wrapped in plastic film) instead of packing them in boxes (Johnsen and Kohmann 1994). This procedure provides more alternatives for thawing seedlings in spring, although it may be more risky than storing seedlings in boxes when it comes to shoot desiccation during and after frozen storage (see Lefevre et al. 1991). Fløistad and Kohmann (2001) showed that there are physiological advantages (e.g. higher carbohydrate content and better frost tolerance at the time of the planting) in thawing seedling bundles rapidly in the air (16 h at 15 ºC) or by immersion in water (20 h at 8 ºC) compared to slow thawing where storage temperature was gradually increased to 5 ºC over a period of 8 weeks. In addition, seedlings thawed rapidly broke bud later after planting than seedlings thawed slowly, which may be beneficial in regions prone to spring frosts. However, when operating with frozen-stored seedlings packed in cardboard boxes, application of rapid thawing procedures would necessitate laborious and cost-increasing removal of seedlings from the boxes.

The easiest and most economical way to thaw seedlings would be to keep them in the boxes they were stored in. However, doing this without any reductions in the physiological quality and subsequent field performance of seedlings requires more knowledge about how long and especially at what temperatures seedlings should or can be kept in the boxes. While high air temperatures would thaw frozen root plugs rapidly, they might also result in depletion of carbohydrates (Puttonen 1986, Silim and Guy 1998) and moulding (Hocking 1971), which suggests that the thawing period should be as short as possible. On the other hand, the time needed to thaw the root plugs may be too short to permit the frozen-stored seedlings to resume normal physiological processes before planting (Grossnickle and Blake 1985, Mattson and Troeng 1986).

3 AIMS OF THE STUDY

In this study, I investigated the risks related to the extension of the planting period of Norway spruce container seedlings from May to June and July. The first aim was to investigate the effect of drought and growth stage on outplanting performance of seedlings in early summer. The second aim was to investigate the effect of thawing practices on outplanting performance of frozen-stored seedlings used as stock material for an extended planting period. The main aims were divided into the following specific questions, to which I tried to find answers in the original articles:

i. What is the effect of pre- and postplanting drought on outplanting performance of actively growing seedlings planted in early July? (I, II, additional data)
ii. Is it possible to decrease the risk of plantation failure due to drought in late June by planting dormant seedlings instead of growing ones? (III)
iii. Is it risk free to plant frozen-stored seedlings without thawing either in cold (May–early June planting period) or in warm soil (June–July planting period)? (IV)
iv. What is the effect of different thawing durations and thawing temperatures on outplanting performance of frozen-stored seedlings planted in June? (V)

In this study, outplanting performance is defined by survival, root egress or height growth of seedlings measured after a given growing period in the greenhouse (IV), in the nursery field (I, II, III and V) or in the clearcut (V). Seedlings were considered growing (or actively growing) when shoots were elongating, and dormant when they possessed terminal buds without any visible sign of bud swelling or bud burst. In a strict physiological sense, ’’dormant’’ seedlings in this study were already in a quiescent stage (Grossnickle 2000), i.e. capable of breaking buds and resuming growth under favourable conditions.

4 MATERIAL AND METHODS

4.1 Seedlings, experimental sites, designs and treatments

The five articles (I, II, III, IV and V) of this thesis are based on seven different experiments (1, 2a and 2b, 3, 4, and 5a and b) carried out in Suonenjoki in central Finland during 1999-2003 (Table 1). Experiments were conducted with 1 or 1.5-yr-old Norway spruce container seedlings raised either at the nursery of Suonenjoki Research Station [62°39’ N, 27°03’ E, altitude 142 m a.s.l.] (exp. 1, 2a and b, and 3) or at a local commercial nursery [Fin Taimi Oy, Tuusniemi, 62°55’ N, 28°19’ E, altitude 102 m a.s.l.] (exp. 4, and 5a and b) according to normal culturing practices. Seeds were obtained from a registered seed orchard in Kangasniemi producing seeds adapted to conditions in central Finland. Seedlings were overwintered either in open hard plastic containers on an outdoor growing area under the natural snow cover or in cardboard boxes in frozen storage. In experiments, seedlings were exposed to different preplanting drying or thawing treatments, and then grown in a greenhouse, sandy nursery field or clearcut under exposure to different postplanting drought periods or soil temperatures (Table 1, Figure 3). The nursery field site (30 × 10 m) was covered with a transparent plastic rain shelter placed at a height of about 2 m to enable exposure of seedlings to postplanting drought periods. Soil temperature treatments were applied in refrigeration beds in the greenhouse. Randomized block design was used in experiments 1, 2a, 3, 5a and b, and complete factorial design in experiment 4.

During drought periods, the soil water content, measured with a portable TDR (time domain reflectometer), decreased from 3.2% to 2.1%, from 6.7% to 3.6% and from 4.8% to 2.6% in experiments 1, 2a and 3, respectively. Soil water content range in control plots was 13−18% (measured 2 h after irrigation), 8−13% and 9−11% (measured 24 h after irrigation) in experiments 1, 2a and 3, respectively. In experiment 4, the water content of the sand in the pots was increased from the initial 3% during the first 4 days to about 9% for the rest of the growing period.

4.2 Seedling measurements

In experiments 1, 2a, 3 and 4, seedlings were lifted after the growing period and visually rated as dead or alive by the presence of turgid green needles. Height growth of surviving seedlings was determined (± 1 mm) on the basis of the difference between initial and final height (both measured from the surface of the root plug to the terminal bud or meristem). Roots that had grown out from the root plug (root egress) of surviving seedlings were cut, washed and dried in an oven (48 h at 105 °C or 24 h at 60 °C + 24 h at 105 °C) and weighed (± 1 mg). In experiment 4, date for terminal bud burst (i.e. bud scales fully open and new needles visible) was also determined.

In experiment 1, shoot xylem water potential (Ψ_{shoot}) (additional data) and in experiment 3, Ψ_{shoot} and needle chlorophyll fluorescence (F_v/F_m -ratio) (Schreiber et al. 1994, Maxwell and Johnson 2000, Kaakinen et al. 2004) were measured before planting and after postplanting drought periods (1, 2, 3 and 4 weeks). In experiment 2b, Ψ_{shoot} was measured daily between 7 and 12 July on seedlings lifted to dry in the greenhouse. In experiments 1 and 2b, measurements were taken in the morning (0800−1000 h; midmorning shoot xylem water potential; $\Psi_{shoot\ mm}$) and in experiment 3 in the early morning (0500 h; simulated predawn shoot xylem water potential; $\Psi_{shoot\ pd}$) and in the afternoon (1400 h; daytime shoot xylem water potential; $\Psi_{shoot\ d}$) using a pressure chamber (Ritchie and Hinckley 1975). Seedlings used for measurement of $\Psi_{shoot\ d}$ were also used for measurement of the F_v/F_m -ratio.

In experiments 5a and 5b, the height of seedlings was measured immediately after planting and again in September 2001, 2002 and 2003. After each growing season seedlings were also visually rated as vigorous, weakened or dead based on the presence of turgid green needles.

Table 1. General description of the seedling material, pre- and postplanting treatments, planting dates, growing periods and experimental sites used in this study.

Exp. Year Article	Seedling age (yr.) / root plug vol. (cm^{-3})	Over-wintering conditions	Preplanting treatment	Planting date / growing period	Seedling / root plug status at planting	Post-planting treatment	Exp. site
1 1999 I	1.5 / 85	Out-doors	0, 4 or 8 day drying in green-house	5–8 July / 6 weeks	Growing / water content of root plugs 54–95, 40–75 and 16–64%	0–4 week drought + 6–2 week irrigation	Sandy field under rain shelter
2a 2000 II	”	”	0–13 day drying in green-house	5–6 July / 6 weeks	Growing / water content of root plugs 5–80%	0 / 6 week drought + 6 / 0 week irrigation	”
2b 2000 II	”	”	”	Not planted	–	–	–
3 2002 III	”	Frozen storage	Thawing 5 weeks or 5 days prior planting	24–28 June / 6 weeks	Growing or dormant / root plugs well watered	0–4 week drought + 6–2 week irrigation	Sandy field under rain shelter
4 2001 IV	1 / 66	”	7 hour or 4 day thawing at 9 °C	7 June / 5 weeks	Dormant / root plugs thawed or frozen	Soil temp. 9±1 or 18±1°C	Refrigeration beds in greenhouse, fine sand
5a 2001 V	”	”	7 hour or 4, 8 or 16 day thawing at 4 or 12 °C	14 June / 2.5 years	”	–	Patch-scarified Myrtillus-type clearcut
5b 2001 V	”	”	”	15 June / 2.5 years	”	–	Sandy field

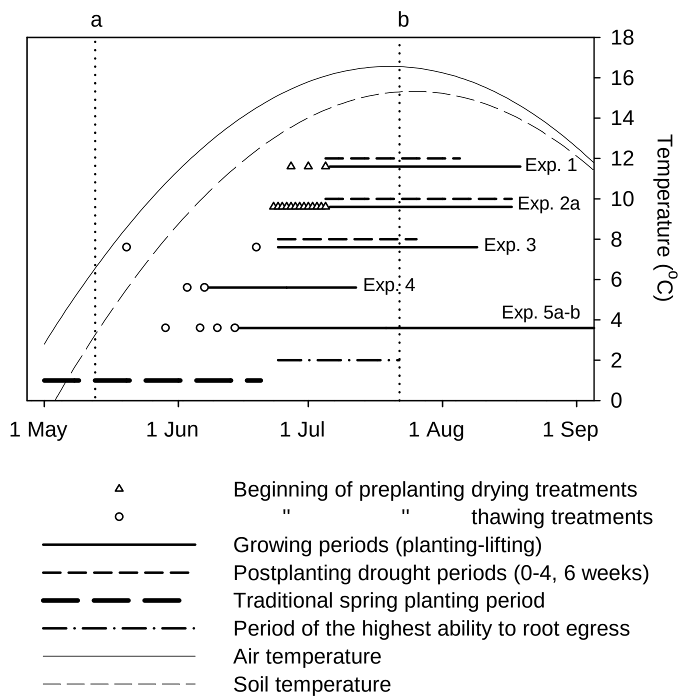

Figure 3. Line illustration of the timing of the growing periods and pre- and postplanting treatments in the experiments of this study in relation to 1) traditional spring planting period, 2) period of the highest ability to root egress, 3) estimated mean daily air (at 2 m) and soil (at a depth of 10 cm) temperatures in central Finland, and 4) the timing of the annual height growth of Norway spruce in central Finland. The period of highest ability to root egress is redrawn from Luoranen et al. (2001) and the temperatures are redrawn and modified from Luoranen et al. (2003). Dotted vertical lines indicate the dates when the long-term (1972–2003) average accumulative temperature sum (threshold value 5 °C) has reached the approximate values for height growth onset (a) (50 d.d.) and cessation (b) (about 700 d.d.) of Norway spruce in central Finland (Raulo and Leikola 1974).

4.3 Weather conditions

Air temperature and relative humidity were monitored with a thermohygrograph at the seedling shoot level (exp. 1, 2a, 3 and 4). Meteorological data was also obtained from the weather station database at the Suonenjoki Research Station. The summers of 1999 (exp. 1) and especially 2002 (exp. 3, 5a and b) were warmer than the long term average in Suonenjoki (Table 2). In summer 2000 (exp. 2a), 2001 and 2003 (exp. 5 a and b) monthly mean air temperatures and precipitation sums were close to the long term average (excluding high mean air temperatures in July in 2001 and 2003, and high precipitation in June 2000). Due to differences in the duration of overwinter storage, planting dates and weather, accumulative temperature sums (threshold value 5 °C) were 601, 508 and 358 d.d. for actively growing seedlings at the beginning of the growing periods in experiments 1 (1999), 2a (2000) and 3 (2002), respectively. Mean daily air temperature, relative humidity and vapor pressure deficit (VPD) during the growing periods were 17.3, 16.4, 18.6, 22 (°C), 66, 74, 61, 53 (%) and 1.9, 1.4, 2.3, 2.6 (kPa) in experiments 1, 2a, 3 and 4, respectively. Cumulative VPD, i.e. sum of daily mean VPD, was used to quantify the atmospheric drought over the time seedlings were exposed to in experiments 1, 2a, 3 and 4 (Figure 4) (cf. Berg and Chapin 1994).

4.4 Statistical analyses

Logistic regression (McCullagh and Nelder 1989) was used in the analysis of mortality and vigour (I and II), and nonlinear regression (Ratkowsky 1990) in the analysis of growth and water status (II) of the seedlings exposed to drought. Analysis of variance (ANOVA) (I, III, IV and V), Tukey’s and Dunnett’s test (I) and paired t-test (III) were used to analyze statistical differences between treatment means. Logarithmic and arc sine -transformations of values and proportions were made when necessary. Non-parametric Mann-Whitney U-test (III) and Kruskal-Wallis one-way analysis of variance (IV) were used when it was not possible to transform distributions to normal and homogenize variances. Additional xylem water potential data collected in 1999 was subjected to ANOVA. Differences between preplanting drying treatments were analyzed with paired t-test after each drought period.

Table 2. Mean monthly air temperatures (°C) and precipitation (mm) during the growing season (May–September) between 1999 and 2003, and a long term (1972–2003, except precipitation where 1975–2003) average (mean ± SD) at the Suonenjoki Research Station.

	Year / Month	1999	2000	2001	2002	2003	1972–2003
Temperature (°C)	May	6.4	9.2	7.6	10.8	10.1	9.0 ± 1.8
	June	18.4	14.1	14.2	15.7	12.0	14.4 ± 2.0
	July	17.3	16.6	18.7	18.3	19.9	16.7 ± 1.7
	August	13.4	13.9	14.6	17.1	14.3	14.2 ± 1.4
	September	10.6	8.2	10.4	8.7	10.0	9.0 ± 2.4
							1975–2003
Precipitation (mm)	May	50	30	55	32	56	39 ± 18
	June	49	115	61	105	72	69 ± 34
	July	92	87	81	73	68	82 ± 29
	August	25	90	80	48	81	76 ± 35
	September	38	23	74	36	28	58 ± 31
	Total	254	345	351	294	305	324 ± 53

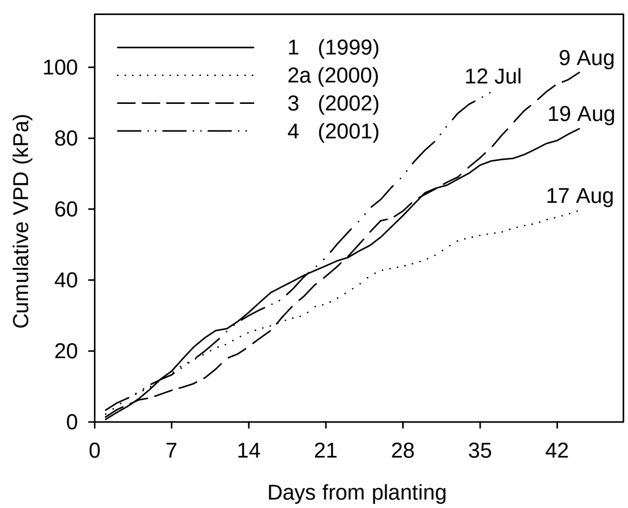

Figure 4. Cumulative mean daily vapor pressure deficit (VPD) during the growing periods in experiments 1, 2a, 3 (6 weeks) executed outdoors, and in experiment 4 (5 weeks) executed in the greenhouse. Dates of termination of the growing periods are given at the end of each curve. VPD is calculated on the basis of daily maximum and minimum air temperature and relative humidity.

5 RESULTS

5.1 Temporal variation in the water content of the root plugs after outplanting

The water content of the root plugs not exposed to preplanting drying was 70−80% at planting. Most of the irrigation water retained in the root plugs was depleted into the surrounding dry soil and transpired into the air in 3 or 4 days following planting (Figure 5, I). In most cases, the water content of root plugs decreased below 15% in one week and below 6% in four weeks after planting when seedlings received no irrigation. There was a considerable difference in the rate of rewetting of the root plugs after drought periods. In general, the longer the drought period and the drier the root plugs at the time of irrigation, the slower the rate of rewetting (Figure 5, I).

5.2 Effect of pre- and postplanting drought on actively growing seedlings

Preplanting drying of root plugs increased mortality of actively growing Norway spruce container seedlings planted in early July (Figure 6a). The decrease in the water content of the root plug below 7% was already lethal even before planting (II). Mortality of predried seedlings increased during postplanting drought periods as affected by soil water content at the time of the planting and cumulative VPD during drought periods (Figure 4 and 6a). However, mortality of well-watered seedlings exposed to drought periods of up to 3 weeks was relatively low (< 15%) regardless of the year (Figure 6a).

Preplanting drying of root plugs, as well as the lengthening of the postplanting drought period reduced height growth of actively growing seedlings planted in late June-early July (Figure 6b). On a percentage basis, height growth (in mm) was reduced less than root egress (in mg) when seedlings were exposed to the 4-week drought period compared to control seedlings (I and III). On the other hand, the decrease in the water content of the root plug below 10% at planting resulted in permanent cessation of height growth but not root egress during the 6-week drought period in 2000. Saturation of root plugs with water before planting was beneficial for height growth especially when seedlings were exposed to long drought periods after planting (I and II).

Root egress of actively growing seedlings decreased gradually along with the increase in the length of the postplanting drought period in 1999 and 2002 (Figure 6c). Exposure to the 4-week drought period resulted in approximately an 80% decrease in root egress compared to seedlings irrigated regularly in both years, although magnitudes were different. Despite the same length of drought periods and the same amount of subsequent irrigation, root egress of actively growing seedlings in 2002 was, in general, twice that of 1999 (Figure 6c). Contrary to 1999 and 2002, in 2000 root egress was on average higher in seedlings exposed to postplanting drought than in seedlings irrigated regularly.

In addition to postplanting drought, root egress was affected by the preplanting drying of root plugs, seedlings, or both, depending on edaphic and atmospheric conditions during drought periods (Figure 6c). In 1999, high water content of the root plugs at planting improved root egress especially when seedlings were exposed to long (3−4 weeks) postplanting drought periods. Instead, in 2000, root egress was affected only when the water content of the root plugs decreased below the threshold value (20%) before planting, where the seedling water status was also affected (II).

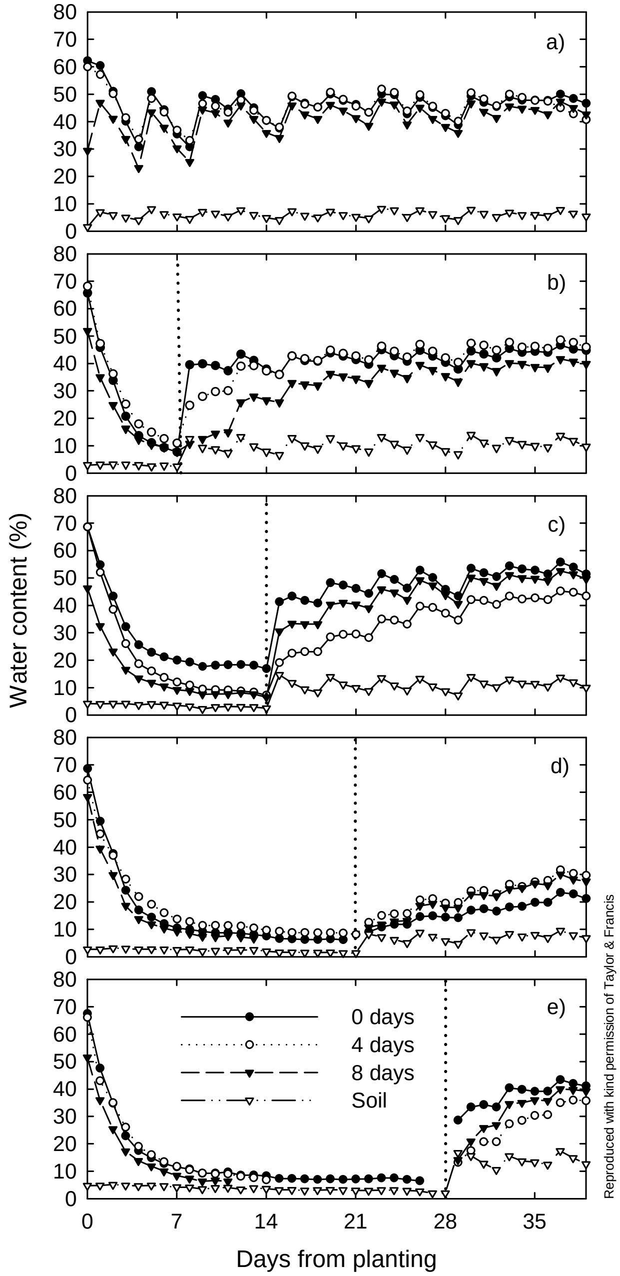

Figure 5. Changes in the water content of soil and root plugs in seedlings exposed to 0-, 4-, and 8-day preplanting drying treatments in control plot (0-week postplanting drought period, panel a) and in plots exposed to 1-, 2-, 3- and 4-week postplanting drought period (panels b-e, respectively). After the drought periods, plots were irrigated twice a week with 16 mm tap water until the end of the experiment (dotted vertical line = first irrigation). From article I.

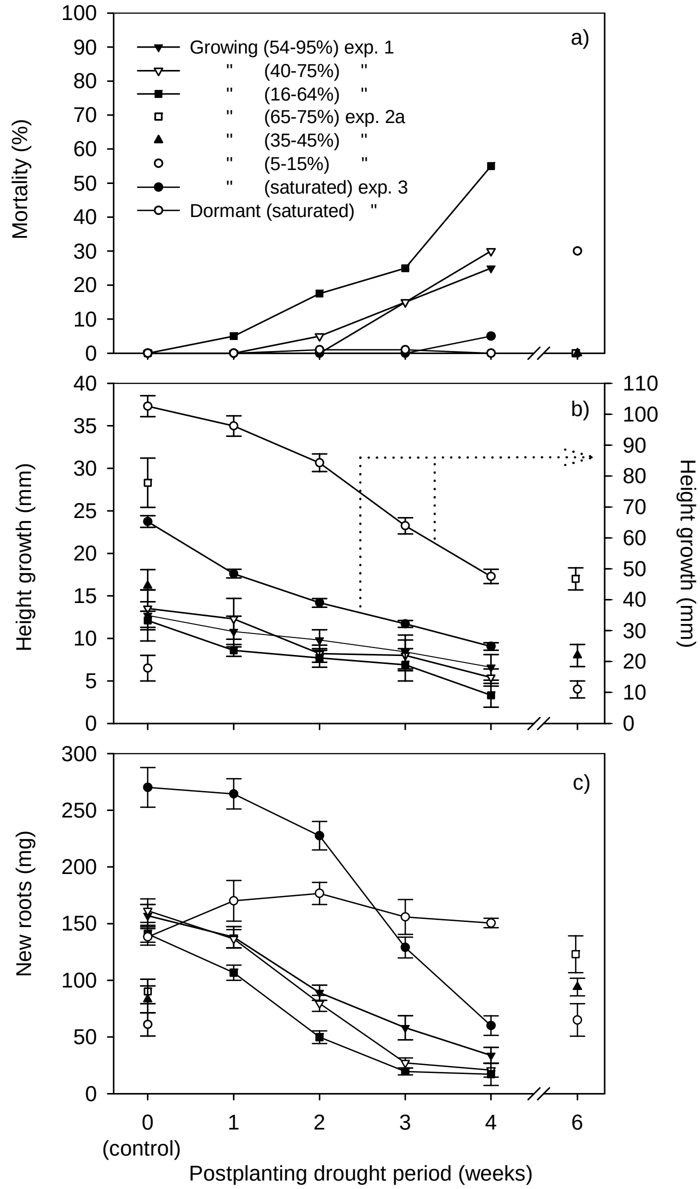

Figure 6. Mortality (a), height growth (b) and root egress (c) of Norway spruce seedlings planted while growing (exp. 1, 2a and 3) or dormant (exp. 3), when exposed to different postplanting drought periods during the 6-week growing period. Water content (v/v) of the root plugs at planting is given in the brackets in the legend. After drought periods, seedlings were irrigated twice a week so that the drought period plus irrigation lasted 6 weeks (i.e. 1-week drought period + 5-weeks irrigation etc.). Due to large year to year variation, height growth in experiment 3 is plotted against a secondary y-axis (indicated by dotted arrow). Vertical bars indicate the standard error of the mean. Redrawn from articles I–III.

There was no difference in the preplanting $\Psi_{shoot\ mm}$ of seedlings dried 0 or 8 days in the greenhouse in 1999 (Figure 7). Corresponding water contents of the root plugs were 79% and 40%. Similarly in 2000, preplanting drying of root plugs from a water content of 80% to 30% had only a slight effect on $\Psi_{shoot\ mm}$ (−0.7 and −0.9 MPa, respectively) (Figure 8, model 1 in II). However, a further decrease below 30% resulted in a steep decline in $\Psi_{shoot\ mm}$ reaching −1.5 MPa at a water content of 15% and a lethal −2.8 MPa at approximately 7% (Figure 8, II).

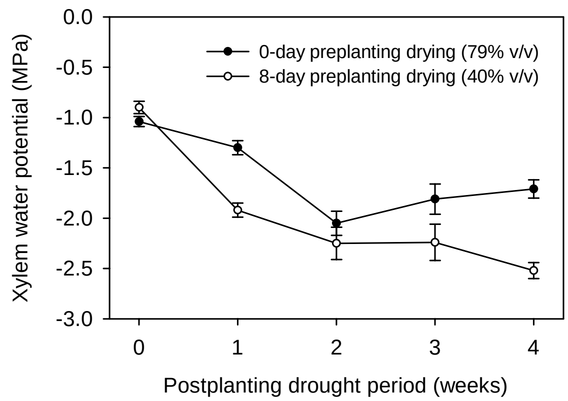

Figure 7. Shoot xylem water potential of seedlings exposed to 0- and 8-day drying treatments before planting (0) and after 1, 2, 3 and 4 weeks of drought (the number of observations were 10 / 10, 9 / 10, 9 / 8, 10 / 9 and 8 / 6, respectively). Measurements were taken in the morning (0800–0900 h; $\Psi_{shoot\ mm}$). Vertical bars indicate the standard error of the mean. Data was collected during experiment 1 (1999) and is presented here as additional data.

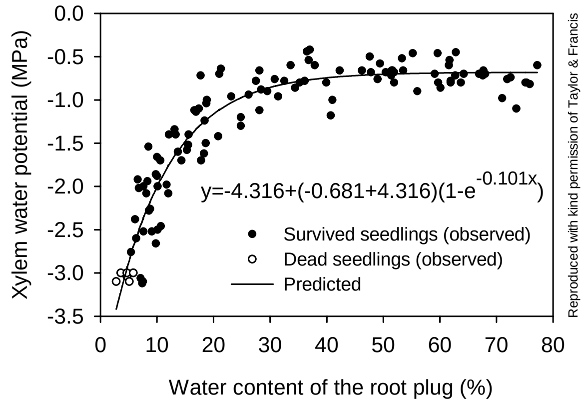

Figure 8. Observed and predicted response of the xylem water potential ($\Psi_{shoot\ mm}$) and observed survival of Norway spruce container seedlings to the decreasing water content (v/v) of the root plug. After the water potential measurement, root plugs were rewetted in a water tub for two hours and then irrigated regularly in the greenhouse for two weeks. Thereafter seedlings were visually rated as dead or alive based on the presence of turgid green needles on the branches. From article II.

Following planting, $\Psi_{shoot\ mm}$ of seedlings dried 8 days prior planting in 1999 declined considerably already after the first week of drought. However, after the second week of drought, $\Psi_{shoot\ mm}$ was again almost equal with that of seedlings dried 0 days before planting. From that point on (i.e. after the third and fourth week of drought), $\Psi_{shoot\ mm}$ diverged in these groups (Figure 7). Seedlings planted with saturated root plugs (0-day drying) had grown a small amount of new roots during the 4-week drought period, whereas no new root growth occurred in seedlings dried 8 days before planting (data not shown).

5.3 Effect of growth stage and postplanting drought on outplanting performance

Frozen storage duration of 30 weeks at –3.5 °C resulted in a 24% depletion in soluble sugar concentration of needles but had no effect on starch concentration (III). However, the prolongation of the frozen storage from 30 to 34 weeks to keep seedlings dormant until planting had no observable effect on sugar or starch concentration (Figure 9).

Survival, root egress and needle F_v/F_m -ratio of dormant seedlings were unaffected by the postplanting drought periods (III). In addition, $\Psi_{shoot\ pd}$ of dormant seedlings remained at a rather constant level during 1-, 2- and 3-week drought periods. Instead, in growing seedlings, both F_v/F_m -ratio and $\Psi_{shoot\ pd}$ declined rapidly after the 3-week drought. However, when seedlings were not exposed to drought, root egress for seedlings that were growing at planting was twice that for dormant seedlings. The benefit from planting dormant seedlings to root egress was apparent only when seedlings were exposed to 3- or 4-week drought periods (Figure 6c). There was also a significant interaction between the growth stage of the seedlings and postplanting drought on root egress, $\Psi_{shoot\ pd}$ and $\Psi_{shoot\ d}$, and F_v/F_m -ratio (Figure 1 and 2 in III).

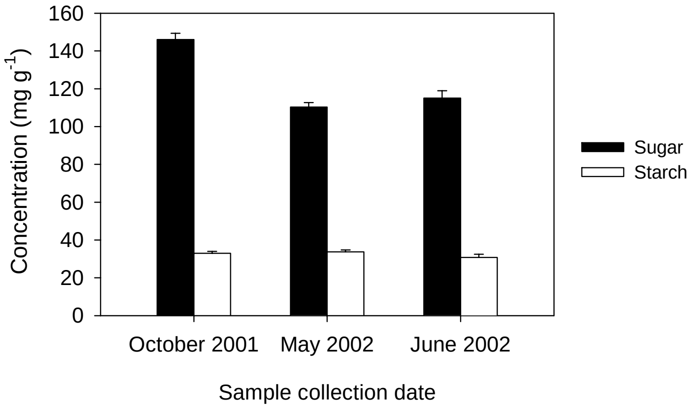

Figure 9. Effect of frozen storage duration on needle sugar and starch concentration (mg g^{-1} dry weight). Needle samples were collected on three occasions: (I) 23 October 2001, before the seedlings were placed into frozen storage, (II) 20–22 May 2002, after the 30-week storage, and (III) 19–21 June 2002, after 34-week storage. Vertical lines indicate the standard deviation. Drawn from article III.

Due to the 4-week difference in frozen storage duration, dormant seedlings were about 9 cm shorter than growing seedlings at the time of planting (Figure 1b in III). Height growth decreased almost linearly along with the increase in the length of postplanting drought period, both in dormant and growing seedlings. Despite weak significant ($p=0.043$) interaction between growth stage and postplanting drought on height growth, in general, height growth in dormant seedlings was twice that for growing seedlings during the 6-week growing period.

5.4 Thawing methods and outplanting performance of frozen-stored seedlings

Thawing rate of the root plugs of frozen-stored seedlings varied greatly within the tray. When thawed at 9 °C, time needed for complete thawing of the root plugs (as indicated by rapid increase in root plug temperature) was threefold (over 30 hours) in the middle of the tray compared to the root plugs at the edge of the tray (Figure 1 in IV). Similarly, when thawed at 4 °C, only the root plugs in the middle of the tray were still frozen after 4 and 8 days (V). Extended thawing period (16 days) indoors at 12 °C resulted in growth of mould, which disappeared soon after planting (V).

Planting seedlings with frozen root plugs increased mortality (IV and V, except in the clearcut), delayed bud burst and retarded root egress and height growth (Figure 10a-d). The negative effect of frozen planting on root egress and height growth increased in cold soil (9 °C) compared to warm soil (18 °C) (Figure 10c and d). Survival rate and days to bud break were however, similar at both soil temperatures. In cold soil, root egress was strongly retarded whether seedlings were frozen or thawed when planted, and especially in seedlings planted with frozen root plugs root egress was almost negligible (Figure 10c). Height growth of thawed seedlings was the same in cold and warm soil.

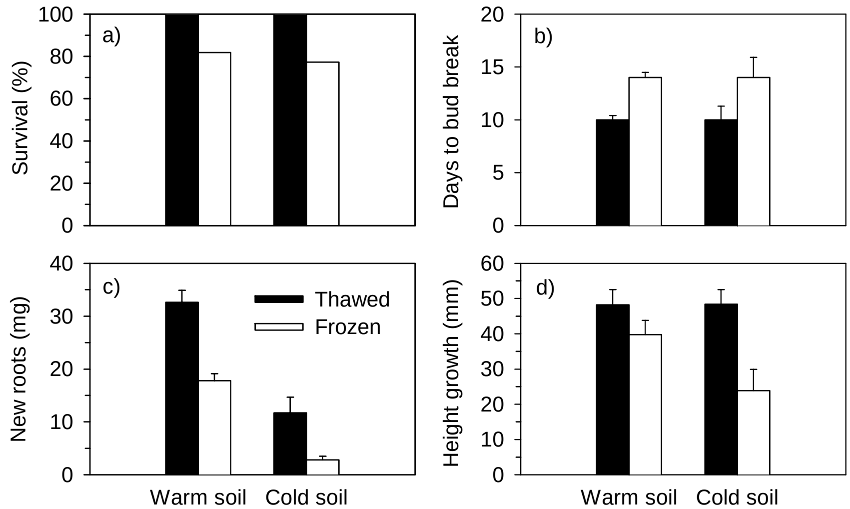

Figure 10. a) Survival, b) days to bud break, c) new root growth (root egress) and d) height growth of frozen-planted and thawed Norway spruce container seedlings (thawing period in thawed seedlings 4 days and in frozen-planted seedlings 7 hours at 9 °C) during the 5-week growing period in warm (18 ± 1 °C) and cold (9 ± 1 °C) soil (mean ± SE). After 7 hours thawing (frozen-planted seedlings), no sign of softening was detected in the root plugs, but they could be separated without any visible damage to the roots. From article IV.

6 DISCUSSION

6.1 Outplanting performance under drought in early summer

In this study, the effect of postplanting drought on seedling performance was examined outdoors in 1999 (I), 2000 (II) and 2002 (III). As could be expected, there was a large variation in weather conditions before and during growing periods, resulting in different degrees of soil drought and atmospheric evaporative demand outplanted seedlings experienced during these years. For example in 1999, soil was exceptionally dry at the time of planting due to low precipitation before the nursery field site was covered with a plastic rain shelter, whereas in 2002 and especially in 2000 soil water content was higher. The weather during drought periods was warm and dry in 1999, but relatively cool in 2000, excluding the first week of drought treatment. In 2002 the weather was cool for 9 days from planting but got very warm during the rest of the growing period. Zweifel et al. (2005) showed that in adult trees water deficit can be well estimated with soil water potential and atmospheric VPD, although radiation and wind are also always involved (Baig and Tranquillini 1980, Simpson 2000, Zweifel et al. 2002). Quantifying the degree of atmospheric evaporative demand by means of cumulative VPD shows that the 4-week drought periods in 1999 and 2002 were as severe as the 6-week drought period in 2000, i.e. cumulative VPDs were equal (Figure 4). When the degree of initial soil drought (i.e. soil water content) is also taken into account, it can be estimated that in this study the most severe drought stress occurred in 1999 and least severe drought stress occurred in 2000.

Large variation in environmental conditions at the beginning and during drought periods between the experiments of this study provides an excellent opportunity to assess the chances to successfully extend the planting period of Norway spruce container seedlings. The most severe edaphic and atmospheric conditions during the 4-week drought period encountered in the experiments of this study resulted in 25% mortality for well-watered, actively growing seedlings planted in early July, and twice that for seedlings dried for 8 days before planting (1999). On the other hand, only an average of 6% of the seedlings grown in the field for 6 weeks without irrigation were dead when planted in early July in relatively moist soil and exposed to low levels of atmospheric drought (2000). In addition, the 6-week drought period was lethal only when the water content of the root plugs of seedlings was below 10% and seedlings were already suffering from water stress at the time of the planting. Accordingly, when no preplanting drying was applied for actively growing seedlings in 2002, only 5% of the seedlings planted 2 weeks earlier than in 1999 and 2000 were dead after 4 weeks of drought. These results indicate that actively growing seedlings planted in moist soil have a good chance of surviving drought periods normally occurring in central Finland in July and August. However, it should be noted that survival of a single drought period after planting does not guarantee successful future field performance, if for example root growth during drought is strongly reduced.

Equal $\Psi_{shoot\ mm}$ of seedlings dried for 0 and 8 days before planting in 1999 indicates that the 8-day drying failed to induce water stress to seedlings (Figure 7). In fact, the water content of the root plugs dried for 8 days (34%) was only slightly below the recommended ranges of the water content of the peat based growth media for growing seedlings at the nursery (Puustjärvi 1977, Heiskanen 1995, Lamhamedi et al. 2001). This failure actually motivated the experiment carried out in 2000, which then showed that the $\Psi_{shoot\ mm}$ declines markedly only after the water content of the root plug decreases below 30% (II). However, water stress was indeed induced in seedlings dried 8 days before planting already during the first week of drought period as indicated by a steep decline in $\Psi_{shoot\ mm}$ (Figure 7). This decline can be attributed to the depletion of initially small water storage of the root plug due to high evaporative demand during the first two weeks of the growing period, and water movement from the root plug to the surrounding dry soil. On the other hand, saturation of the root plugs with water before planting resulted in a postponed decline in Ψ_{shoot} (Figure 7) accompanied by lower mortality and smaller reductions in height growth and root egress during drought periods compared to seedlings with non-saturated root plugs (Figure 6a-c). In fact, after the initial decline, $\Psi_{shoot\ mm}$ of seedlings planted with saturated root plugs seemed to increase slightly during the 3 and 4 week drought (Figure 7), which was probably attributed to the growth of new roots into the soil to enable water uptake. For example, in pine species it has been reported earlier that a relatively small amount of new root growth can significantly improve seedling water relations (Brissette and Chambers 1992) and increment of total fresh weight (Rose 1992) following planting. In this study, actively growing seedlings began to die when $\Psi_{shoot\ mm}$ reached −2.8 MPa, which is close to that (−3 MPa) reported earlier by Christersson (1976) for both Norway spruce and Scots pine seedlings.

Results from the temporal variation in the water content of the root plug after planting are in accordance with those reported earlier by Day and Skoupy (1971) and Heiskanen and Rikala (2000). When it comes to the available water for seedlings in the root plugs following planting, benefit gained from the saturation of root plugs with water before planting is short-lived. For example, most of the irrigation water retained in the root plugs was released into the soil in 3 or 4 days after planting in the present study (I). However, water release from the root plugs and corresponding water gain in the surrounding soil could promote rapid root growth out from the root plug as was suggested by Heiskanen and Rikala (2000). This, together with postponed induction of water stress following planting (Figure 7), could account for the greater root growth in seedlings planted with saturated root plugs compared to seedlings dried 8 days before planting, especially during long drought periods (Figure 6c).

Dry root plugs can also absorb water from the surrounding soil after planting if a sufficient hydraulic gradient prevails between soil and the medium and if there is good soil - root plug contact (Heiskanen 1999, Heiskanen and Rikala 2000). This was probably the reason for the minor effect of increasing water content of the root plug on root growth and mortality even in plots receiving no irrigation during the growing period in 2000 (II). It is possible that if the soil had been drier (< 6.5%) at the time of the planting (dry enough to prevent any absorption of water from the soil), the initial water content of the root plugs would have affected seedling outplanting performance more. In addition to the hydraulic gradient between the root plug and the soil, the rate at which the root plug absorbs water can be affected by the water repellency and other physical properties of root plug media (Heiskanen 1993a, Heiskanen 1999). Water repellency was probably one reason for the great variation found in the rate of rewetting when irrigation was applied after the drought periods (Figure 5). Considering the abundant irrigation (15 mm twice a week) seedlings received, poor rewetting of dry root plugs after drought may be of great concern when it comes to the survival of seedlings on actual reforestation sites.

Root egress was strongly retarded when actively growing seedlings were exposed to postplanting drought periods in late June-early July (I and III). In both experiments, actively growing seedlings had increased shoot to root ratios (Table 1 in III) and succulent new shoots at the time of the planting. Consequently, actively growing seedlings had for example more transpiring needle area than dormant seedlings (III), and they were probably not readily able to control water loss through needles (both stomas and cuticles) during the first few weeks after planting. For example, Blake (1983) found that needles in the new shoot transpired 4 to 5 times the rate found in older needles of white spruce seedlings. Hallgren and Helms (1988) reported that in white fir [*Abies concolor* (Gord. and Glend.) Lindl.] and red fir (*A. magnifica* A. Murr.) rapid development of moisture stress under an unwatered regime during the second growing season in the field occurred at the same time that seedlings were expanding the spring flush. In spruce needles, complete cuticular development takes a minimum of 3 months after budburst (Tranquillini 1979). Thus, the rate of water loss from the seedlings is likely attributable to the variation in atmospheric evaporative demand. In 1999 VPD was higher during the first two weeks after planting than in 2002 (Figure 4), which resulted in a more rapid decline of Ψ_{shoot} (Figure 7) and thus more rapid induction of growth limiting water stress than in 2002 (Figure 2a in III). This may partly explain the marked difference in root egress of actively growing seedlings between the two years. The difference in root egress may also relate to the natural growth rhythm of roots. At the beginning of the growing period in 1999, the ability of actively growing seedlings to root egress was already at its seasonal maximum and started to decline (Luoranen et al. 2001, Kaakinen et al. 2004). In 2002, seedlings were planted two weeks earlier than in 1999, which together with frozen storage until 20–24 May resulted in lower accumulated temperature sum prior to planting than in 1999. Thus it is possible that the timing of the entire 6-week growing period in relation to the ability to grow roots was more favourable in 2002 than in 1999. A third possible explanation for the difference in root egress is spring frost (-10 °C at soil surface level) which occurred in early May 1999 that might have damaged the root systems of seedlings stored outdoors (cf. Bigras and Hébert 1996). For example, part of the seedlings reserved for the experiment lost their terminal bud because of the frost and had to be replaced. Had there been severe spring frosts in early May also in 2002, possible damages could have been avoided because seedlings planted actively growing were kept in frozen storage until 20 May (cf. Kohmann 1991).

The response in the growth of seedlings to postplanting drought was more evident (on a percentage basis) in new root dry mass than in height growth when actively growing seedlings were planted in early July (I and III). Although the change in height growth of seedlings due to drought can not be directly compared with that of new shoot dry mass, it seems likely that also new shoot dry mass was much less affected than new root dry mass. For example, in the study of Roberts and Cannon (1992) a 33% decrease in height growth of red spruce (*Picea rubens* Sarg.) seedlings due to drought induced at bud break corresponded to a 21% decrease in new-shoot dry mass. However, in their study, root dry mass was somewhat less in drought-stressed seedlings than in well-watered seedlings, but the differences were not significant. On the other hand, when 2-yr-old red spruce container seedlings were exposed to 11 weeks of water stress 7 weeks after bud break, root dry mass was reduced more than shoot dry mass (Seiler and Cazell 1990). In the present study, greater reduction in root growth compared to height growth in response to drought may simply be attributed to the timing of water stress in relation to the growth dynamics of shoot and roots (cf. McMillin and Wagner 1995), i.e. there was proportionally more seasonal potential belowground growth left to be affected by water stress than aboveground growth at the beginning of the drought periods in early July.

Growth stage of seedlings at planting had a major impact on outplanting performance in the present study. Seedlings that were growing at planting showed much greater root egress than dormant seedlings when irrigated regularly or exposed to only short drought periods (1−2 weeks) after planting (III). On the other hand, height growth of dormant seedlings was, in general, twice that for growing seedlings during the 6-week growing period regardless of the drought period. It seems evident that this is due to the different timing of shoot and root growth. After budbreak, provided that seedlings are not exposed to drought severe enough to affect growth and translocation of photosynthates, the shoot is the primary sink of photosynthates, which results in increased shoot growth and decreased root growth (Kramer and Kozlowski 1979). Instead, in growing seedlings, allocation of photosynthates to roots probably increased during the 6-week growing period. For example Kaakinen et al. (2004) found a considerable increase in root biomass simultaneously with ceasing stem elongation after mid-July in 1-yr-old hydroponically grown Norway spruce seedlings that had initiated stem elongation in early June. Rapid height growth together with reduced root egress in dormant seedlings during the growing period also indicates that the normal growth rhythm was not affected during the prolonged (34 weeks) frozen storage.

The decrease in the concentration of soluble sugars in needles during the frozen storage was smaller than reported by Ritchie (1982) and Jiang et al. (1994), but is probably mainly attributed to the lower storage temperature used in the present study (III). For example Wang and Zwiazek (1999a) found significantly higher total non-structural carbohydrate (sugar + starch) levels in white spruce needles and roots stored 7 months at −4 and −6 °C compared to seedlings stored at −2 °C. Lack of any differences in needle sugar and starch concentration between seedlings stored for 30 and 34 weeks in the present study indicates that such prolongation of frozen storage is safe at least when it comes to the carbohydrate reserves at storage temperatures close to −3.5 °C. In addition, in the study of Jiang et al. (1994) the largest decline in needle sugar concentration occurred during the first 12 weeks of cold storage. Jiang et al. (1994) also postulated that the decline in needle sugar concentration is not completely attributable to respiratory consumption, but also to the conversion of sugar to starch. Thus, the effect of long frozen storage on carbohydrate reserves may not be as detrimental as could be expected on the basis of the decrease in soluble sugar concentration alone. However, prolonged frozen storage would eliminate any restoration of carbohydrate reserves prior to planting observed in outdoor-stored seedlings early in spring when photosynthesis recover (Wang and Zwiazek 1999b, 1999c).

When actively growing and dormant seedlings were exposed to drought after planting, root egress of actively growing seedlings decreased considerably, whereas root egress in dormant seedlings was rather insensitive to drought (III). In fact, root egress of dormant seedlings increased slightly by short (1−2 weeks) exposure to drought (Figure 6c). It is possible that a short period of low soil water content stimulates root egress of newly planted seedlings, at least as long as severe water deficit is avoided. Correspondingly, constant high soil water availability near the root plug may reduce the need for rapid root egress (cf. Livingston and Black 1988). This observation is reinforced by the smaller root egress (on average) for actively growing seedlings in wet soil compared to dry soil in 2001 (II). Similarly, Brand (1991) reported that as availability of a particular resource (e.g. water, nutrient or light) improved for newly planted spruce seedlings, growth allocation was shifted away from tissues that are used to acquire that resource.

6.2 Outplanting performance and thawing methods

Results of planting seedlings with their root plugs still frozen were contradictory in this study. When frozen seedlings were planted in dry soil in the greenhouse environment, mortality increased and both height and root growth decreased compared to seedlings planted with thawed root plugs (Figure 10). In addition, low soil temperature increased the negative effect of frozen-planting on subsequent height and root growth. However, when frozen seedlings were planted outdoors, field performance was adversely affected only in the nursery field but not in the clearcut (V). The result from the clearcut is in accordance with the findings of Kooistra and Bakker (2001). In their study, no major differences were found in field performance between frozen-planted and thawed lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var. *latifolia* Engelm.), western larch (*Larix occidentalis* Nutt.) and interior spruce container seedlings, except for bud break and height growth of western larch under irregular watering regime. However, poor height growth of frozen-planted western larch was concluded to result from the smaller amount of irrigation (i.e. drought stress) compared to thawed seedlings, rather than the effect of the frozen root plug as such. The contradiction in the present study may be partly explained by the differences in edaphic conditions frozen seedlings were exposed to in the greenhouse (IV) and in the nursery field and clearcut (V). In the greenhouse, the water content of the sand was low for four days after planting. Consequently, the thermal conductivity of the sand was also low (Grossnickle 2000), which probably delayed the thawing of the root plugs and caused increased mortality and reduced growth. Instead in the nursery field and in the clearcut the soil was initially wet due to rain showers on the days preceding planting. In the clearcut, soil water content (although not measured) probably also remained higher due to finer soil texture compared to the nursery field, which could explain the difference in mortality of frozen-planted seedlings between the two sites. When it comes to the frozen-planting in general, one potential problem is the shrinkage of the root plugs that must necessarily occur upon thawing. This shrinkage may then result in poor hydraulic conductivity between the root plug and the soil, and further, reduced outplanting performance of seedlings.

Lower soil temperature (9 °C) used in study IV corresponds to that encountered in central Finland at the end of May (Figure 3). Root growth at this temperature was considerably reduced whether seedlings were thawed or frozen at planting, confirming previous and recent findings for several conifers (Tabbush 1986, Lopushinsky and Max 1990, Balisky and Burton 1997) also including Norway spruce (Vapaavuori 1992, Heiskanen 2005). On the other hand, low soil temperature had no effect on height growth of thawed seedlings (Figure 10d). This together with a lack of any visible wilting of succulent new shoots even during warm and sunny days indicates that water uptake, and seedling water balance, were not seriously affected by the low soil temperature as such. Dang and Cheng (2004) reported rapid increase in mid-day xylem water potential along with the increase in soil temperature from 5 to 10 °C, but only moderate increase from 10 to 15 °C for white and black spruce [*Picea mariana* (Mill.) B.S.P.] seedlings growing in the greenhouse. It should be noted, however, that the potential transpiration in the greenhouse during the growing period in this study might not have been high enough to reveal the adverse effect of low soil temperature on seedling water balance (cf. Rikala and Puttonen 1988). In addition, after the initial short-term drought, seedlings received abundant irrigation for the rest of the growing period. Insofar as reduced root growth must eventually translate into reduced ability to take up water in relation to the increased surface area exposed to loss of water (due to unaffected height growth), desiccation may occur in seedlings planted in cold soil especially under conditions of low soil water availability and/or high radiation and wind present on actual reforestation sites.

Excluding the frozen-planting, no clear differences were found in the long-term outplanting performance between seedlings exposed to different thawing duration and thawing temperature treatments (V). It appears that the physiological quality of frozen-stored seedlings is not likely to be reduced during thawing at relatively low temperatures (≤ 12 °C) to affect outplanting performance, provided that ventilation is ensured in seedling boxes to prevent the growth of mould. Although the highest thawing temperature (12 °C) used in study V was chosen to represent the mean outdoor air temperature in the end of May in central Finland, the results may not be readily applicable to thawing seedlings outdoors due to diurnal variation in air temperature and solar radiation. Further studies should focus on thawing seedlings outdoors, since frozen storage facilities, where temperature can be adjusted, are not normally available for thawing purposes, especially in the case of prolonged storage. It is likely that the rate of thawing in boxes will vary considerably with specific conditions (local temperature, irradiance, rain, ventilation, positioning etc.) and resulting heat flux.

6.3 Constraints of the study and needs for further research

All experiments in the present study, excluding 5b, were carried out in conditions that differ from those encountered on actual reforestation sites. For example reduced solar radiation under the rain shelter probably reduced seedling transpiration, which may have decreased water stress and mortality during long drought periods in experiments 1, 2a and 3 (cf. Kaufmann 1979, Livingston and Black 1988). However, when it comes to the outplanting performance under available soil water, Khan et al. (2000) reported only minor changes in morphological and physiological parameters of several conifers grown in 35% shade compared to full sunlight. Similarly, Dehlin et al. (2004) found that shading even up to 70% of the average PAR had no effect on height growth of Norway spruce seedlings during a 22–27 week growing period in a climate chamber. However, they did report decreased root growth for Norway spruce seedlings under the shade. In the present study, seedlings were also grown completely free from competition for water, nutrients and light, which has been shown to affect growth and survival of newly planted spruce seedlings (Brand 1991, Fleming et al. 1994, Nilsson and Örlander 1999, 2003, Archibold 2000, Thiffault et al. 2003). On actual reforestation sites, ground vegetation is usually controlled by soil scarification during the previous year to allow soil stabilization in mounds during winter. However, invasion or regrowth of ground vegetation may occur by early July in the year of planting, especially on rich sites with dense ground vegetation present prior to clearcutting (Nilsson and Örlander 1995).

The outcome of ground vegetation regrowth on a reforestation site can be twofold: depletion of available soil water in the rooting zone may increase the risk of water stress for seedlings planted in July, whereas decreased evaporative demand due to shading and reduced wind speed may decrease it (cf. Jobidon et al. 1998). Thus, if the traditional planting period is to be extended to June and July, the timing of soil scarification as well as the choice of soil scarification method itself needs further investigation. For example, Bassman (1989) found that the positive effects of improved soil temperatures and root growth in mounds were negated to a large extent by increased water stress during the first two growing seasons following planting. Assuming it is more important to decrease the risk of low rather than excess soil water following planting, for example inverting might provide more favourable edaphic conditions for extended planting period than mounding (cf. Hallsby and Örlander 2004).

The growing periods in the experiments of this study, excluding 5a and b, were rather short. Consequently, the results of this study may have provided only suggestive information about the long-term success of Norway spruce container seedlings planted in June and July on actual reforestation sites. It may take two or three years before the response to any given cultural treatment appears (cf. Johansson 2004). For example, drought has been shown to decrease the number of needle primordia in the developing buds (Pollard and Logan 1977, 1979, Hallgren and Helms 1988, Khan et al. 1996), which has a direct bearing on the second year height growth potential through predetermined growth (Grossnickle and Folk 2003). Considering the differences in root egress and final heights between dormant and growing seedlings after the experiment (III), it is likely that the dormant seedlings have the potential to catch up on actively growing seedlings only if unusually long dry periods occur after planting.

7 CONCLUSIONS

The results of this study suggest that there is minimal risk of excessive mortality occurring due to drought when well-watered, actively growing Norway spruce container seedlings are planted in late June - early July, provided that the soil is not exceptionally dry at the time of the planting. Preplanting drying of root plugs and especially seedlings, and long postplanting drought periods reduced survival, height and root growth of seedlings following planting, largely depending on the water content of the soil at planting and atmospheric evaporative demand during postplanting drought periods.

Prolonged frozen storage (from 30 to 34 weeks) in cardboard boxes at −3.5 °C was a useful method, with no observable negative effect on seedling carbohydrate reserves, to maintain dormancy until planting in late June**.** Dormant seedlings showed less reduction in root growth, Ψ_{shoot} and F_v/F_m -ratio in response to postplanting drought than actively growing seedlings from the same stock. However, when it comes to root growth, the benefit from planting dormant seedlings instead of growing ones is realized only if very long dry periods (3 weeks or longer) occur after planting.

Planting frozen Norway spruce container seedlings at soil temperatures normally prevailing in spring or early summer in central Finland may adversely affect the outplanting performance especially if soil is dry at the time of the planting. A 4 to 8 day thawing period at 9 - 12 °C was long enough for frozen-stored container seedlings to be thawed and ready for planting.

Considering the short study periods used in the present study, the shelter effect, year to year variation in weather conditions, and the variation in edaphic conditions encountered on actual reforestation sites, these results can be considered only suggestive in Finnish conditions. Further studies on actual reforestation sites with different soil scarification methods and schedules are needed to ascertain the effect of drought and thawing practices on seedling outplanting performance in the long run.

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