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Effect of Physiological Status on the Cold Storage Tolerance and Field Performance of Ash, Oak and Sycamore in Ireland

By

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With 4 Figures

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Summary

O'REILLY C., MORTAZAVI M. & KEANE M. 2003. Effect of physiological status on the cold storage tolerance and field performance of ash, oak and sycamore in Ireland. – Phyton (Horn, Austria) 43 (2): 335–350, with 4 figures. – English with German summary.

The relationship between physiological condition at the time of lifting and cold (1 °C) tolerance was investigated in ash (*Fraxinus excelsior* L.), sycamore (*Acer pseudoplatanus* L.) and oak [*Quercus petraea* (MATT.) LIEBL.] seedlings lifted in the nursery in Ireland in 1996/97. Cold storage reduced bud dormancy intensity to less than a few days in all species and lift date effects were small. Cold storage increased or had little effect on xylem pressure potential (Ψ) in most cases, probably because it helped to release or maintain dormancy levels. However, cold storage decreased Ψ in a few cases, perhaps because the plants lost water while in storage. Cold storage greatly increased root growth potential (RGP) or maintained a high RGP compared with values at the time of lifting in ash and sycamore, but had little effect in oak. Fine root electrolyte leakage (REL) was higher or about the same after cold storage as

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at the time of lifting in all species. The RGP and REL results indicated that there was little deterioration in root quality during storage. Ash and oak lifted to cold storage from December to March performed well in the field, although not as well as those freshly planted on some dates. Sycamore grew relatively poorly after planting, regardless of storage date.

Zusammenfassung

O'REILLY C., MORTAZAVI M. & KEANE M. 2003. Einfluss des physiologischen Zustandes von Esche, Eiche und Ahorn auf die Toleranz der Kältelagerung und deren Leistungsfähigkeiten im Freiland in Irland. – Phyton (Horn, Austria) 43 (2): 335–350, 4 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die Zusammenhänge zwischen physiologischem Zustand zur Zeit des Ausgrabens (Ernte) und der Kältetoleranz (1 °C) wurden bei Sämlingen von Esche (*Fraxinus excelsior* L.), Ahorn (*Acer pseudoplatanus* L.) und Eiche [*Quercus petraea* (MATT.) LIEBL.] untersucht, welche in einer Baumschule in Irland 1996/97 geerntet wurden. Die Lagerung bei Kälte verminderte die Intensität der Knospenruhe bei allen Arten auf wenige Tage und das Erntedatum hatte nur geringen Einfluss. Kältelagerung ließ das Xylemwasserpotential (Ψ) ansteigen oder hatte in den meisten Fällen nur geringe Auswirkungen, wahrscheinlich deshalb, da sie dazu führte, entweder die Ruhe aufzugeben oder beizubehalten. In einigen Fällen nahm Ψ jedoch nach Kältelagerung ab, was vermutlich auf Wasserverluste während der Lagerung zurückzuführen war. Kältelagerung steigerte stark das Wurzelwachstumspotential (RGP) oder hielt ein hohes RGP im Vergleich mit Werten zur Zeit der Ernte in Esche und Ahorn aufrecht, bei der Eiche war kaum ein Effekt zu beobachten. Der Elektrolytverlust der Feinwurzeln (REL) aller drei Arten war größer oder nahezu gleich nach der Kältelagerung als zur Zeit der Ernte. Die Ergebnisse von RGP und REL weisen darauf hin, dass nur eine geringe Beeinträchtigung in der Wurzelqualität während der Lagerung erfolgte. Eschen und Eichen, welche für eine Kältelagerung von Dezember bis März ausgegraben wurden, ging es im Freiland gut, jedoch nicht so gut wie jenen, die frisch gepflanzt wurden. Ahorn wuchs nach der Auspflanzung unabhängig vom Lagerdatum relativ schwach.

Introduction

Broadleaf species now account for a significant proportion of the current annual planting programme of about 15,000 ha in Ireland. Broadleaves represented only 5% of the planting programme 10 years ago, but the proportion increased to about 20% by 1995 (ANONYMOUS 1998). The logistics of scheduling lifting and planting operations in this programme are difficult, especially since many of the planting sites are small and scattered throughout Ireland. The use of cold storage allows some flexibility in such a programme, especially in extending the planting season (McKAY 1992). Stock can be maintained in a 'dormant' state in the cold store and then dispatched when required for field planting. However, seedlings may perform poorly in the field after planting, especially if they are lifted too early or late in the 'dormant' season and placed in storage when stress resistance levels are low (WEBB & VON ALTHEN 1980, MCKAY 1997).

Broadleaved seedlings are generally more expensive to produce and plant than conifers (JOYCE & al. 1998), so there is a high cost penalty if survival is low and seedlings need replacing. Seedlings that survive are likely to grow slowly and need extra tending such as weed control (INSLEY 1980, MCCREARY & DURYEA 1985). Seedlings are generally considered to be most resistant to storage and handling stresses when 'dormant'. Since the physiological condition of seedlings may vary during the lifting season (normally November to March or April in Ireland), the tolerance of the seedlings to storage may also vary seasonally. There is little information for Ireland on the effect of physiological status at the time of lifting on the cold storage tolerance of broadleaf species and on their field performance potential. Such information is available for Douglas fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] (O'REILLY & al. 1999a, O'REILLY & al. 1999b), Sitka spruce [*Picea sitchensis* (BONG.) CARR.] (O'REILLY & al. 1999a, O'REILLY & al. 2000) and hybrid larch (*Larix* x *eurolepsis* Henry) (O'REILLY & al. 2001), limited information is available for ash (*Fraxinus excelsior* L.) and sycamore (*Acer pseudoplatanus* L.) (O'REILLY & al. 2002), but none is available for sessile oak (*Quercus petraea* (MATT.) LIEBL.

The objective of this study was to determine the effect of physiological status at the time lifting on the cold storage tolerance and field performance potential of ash, sessile oak and sycamore seedlings, important species in Irish forestry. The physiological condition of the seedlings was assessed using measurements of shoot dormancy intensity, shoot xylem pressure potential (Ψ), root electrolyte leakage (REL) and root growth potential (RGP). These parameters are important determinants of stock quality (RITCHIE 1984, MCKAY & al. 1994). The survival and first-year height increment of the seedlings were evaluated in a field trial established in tandem with the physiological work.

Material and Methods

Plant Material and Sampling

Commercial nurseries supplied the seedlings used in this study. Two-year old (1u1) ('undercuts' or non-transplanted stock) bare-root seedlings of ash and oak grown at Ballymurn Nursery, Co. Wexford (52° 27′ N, 6° 29′ W, 110 m) and sycamore produced at Ballintemple Nursery, Co. Carlow (52° 44′ N 6° 42′ W, 100 m) were sampled at 2–6 week intervals from October 1996 to March 1997. The stock characteristics are shown in Table 1. On each occasion, about 500 seedlings per species and lift date were loosened with an undercutting machine and hand lifted, sealed in co-extruded black and white poly-bags (50 per bag) and dispatched that day to University College Dublin (about 105 km from nursery) and field planting (about 80 km from nursery).

Table 1. Details of planting stock used in the experiments.

Species	Mean Height[1] (cm)	Mean Diameter[1] (mm)	Seed source	Provenance description
Ash	36.60 (1.58)	8.12 (0.14)	Ireland	(417) South West
Oak	45.20 (1.48)	6.77 (0.14)	France	(44) 05F/1 SW Vallées
Sycamore	56.30 (1.17)	8.44 (0.22)	Ireland	(417) South West

[1] Mean height and diameter and associated standard errors (in parentheses) are based upon nine replications per species, with 18 seedlings per replication per lift date.

Cold Storage and Physiological Tests

The seedlings were held in a directly refrigerated cold room at 1–2 °C until the time of testing. Humidity levels could not be controlled, but desiccation was minimised by keeping the plants in sealed heavy-duty co-extruded polythene bags. The physiological condition of the seedlings was assessed within 48 hours of lifting and immediately after cold storage until May.

Dormancy Intensity and Root Growth Potential

The seedlings of each species were randomly selected to determine dormancy intensity and root growth potential on each lifting date and after cold storage. After washing the roots of each plant, the root system was pruned to approximately 12 cm below the root collar and any new white root tips were removed. New root growth was determined after keeping the roots of seedlings in an aerated hydroponics system (Ritchie 1984, DeWald & al. 1985, Ritchie & Tanaka 1990). The seedlings were suspended in plastic boxes (35 × 60 × 90 cm) containing approximately 50 l tap water. There were three boxes (replications) per lift date, each containing six seedlings per species. The boxes were placed on benches in a greenhouse set at 20/15 °C (day/night). Temperatures were a little below the set points during very cold weather and were a little above them during warm weather (actual, 18–23 °C day/ 13–17 °C night). Photoperiod was extended to 16 hours using high-pressure sodium vapour lights and relative humidity was maintained above 50% using time-controlled fine mist nozzles.

The dormancy intensity of the buds was estimated by determining the number of days for buds to break (DBB) for seedlings in the RGP tests (Ritchie & Dunlap 1980, Ritchie 1984, Johnsen & al. 1989). The total number of seedlings having flushed lateral buds was recorded at 2-3 day intervals. After all seedlings had flushed, the average number of DBB was calculated. After six weeks, the number of new roots (>1 cm in length) per plant was recorded. Because of space constraints in the greenhouse, seedlings were retained there for a maximum of 120 days, even if the buds did not flush. Since the roots were kept moist during the root counts, it unlikely that the flushing date was influenced by this factor for seedlings retained more than six weeks.

Shoot Xylem Pressure Potential

The terminal 7–10 cm of the leading shoot was excised from each of 15 seedlings per species and lift date to determine shoot xylem pressure potential (MPa) using a

Scholander type pressure chamber (Skye Instruments Ltd., SKPM 1400, Powys, Wales), following the method described by (RITCHIE & HINKLEY 1975).

Root Electrolyte Leakage

Electrolyte leakage from the fine roots (< 2 mm diameter) of seedlings lifted on each occasion was determined using a method similar to that described by McKAY 1992. The roots of 15 randomly chosen seedlings per species and lift date were washed in tap water to remove excess soil. Root portions (300–500 mg, fresh weight) were excised from each plant, rinsed in tap water and then in deionised water to remove surface ions. After washing, the roots were placed in 28 ml universal vials to which 17 ml deionised water was added. The vials were immediately agitated and then allowed to sit at room temperature. After 18 hours, the vials were agitated again and the conductivity of the bathing solution was measured using a conductivity probe with in-built temperature compensation (Delta Ohm conductivity meter, HD 8706, Padova, Italy). All samples were then placed in an oven for 2 hours at 90 °C to kill the cells. After cooling to room temperature (ca 4 hours), a second conductivity reading (the total potential conductivity) of each sample was taken. The 18-hour value was expressed as a percentage of the second reading.

Field Performance

Shortly after lifting and after cold storage until 19 May 1997, seedlings of each species were dispatched for planting to a nursery site at the Coillte Teo., Tree Improvement Centre, Kilmacurragh, Co. Wicklow (52° 56′ N, 6° 0′ W, 120 m). The site was prepared for planting in August/September 1996. After applying herbicide (glyphosate) to kill the weeds, the site was ploughed and tilled to 30 cm depth. After planting, weed competition was minimised by manual weeding. The field experiment was laid down as a randomised block design. Each of the four blocks contained one replicate of each species and lift combination. A single replication was a plot containing 20 seedlings. Seedlings were planted at 30 cm within rows and 50 cm between rows. Initial heights of seedlings were recorded shortly after planting. The number of surviving seedlings per plot and seedling height was recorded in the winter at the end of the first growing season after planting. Increment was expressed as a percentage of initial height to minimise the effect of variation in initial height and planting depth on height growth.

Data Analyses and Presentation

Because each species was sampled from a different nursery bed (and a different nursery for sycamore), species differences were treated as a split-plot factor in the statistical models for analysing the physiological data. Transformed values were used to standardise variation where indicated. The effects of species, lift date, cold storage and their interactions on the number of days to bud break, root electrolyte leakage (after arc-sine square root transformation), and shoot xylem pressure potential (transformed to natural logs) were analysed using an ANOVA (SAS 1989). LSD tests were used to compare species means within lifts, and lift means within species. For the freshly lifted stock, the effect of species on RGP (using ranked values within lift dates) was evaluated, but lift effects were not tested because seasonal changes in temperatures (and light intensity to lesser extent) in the greenhouse may have influenced RGP. However, lift date effects on DBB were also evaluated because the effect of these seasonal variations was considered to be too small to be of consequence for this parameter.

An ANOVA following a randomised block design was used to test for the effects of species and lift / planting date and their interactions on survival (after arc-sine square root transformation) and percent height increment.

Results

Physiological Responses

Cold storage, species and lift date and their interactions significantly influenced DBB (all $p < 0.001$); most of these interaction effects reflected differences among lift dates for the freshly lifted stock. The number of days to bud break was >120 days for stock freshly lifted in October, but DBB declined to 9–13 days for those lifted in March. Cold storage reduced DBB to <7 days regardless of species or lift date. The buds of sycamore seedlings lifted to storage in October had already flushed prior to the time of removal from cold storage.

Species, lift date and the three-way interaction of treatments influenced shoot xylem pressure potential (all $p < 0.01$). For the freshly lifted stock, Ψ was high (less negative) for seedlings lifted in October in ash and oak (>1.0 MPa), but lift date effects were small or negligible in sycamore (Fig. 1). Pressure potential was low for seedlings lifted in January (–3.4, –2.1 and –0.8 MPa in ash, oak and sycamore, respectively), and to a lesser extent for plants lifted in December (–1.0, –1.2 and –0.4 MPa) and March (–2.3, –1.5 and –0.2 MPa). After cold storage until May, Ψ increased (became less negative) or stayed about the same as at the time of lifting in most cases, but Ψ decreased in ash and oak lifted in late October, and in oak lifted in March. Many of these differences were significant. After cold storage, Ψ ranged from –0.5 to –1.1 MPa in ash, –0.3 to –2.5 MPa in oak, and –0.2 to –0.3 MPa in sycamore.

Species, cold storage and the three-way interaction significantly affected fine root electrolyte leakage (all $p < 0.01$), but the main effect of lift date or other interactions were not significant. Root electrolyte leakage was generally lower in ash (<23%), regardless of lift date or cold storage date, than in oak or sycamore (24–40%) (Fig. 2). Seasonal differences were small in freshly lifted stock, although values were generally higher in October than on other lift dates. Root electrolyte leakage was higher or about the same after cold storage than at the time of lifting, except for oak lifted in early October, which showed the reverse trend. Many of these differences were significant, although their magnitude was generally small.

Species differences in RGP were highly significant for freshly lifted stock ($p < 0.001$). Lift date and its interaction with storage effects were not evaluated for freshly lifted stock because conditions in the greenhouse

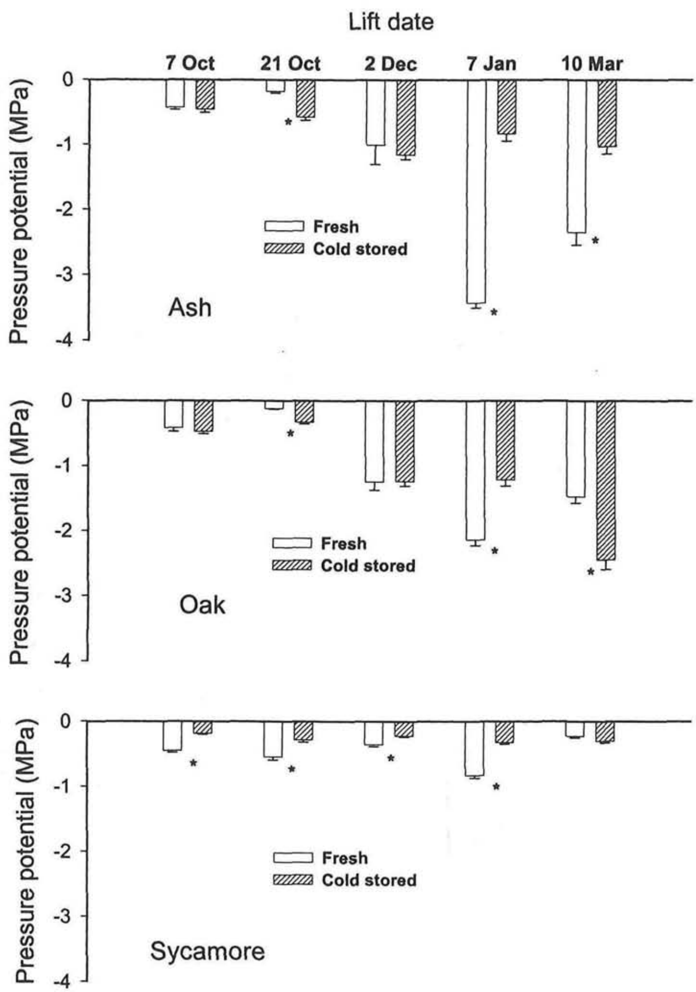

Fig. 1. Shoot xylem pressure potential (Ψ) in ash, oak and sycamore seedlings freshly lifted or after cold storage until May. Significant differences ($p < 0.05$) between means for the freshly lifted and cold stored stock of each lift date are indicated (*). Vertical lines on symbols are standard errors.

were not identical (although similar) for each lift date. Species significantly affected RGP for cold stored stock ($p < 0.001$), but lift date and its interaction with species were not significant. Freshly lifted ash and oak plants had low or negligible RGP (except ash lifted in March), but values were higher in sycamore (especially in March) (Fig. 3). Cold storage greatly increased RGP in ash and sycamore, except for sycamore lifted in March (but RGP at time of lifting was very high on this date). Lift effects were not

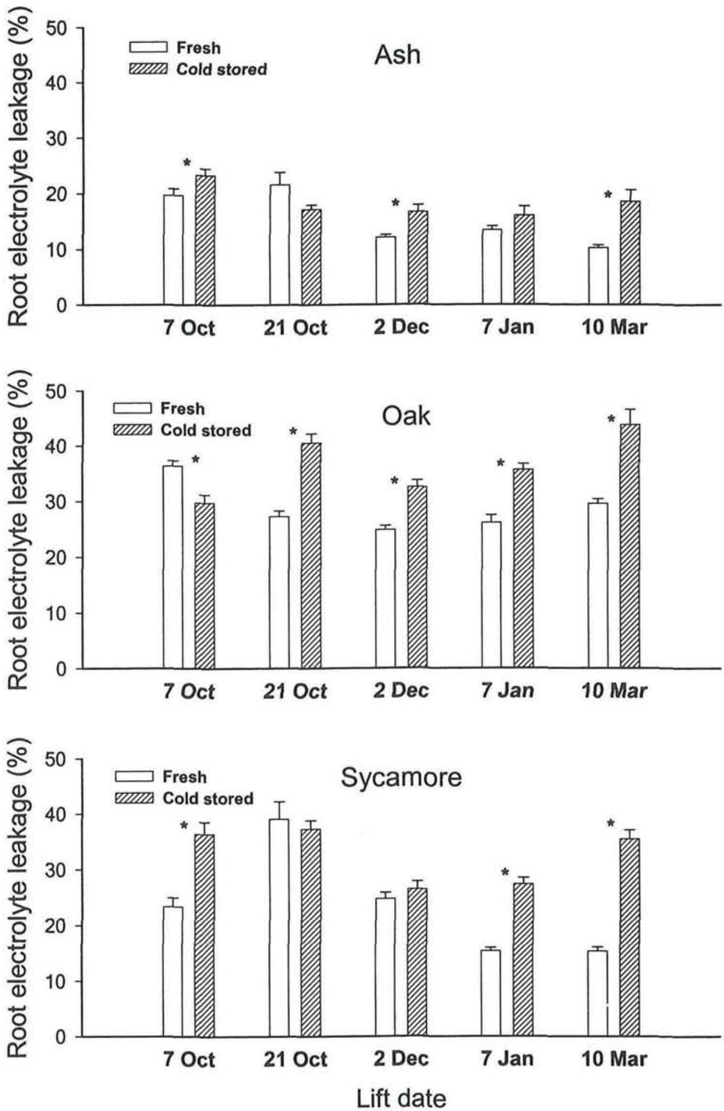

Fig. 2. Fine root electrolyte leakage in ash, oak and sycamore seedlings freshly lifted or after cold storage until May. Significant differences ($p < 0.05$) between means for the freshly lifted and cold stored stock of each lift date are indicated (*). Vertical lines on symbols are standard errors.

significant for all cold stored stock. Cold storage effects on RGP in oak are difficult to evaluate because RGP was very low regardless of lift or storage date.

Table 2. End-of-season survival (%) of ash, oak and sycamore seedlings freshly lifted or cold stored until May and planted two or three days later.

Lift	Ash		Oak		Sycamore	
	Fresh	Cold stored	Fresh	Cold stored	Fresh	Cold stored
7 Oct	99	100	93	91	100	99
21 Oct	100	98	96	84	100	100
2 Dec	100	100	100	99	99	99
7 Jan	100	96	100	100	98	96
10 Mar	100	100	95	99	100	84

Field performance

Survival after planting was very good and was not significantly affected by species, lift date or storage treatment or their interactions (Table 2). Survival was >90%, except for sycamore lifted to storage in March (84%) and oak stored in late October (84%).

Species, cold storage date and lift date and all interaction effects (all $p<0.01$), except species by storage date, significantly influenced height increment. On average, freshly lifted ash grew more (in percentage terms) than oak or sycamore. Freshly lifted ash (>90%) and sycamore (>35%) planted early in October grew better than those planted on later dates (Fig. 4). In contrast, oak freshly planted in December (45%) and January (50%) grew best. In general, cold storage reduced height increment in all species compared to values for freshly lifted stock, but the effect varied with lift date. Seedlings lifted to storage in early October grew poorly. Sycamore seedlings cold stored from October grew poorly compared with those freshly planted in October, and those stored from March died back (negative increment; shown as zero increment in Fig. 4). However, the increment of cold stored sycamore was similar to that achieved by stock freshly planted in December or January. Ash lifted to cold storage from late October to March and oak lifted from December to March grew relatively well after planting, although in some cases increment was less than that achieved by the freshly lifted stock of same lift date.

Discussion

Physiological Responses

Cold storage reduced bud dormancy intensity to less than a few days in all species and lift effects were small. Dormancy is released mainly in response to chilling accumulation (Lavender 1984, Burr 1990) and chilling greatly reduces the post-chilling heat requirement for bud burst in broadleaf trees (Webb 1977, Webb & von Althen 1980, Westergaard & Riiksen 1997). Therefore, the buds of the seedlings in this study were probably quiescent or post-quiescent in response to chilling experienced during cold storage. Furthermore, the buds of sycamore seedlings placed in storage in

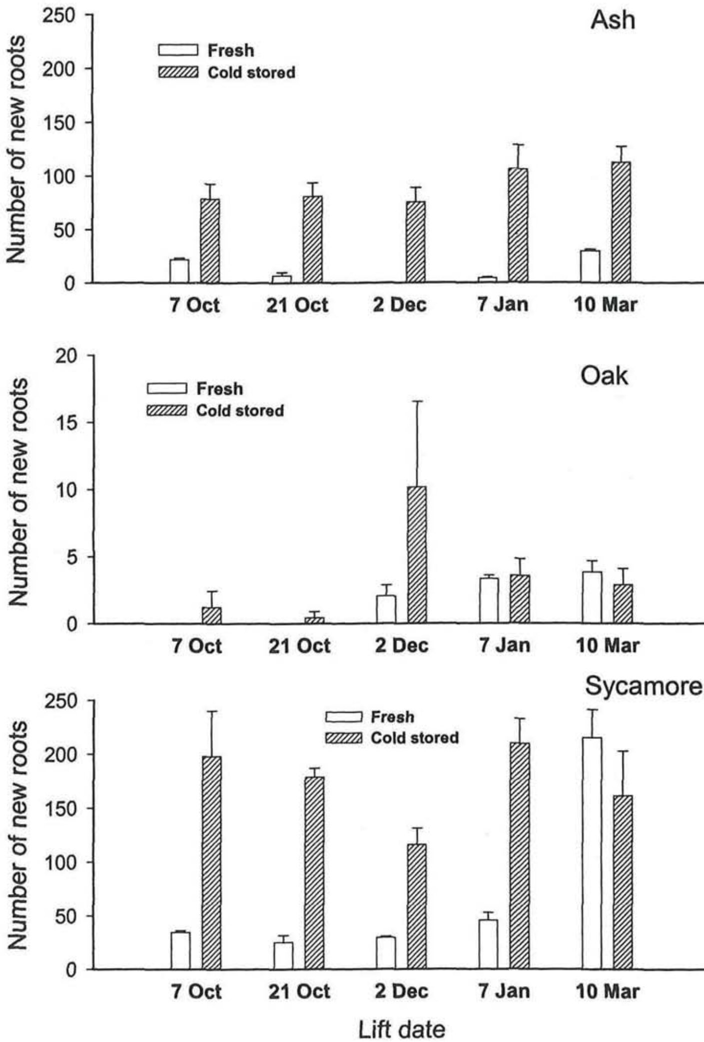

Fig. 3. Root growth potential in heated greenhouse in ash, oak and sycamore seedlings freshly lifted or after cold storage until May. Means for the freshly lifted stock were not compared statistically with those for the cold stored stock of each lift date because conditions in greenhouse were not identical on each test date. Vertical lines on symbols are standard errors. Note difference in the Y-axis scale between species.

October flushed while in cold storage, a phenomenon reported previously for *Acer* species (WEBB & VON ALTHEN 1980). It is likely that dormancy was broken earliest in stock lifted in October, thus allowing sufficient time for the buds to break while in storage.

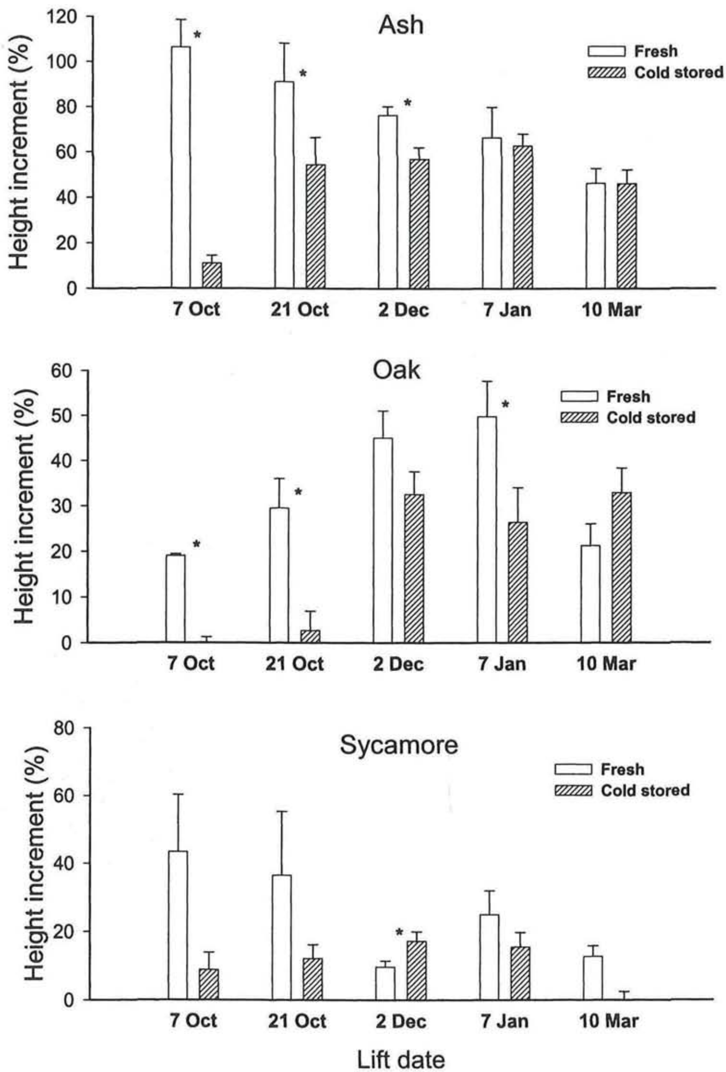

Fig. 4. End-of-season height increment as a percent of initial height for ash, oak and sycamore seedlings freshly lifted or after cold storage until May. Significant differences ($p < 0.05$) between means for the freshly lifted and cold stored stock of each lift date are indicated (*). Vertical lines on symbols are standard errors. Note difference in the Y-axis scale between species.

Cold storage increased or had little effect on xylem pressure potential in most cases. The increase in Ψ was probably associated with the process of dormancy release and concomitant decrease in sugar concentrations. Plants that are released from dormancy would be expected to have higher

Ψ than more dormant plants (WEBB & VON ALTHEN 1980, RITCHIE 1982, RITCHIE & SCHULA 1984, LAKSO 1990, MURAKAMI & al. 1990, ENGLERT & al. 1993, O'REILLY & al. 2002). However, cold storage reduced Ψ in oak lifted in March, and in ash lifted in late October (although absolute effects were small for the latter stock) (Fig. 1). Perhaps Ψ declined in these plants because they lost some water while in storage, although they were kept in sealed polythene bags to minimise desiccation.

Root electrolyte leakage is an indicator of root membrane integrity and is especially useful in detecting root deterioration during cold storage (MCKAY & MASON 1991). Root electrolyte leakage was higher or about the same after cold storage as at the time of lifting in all species in this study (Fig. 2). While these results indicate that some deterioration might have occurred during storage in some cases, the level of deterioration was probably small (no value exceeded 44%). The fact that cold storage did not significantly affect survival after planting supports this view.

Cold storage greatly increased RGP compared with values at the time of lifting in ash and sycamore, but had little effect for sycamore lifted in March (when RGP at the time of lifting was already high). This result is not surprising since RGP generally increases in broadleaves (RICHARDSON 1958, WEBB 1976, 1977, FARMER 1979, WEBB & VON ALTHEN 1980, HARRIS & al. 1993) and deciduous conifers such as larch (O'REILLY & al. 2001) after the buds have become quiescent. However, oak had very low or near zero RGP at the time of lifting, and cold storage increased values only slightly for seedlings lifted on some dates. RGP might be expected to decrease if plant quality deteriorated during storage (RITCHIE & DUNLAP 1980, STRUVE 1990), but there was little evidence of this (Fig. 3). In contrast, the RGP of Sitka spruce and Douglas fir seedlings was lower following cold storage than at the time of lifting, regardless of lift date (BURR & TINUS 1988, MCKAY & MASON 1991, MCKAY 1992).

Field Performance

Cold storage until May had no significant effect on post-planting survival in all species, despite fact that some plants were stored from October. These results were in agreement with the REL and RGP data. It appears that these broadleaf species achieve and maintain high levels of stress resistance early in the 'dormant' period, as found previously for several broadleaf species (WEBB & VON ALTHEN 1980, LINDQVIST 1998, 2001). In contrast, most conifer species are highly sensitive to date and duration of cold storage (RITCHIE & al. 1985, MCKAY & MASON 1991, MCKAY 1992, 1993, O'REILLY & al. 1999a, O'REILLY & al. 1999b).

However, the window of opportunity for placing plants in cold storage is narrowed if height after planting is considered in addition to survival. Cold storage reduced height increment after planting for seedlings lifted on some dates, causing shoot dieback in some cases. Ash grew well after planting, except for those stored from early October, while oak grew well if lifted to storage from December to March. Although ash cold stored from late October performed adequately in this study, it performed poorly when store from late October in another experiment carried out in Ireland (O'REILLY & al. 2002). Sycamore grew poorly after planting regardless of storage date. Sycamore seedlings were more highly active at the time of lifting than the other species, as indicated by their higher Ψ and RGP values at these times, suggesting that this species was probably least resistant to storage stresses. In paper birch (*Betula papyrifera* Marsh.) and green ash (*Fraxinus pennsylvanica* Marsh.) sampled in the US, shoot growth of all species was little affected by cold storage duration (HARRIS & al. 1993). In another study carried out in the US, however, long periods of cold storage caused plant mortality and stem dieback after planting in two-year-old Norway maple (*Acer platanoides* L.), red oak (*Quercus rubra* L.), European mountain ash (*Sorbus aucuparia* L.), paper birch, and Washington hawthorn (*Crataegus phaenopyrum* L.) seedlings (ENGLERT & al. 1993).

None of the physiological parameters were consistently reliable indicators of post-planting height increment (data not shown), perhaps because increment was generally good regardless of lift/ planting date. The physiological parameters may have been more predictive if the stock was handled poorly prior to planting or if post-planting conditions were more stressful (MCKAY 1997). The relationship between physiological responses and field performance has been examined in many studies (WEBB & VON ALTHEN 1980, LOPUSHINSKY 1990, MCKAY & al. 1999, GARRIOU & al. 2000, LINDQVIST 2001), but the results were generally not highly consistent.

Conclusions and Operational Implications

The results of this study showed that ash and oak lifted to cold storage from December to March performed well in the field. Sycamore from cold storage grew relatively poorly after planting, regardless of storage date. However, it is still preferable to use sycamore stock cold stored from December or January than freshly lifted seedlings for planting later in the season. Unfortunately, none of the physiological parameters were consistently reliable indicators of post-planting height increment.

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