Ann. For. Sci. 56 (1999) 391–402

Original article

The effect of desiccation and rough-handling on the survival and early growth of ash, beech, birch and oak seedlings

Helen M. McKay[a*], Richard L. Jinks[b], Colin McEvoy[a]

[a] Forestry Commission Research Agency, Northern Research Station, Roslin, Midlothian, EH25 9SY, UK
[b] Forestry Commission Research Agency, Alice Holt Lodge, Wrecclesham, Farnham, Surrey, GU10 4LH, UK

(Received 16 September 1997; revised 28 January 1998; accepted 8 March 1999)

Abstract – *Fraxinus excelsior* L., *Fagus sylvatica* L., *Betula pendula* Roth. and *Quercus robur* L. seedlings were grown for 1 year with or without an undercutting treatment in July of their first growing season. In the following March, seedlings were lifted from the nursery and subjected to 0, 12 or 36 h desiccation followed by 0 or 10 drops from 1 m. Morphological measurements, moisture content and root electrolyte leakage were determined. Field performance was measured after 1 year. The effects of undercutting, rough-handling and exposure were highly species dependent. Undercutting tended to improve both moisture content and root electrolyte leakage but decrease the root/shoot (R/S) ratio. Rough-handling increased fine root leakage and decreased final height and diameter but had no significant effect on survival. Desiccation had a major effect on the electrolyte leakage from fine roots, increasing it, on average, three-fold over a 36-h exposure. Ash and oak survival was high irrespective of desiccation treatment, whereas survival of beech and especially of birch was impaired by drying. The effect of rough-handling was minor compared with desiccation but there was a detrimental interaction between dropping and 36-h desiccation on birch performance. Species differences in survival were related to differences in R/S ratios, stem height and tap root biomass at the time of planting. (© Inra/Elsevier, Paris.)

desiccation / rough-handling / interaction / deciduous / performance

Résumé – **Les effets du dessèchement et de la mauvaise manipulation sur la survie et les nouvelles pousses de frênes, de hêtres, de bouleaux et de chênes.** Des plants de *Fraxinus excelsior* L, *Fagus sylvatica* L, *Betula pendula* Roth. et *Quercus robur* L ont été cultivés pendant un an avec ou sans cernage au mois de juillet de leur première saison de pousse. Au mois de mars suivant, ils ont été arrachés et stockés en conditions ambiantes pendant 0, 12 ou 36 h, puis ont été soumis, de 0 à 10 fois, à des chutes de 1 m. Les mesures morphologiques, la teneur en eau et les partes d'électrolytes au niveau des racines ont été déterminées. Les performances au champ ont été mesurées un an plus tard. Il s'est avéré que les effets du cernage, de la mauvaise manipulation et du stockage variaient fortement suivant les espèces. Le cernage tendait à améliorer la teneur en eau et les pertes d'électrolytes au niveau des racines, mais à réduire le rapport système racinaire/système foliaire. La mauvaise manipulation augmentait la perte au niveau des racines fines et réduisait la hauteur et le diamètre finaux des sujets sans avoir d'effet significatif sur leur survie, Le dessèchement avait un effet majeur sur les pertes d'électrolytes au niveau des racines fines, ces pertes étant en moyenne multipliées par trois avec un stockage de 36 h. Les frênes et les chênes présentaient un taux de survie élevé indépendamment de la longueur du stockage tandis que la survie des hêtres et plus particulièrement des bouleaux était amoindrie par le dessèchement. Les effets de la mauvaise manipulation étaient mineurs par comparaison avec ceux du dessèchement mais on notait que l'interaction de la mauvaise manipulation et du stockage de 36 h avaient un effet négatif sur les performances du bouleau. Les différences de survie au sein des espèces étaient reliées aux différences présentées par le rapport système racinaire/système foliaire, la hauteur de la tige et la biomasse du pivot au moment de la plantation. (© Inra/Elsevier, Paris.)

dessèchement / mauvaise manipulation/interaction / à feuilles caduques / performances

* Correspondence and reprints
h.mckay@forestry.gov.uk

1. Introduction

In Britain, broadleaved species are widely planted for amenity and landscaping purposes [2]; in 1994–1995, for example, 12.6 kha were planted with broadleaved species [3]. Although broadleaved species have not been a major component of commercial forests, recent government incentives such as the Woodland Grant Scheme have stimulated planting of broadleaves especially in England [3].

The majority of planting stock used in the UK is bare rooted; cell-grown stock comprises approximately 15 % of the market (J. Morgan, personal communication). During the interval between lifting and planting, bare-rooted stock may be damaged by a range of stress factors (see [32]) including desiccation and rough-handling. Relatively little is known about the resistance of broadleaved seedlings to these factors.

Hermann [17] concluded that dormant hardwoods were more resistant to drying than conifers. Desiccation reduced survival of Norway maple (*Acer platanoides* L.), sessile oak (*Quercus petraea* Liebl.) and *Nothofagus obliqua* (Mirb.) Blume [22] and narrow-leaved ash (*Fraxinus angustifolia* Vahl.) and downy birch (*Betula pubescens* Ehrh.) [23]. Girard et al. [15] found that 12 d exposure at 8 °C and 60 % relative humidity prevented root regeneration and resulted in mortality in 50 % of red oak (*Quercus rubra* L.) seedlings, whereas all seedlings survived exposure for 8 d or less. Differences among species in survival of bare-rooted stock have been reported by Insley [22], Insley and Buckley [23] and Englert et al. [13]. In some cases, these differences were related to the rate at which seedlings lost water [22], but in others, e.g. [36], differences in sensitivity to desiccation were evident even though species lost water at the same rate. This suggests that both the rate of drying and the ability to overcome water stress after outplanting are important in determining performance. Depletion of reserve carbohydrate by respiration during exposure to desiccating conditions was not thought to be a factor influencing growth and survival in red oak seedlings [15].

There is no reported investigation of the effects of rough-handling on broadleaved species but a variety of rough-handling treatments, such as dropping, knocking against a boot, tumbling and squashing, have been reported to decrease the survival and growth of bare-rooted conifer seedlings [11, 26, 35, 44, 45, 51]. Furthermore, conifer studies have shown that the combination of desiccation and rough-handling can be especially detrimental [11, 37].

Undercutting of broadleaved nursery stock can be used to limit tap root development. This practice modifies root architecture and growth but also affects shoot growth and the balance between root and shoot. In general, undercutting stimulates the production of fine [19] and lateral roots at the expense of tap root development [24, 43], reduces shoot growth and increases the root/shoot (R/S) ratio [19, 20, 25]. Compared with seedlings that were not undercut in the nursery, undercut seedlings had greater root development after one growing season and survival after 4 years [24]. The greater survival of undercut seedlings is often attributed to their greater root development.

This study was designed to investigate differences in resistance to desiccation and rough-handling between uncut and undercut seedlings of four species. We had three main objectives: to examine the effect of undercutting on seedling condition and 1st-year performance; to investigate the impact of desiccation and rough-handling when applied singly or in combination on seedling quality and field performance; and to relate field performance to differences in seedling morphology, moisture content and root cell membrane integrity at planting. The four species (common ash: *Fraxinus excelsior* L.; common beech: *Fagus sylvatica* L.; silver birch: *Betula pendula* Roth. and pedunculate oak: *Quercus robur* L.) are common in amenity and forest planting schemes but differ in their rooting habit and in particular their tendency to develop large tap roots. Resistance to rough-handling was assessed by electrolyte leakage from the root system; resistance to desiccation was assessed by both root electrolyte leakage and moisture content of the stem and root system of a subsample of plants. Electrolyte leakage is an index of cell membrane condition; low leakage rates indicate that the cell membranes have control over the influx and efflux of solutes, whereas high leakage rates indicate some form of cell membrane damage [38]. Root electrolyte leakage (REL) has proved a sensitive indicator of damage caused by rough-handling [35] and especially desiccation [34] of conifer seedlings. Resistance to both stresses was also measured by survival and growth in a field experiment.

2. Materials and methods

Plants of the four species were grown at Headley Nursery, Surrey, UK (51°8' N, 0°50' W, 90 m above sea level). Soil was sterilised using methyl bromide (98 % active ingredient methyl bromide) at 300 kg·ha^{-1} in the spring prior to sowing. Ground magnesium limestone was applied as a base dressing in late winter to raise the soil pH to 5.5. Britain was the seed source for ash and birch while the Netherlands was the source for beech and oak. Forestry Commission seed identity numbers were ash, 91 (20); beech, 93 (492) 2.1; birch, 92 (BRITAIN); and oak, 93 (492) 2. Non-dormant seed was sown in March 1994 to give a target seedling density of 75–100 m^{-2}; seed was sown in five parallel drills, with the exception of birch which was broadcast, with one species per bed in adjacent beds. Each species received three top-dressings of 1N:1P:2K horticultural fertiliser at 50 kg N ha^{-1} in each application; the first application was after the majority of seedlings had emerged, the second was mid-growing season and the final application was in late July. Water was applied using irrigation lines commencing after sowing and continuing once or twice per week depending on the weather conditions and tensiometer readings. Actual seedling densities were: ash 65 m^{-2}, beech 64 m^{-2}, birch 203 m^{-2} and oak 91 m^{-2}. In July, half of the seedlings were undercut at 10 cm in depth using a reciprocating undercutter to produce two plant types (undercuts and uncut); all seedlings were irrigated after the undercutting operation. The seedlings were not wrenched. They were lifted in early January 1995, bundled and bagged with either the entire seedling or the root system enclosed in black and white co-extruded polythene bags. Plants were stored at +2 °C until early March.

There were three desiccation durations (0, 12 and 36 h) followed by two rough-handling treatments (0 or 10 drops from 1 m) in a factorial combination. A total of 840 plants of each species and type was divided at random into six lots of 140 which were then bagged to prevent the roots drying; this procedure was carried out in a cool glasshouse at about 12 °C. Two lots of 140 were set aside for the 0-h desiccation treatment and the remaining seedlings were allocated to a random position along each of four racks running the length of the glasshouse. Each rack was 1.5 m wide and consisted of a wire grid supported 25 cm above the floor. When all the seedlings had been allocated, the bags were quickly removed and the seedlings spread out along the racks before the lights (400 W Son-T Agro lamps + Philips SGR 140 luminaries), suspended over the seedlings at a height of 2 m, and the heater, set to maintain a minimum temperature of 10 °C, were switched on. After 12 h, half of the seedlings were removed and the remainder left for a further 24 h. Conditions at plant level were measured on nine occasions during the 36-h desiccation treatment at six positions across the length and breadth of the greenhouse (*table I*). Seedlings treated for 36 h did not receive exactly three times the desiccation of seedlings treated for 12 h; the latter were treated overnight when temperatures, light levels and vapour pressure deficits were comparatively low, whereas the 36-h treatment included 2 nights and 1 day when temperatures rose to 20 °C and relative humidity fell to 31 %. The water vapour saturation deficit also varied diurnally from, for example, 5.9 m bars at time 0 (0:00 hours) to 15.7 m bars at 13:00 hours the following day.

Within each desiccation treatment, half of the seedlings (140 plants) were carefully handled at all times and the other half was dropped ten times from a height of 1 m but handled carefully at all other times. For each species, plant type and desiccation treatment, all 140 plants to be dropped were bundled into two lots of 50 plants and one lot of 40; the three bundles were placed in a polythene bag and weighed. Since undercutting had influenced plant weight, a bag of sand was added to the centre of each bag to equalise the weight of the undercut and uncut throughout plants within each species and desiccation treatment. Bag weights ranged from 11.3 kg for undesiccated ash to 2.9 kg for oak desiccated for 36 h. Each bag was tied firmly around the plants and dropped with the roots first onto a concrete road.

On completion of the desiccation and rough-handling treatments, 100 plants were allocated to the field experiment and 40 to assessments of plant quality. Seedlings were notch planted the following week on an open field site set in woodland at Alice Holt (latitude 51°10' N, longitude 0°50' W, 110 m asl). The soil type was a slowly permeable fine loamy-clay and the trees were maintained weed free using standard herbicide applications. There were five blocks split first for species and nursery treatment and second for desiccation and rough-handling treatment. Each block contained one 20-plant plot of each species and treatment combination. Assessments of survival, height and stem diameter were made in late November 1995.

Table I. Average conditions with standard errors during the desiccation treatment, mean of six positions.

Time elapsed (h)	0	12	13	15	16	17	21	23	35
Actual time, GMT	21.00	9.00	10.00	12.00	13.00	14.00	18.00	20.00	8.00
Temperature (°C)	11.8 (0.04)	16.6 (0.04)	19.7 (0.03)	20.4 (0.03)	19.8 (0.06)	17.9 (0.05)	12.6 (0.00)	15.4 (0.00)	15.9 (0.03)
Relative humidity (%)	57.0 (0.7)	52.3 (0.7)	44.7 (1.2)	37.8 (0.7)	31.3 (0.2)	39.7 (0.3)	52.5 (0.6)	53.3 (0.7)	35.7 (0.5)
Radiation ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	96.8 (6.1)	413.1 (13.7)	657.1 (45.9)	891.8 (38.1)	553.2 (17.1)	254.3 (9.5)	69.2 (6.8)	81.1 (9.5)	344.1 (27.3)

Assessments of plant quality were made at the Northern Research Station. Seedlings were stored at +4 °C until assessments were completed. The moisture content of shoots, tap roots, lateral roots and fine roots and electrolyte leakage from fine roots and woody roots were measured on 15 plants per species, type and stress treatment within 14 d. Fine roots were defined as any root < 2 mm in diameter, tap roots were the main vertical woody roots and the lateral roots were the roots > 2 mm in diameter branching off the tap roots. Morphological measurements included stem height from the root collar to the top live bud, stem diameter in two directions at 90° to one another at 5 cm above the root collar, dry weights of stem, tap roots, lateral roots and fine roots, and the number of lateral roots emerging from the undercut point and from other points on the tap roots. Fresh and dry weights were determined for all stress treatments but height, diameter, the number of lateral roots and the number and diameter of tap roots were measured on undesiccated plants only.

Morphological and biomass data were used to calculate the dry weight ratios of fine/tap roots, lateral/tap roots, and total root/shoot, the sturdiness quotient (height in cm divided by the stem diameter in mm), Dickson's quality index, and moisture content. Dickson compared the ability of several possible combinations of morphological parameters to predict field performance and concluded that a combination of dry weight, sturdiness ratio and R/S ratio gave the best quality index [12].

$$\text{Quality index:} \left| \frac{\text{total seedling dry weight (g)}}{\frac{\text{height (cm)}}{\text{diameter (mm)}} + \frac{\text{shoot weight (g)}}{\text{root weight (g)}}} \right|$$

$$\text{Moisture content: } \frac{(\text{fresh weight} - \text{dry weight})}{(\text{dry weight})} \times 100$$

Electrolyte leakage from fine roots of 15 replicates was measured using the method of Wilner [55] as modified by McKay [31]. Roots were washed in cool tap water, rinsed in deionised water and a sample of roots from the central bulk of roots removed. This sample was added to a glass bottle containing 16 mL distilled water. Samples were left at room temperature for 24 h, shaken thoroughly and the conductivity of the bathing solution measured using a conductivity probe (K = 1.0) with in-built temperature compensation (CP Instrument Company Ltd, Bishop's Stortford, UK) and an Alpha 800 conductivity meter (Courtcloud Ltd, Dover, UK). Samples were then autoclaved at 110 °C for 10 min. A second conductivity measurement was made on each sample once they had reached room temperature. The REL rate was calculated as:

$$\frac{\text{conductivity after 24 h}}{\text{conductivity after autoclaving}} \times 100.$$

The electrolyte leakage from the tap roots was determined in the same way on a 1.5–2-cm-long section cut from midway down the tap root.

The main effects and interactions of treatments on plant condition and field performance were evaluated using analysis of variance (ANOVA) run through Genstat 5. Survival data were transformed using an arcsine transformation before ANOVAs were used; however, for clarity untransformed means are presented.

3. Results

3.1. Seedling morphology

By the end of production at the nursery, the height of the uncut birch seedlings was more than double the height of the other three species (*figure 1a*); however, there was much less difference between species in the stem diameters of the uncut seedlings (*figure 1b*). The effects of undercutting on seedling morphology varied between species. Undercutting did not significantly affect height growth of either beech or oak seedlings, but caused a slight reduction in the average height of birch (*figure 1a*). In contrast, undercut ash seedlings were significantly taller than uncut seedlings. Stem diameters of birch and oak seedlings were not significantly affected by undercutting, but were reduced in beech and increased in ash (*figure 1b*).

The total dry weight of uncut ash seedlings was about 15 % more than for the other three species (*figure 2b*). The dry weight of shoots and roots differed significantly between species, reflecting differences in the allocation of dry matter between shoots and roots (*figure 2b* and *table II*). R/S ratios of uncut ash, beech and oak seedlings were between 2.5 and 3.8, whereas the majority of the dry matter in birch seedlings was retained in the shoots giving a ratio of about 0.5 (*table II*). Undercutting had no significant effect on shoot dry weight of beech, birch and oak seedlings, but increased the dry weight of ash shoots (*figure 2b*). Root dry weight of ash and birch was unaffected by undercutting, but was reduced by 40 and 20 % in beech and oak, respectively; however, only the R/S ratio of beech was significantly lower (*table II*). The increase in shoot weight in undercut ash also reduced the seedling R/S ratio (*table II*).

Undercutting had no significant effect on either the sturdiness quotient or the quality index of seedlings (*table II*). These two measures only varied significantly between species, in particular reflecting the proportionately greater shoot growth of birch seedlings (*table II*). Consequently, birch had the poorest values and ash the best, with beech and oak intermediate.

Undercutting made no significant difference to the dry weights of fine, lateral or tap roots of either ash or birch (*fig-*

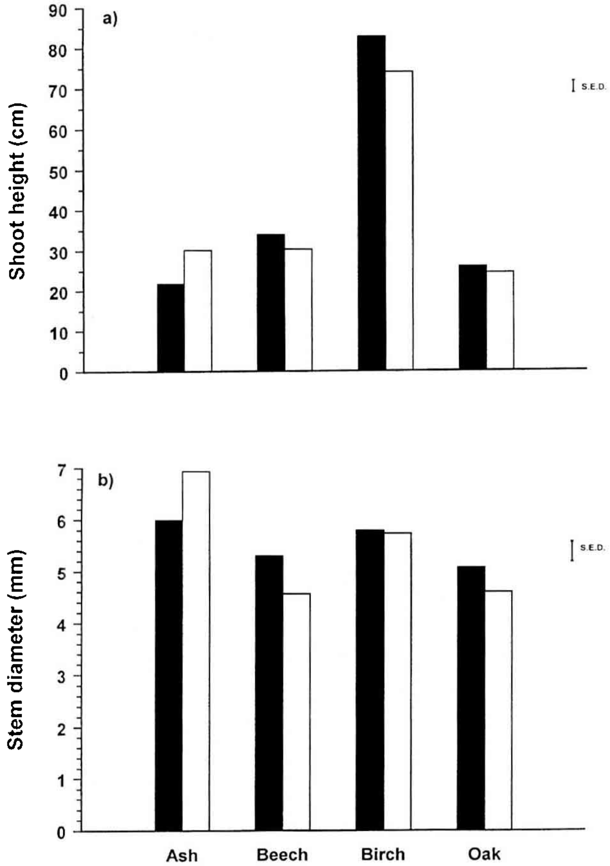

Figure 1. The effect of undercutting on (a) the heights, and (b) stem diameters, of uncut (closed bars) and undercut (open bars) ash, beech, birch and oak seedlings after one season's growth at the nursery.

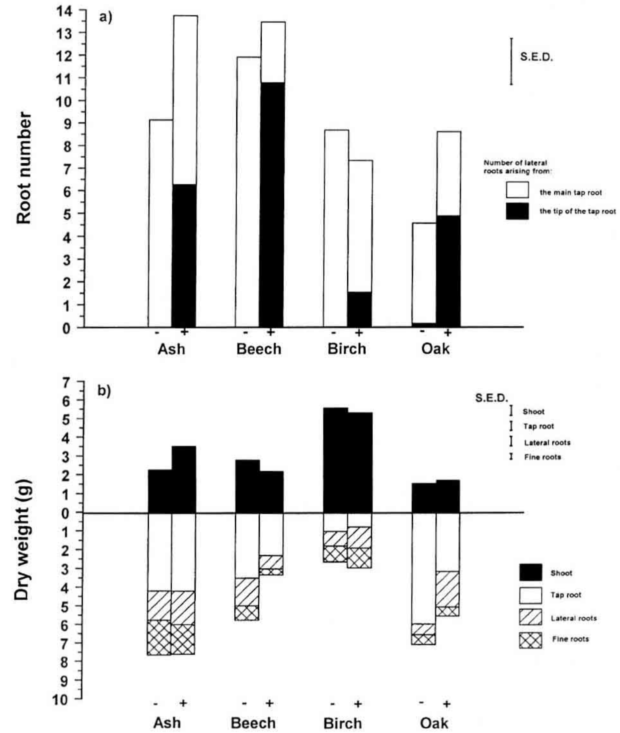

Figure 2. The effect of undercutting seedlings of uncut (–) and undercut (+) ash, beech, birch and oak seedlings on (a) lateral root number and b) shoot and root dry weights.

ure 2b). However, in undercut beech seedlings, the dry weight of the fine and lateral roots was significantly reduced by about half, while the weight of the tap roots was about one-third less than in the uncut seedlings. The only increase in the dry weight of a root category in response to undercutting occurred in oak where the weight of the lateral roots more than doubled; tap root dry weight, however, was reduced by half and undercutting had no significant effect on the dry weight of the fine roots, resulting in a 20 % reduction in total root dry weight.

The ratio of fine root to tap root dry weight was unaffected by undercutting but varied significantly between species with birch having the highest ratio and oak the least

Table II. The effect of undercutting on morphological ratios and indices of ash, beech, birch and oak seedlings.

	Ash		Beech		Birch		Oak		SED	Significance		
	Undercutting											
	–	+	–	+	–	+	–	+		Species (S)	Undercut (U)	S × U
Root/shoot	3.35	2.31	2.49	1.70	0.48	0.53	3.75	3.55	0.457	***	*	NS
Sturdiness quotient	3.66	4.35	6.60	6.70	14.5	13.3	5.14	5.52	0.659	***	NS	NS
Quality index	0.28	0.26	0.14	0.09	0.06	0.07	0.17	0.15	0.029	***	NS	NS
Fine/tap root ratio	0.23	0.19	0.13	0.10	0.31	0.35	0.07	0.09	0.024	***	NS	NS
Lateral/tap root ratio	0.19	0.23	0.19	0.20	0.27	0.33	0.08	0.33	0.038	***	***	***

SED: standard error of deviation; NS: not significant; ***: significant with $P < 0.001$; ** significant with $P < 0.01$; *: significant with $P < 0.05$.

(*table II*). There was a significant interaction between species and undercutting in the ratio of lateral to tap root dry weight. This was due to undercutting increasing the weight of lateral roots relative to tap root in oak (*table II*).

Undercutting significantly increased the number of lateral roots produced on the tap roots of both ash and oak seedlings, but did not affect the total lateral root number in either birch or beech (*figure 2a*). Nearly all of the increase in lateral root production in both ash and oak was due to the production of new roots from the cut end of the tap roots (*figure 2a*). Relatively few new roots were produced from this location in birch. In contrast, undercutting beech seedlings resulted in nearly all of the lateral roots being produced from the cut end of the tap roots, and relatively few from along the sides.

3.2. Moisture content

In brief, the effects of desiccation on shoot and root moisture content varied between species, with differences between undercut and uncut seedlings only evident in beech and birch seedlings. In all species, the fine roots had the highest initial moisture content, followed by lateral roots, tap roots, with shoots having the lowest moisture content (*figure 3*). The amount of moisture lost from fine roots after 12 h of desiccation varied between species. In ash, fine root moisture content only decreased from 400 to 350 %, whereas in oak it declined from 370 to about 100 %; the decline in fine root moisture content in the other two species was intermediate. After 36 h of drying the moisture contents of all tissues tended to converge at around 100 %. Undercutting had no effect on the amount of moisture loss from the different tissues of either ash or oak seedlings, whereas the fine roots of undercut birch seedlings maintained a higher moisture content than uncut roots after 0 and 12 h of desiccation (*figure 3*). Similarly, the fine and lateral roots of undercut beech seedlings also tended to have higher moisture contents after the first 12 h of desiccation. Although statistically significant, much less moisture was lost from the shoots and tap roots during desiccation than from fine and lateral roots.

3.3. Root electrolyte leakage (REL)

In all four species, treatments tended to have much less effect on leakage from tap roots than from fine roots (*figures 4* and *5*). Compared with the other three species, the fine roots of untreated ash seedlings had a very low REL (< 10 %); this was less than from the tap root. There was no obvious trend between REL from tap roots and desiccation time (*figure 4*). In the absence of desiccation, there was a tendency for the tap roots of undercut, roughly handled

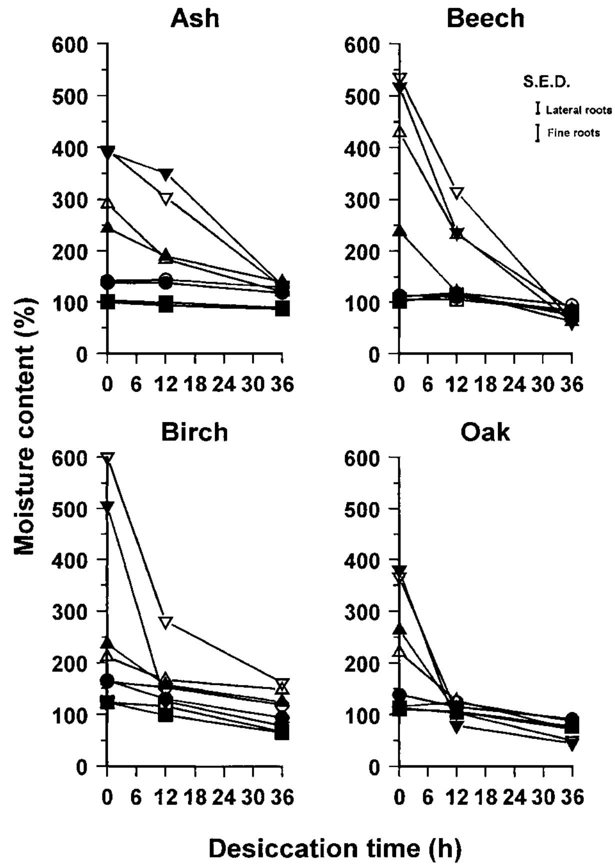

Figure 3. Changes in shoot and root moisture contents with desiccation time in undercut and roughly handled seedlings of ash, beech, birch and oak. ■□ Uncut and undercut shoot; ●○ uncut and undercut tap root; ▲△ uncut and undercut lateral roots; ▼▽ uncut and undercut fine roots.

seedlings of beech, birch and oak to have about a 5 % higher REL than the other three treatment combinations (*figure 4*). However, once seedlings had been desiccated, roughly handled uncut tap roots generally had the highest REL values in all species.

In fine roots, there was a linear trend in the increase in REL with desiccation time in beech and uncut oak seedlings. In all other cases there was little change in REL after 12 h desiccation, but much higher leakage after 36 h (*figure 5*). Undercutting and rough-handling had no effect on the REL from fine roots of ash, and had little effect in birch. However, leakage was lower in undercut seedlings in both oak which had been desiccated for 12 h, as well as in beech. There was also a tendency, particular in beech and birch after the longest desiccation time, for rough-handling to produce slightly higher REL values.

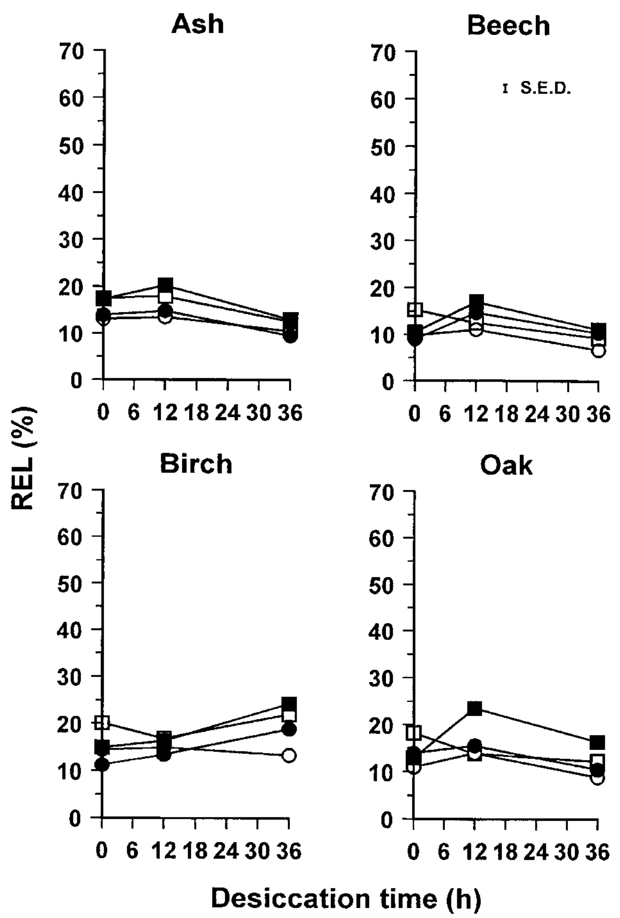

Figure 4. The effects of duration of desiccation and rough-handling on the electrolyte leakage of the tap roots of uncut and undercut ash, beech, birch and oak seedlings. ●○ Uncut and undercut, carefully handled; ■□ uncut and undercut, roughly handled. REL: root electrolyte leakage.

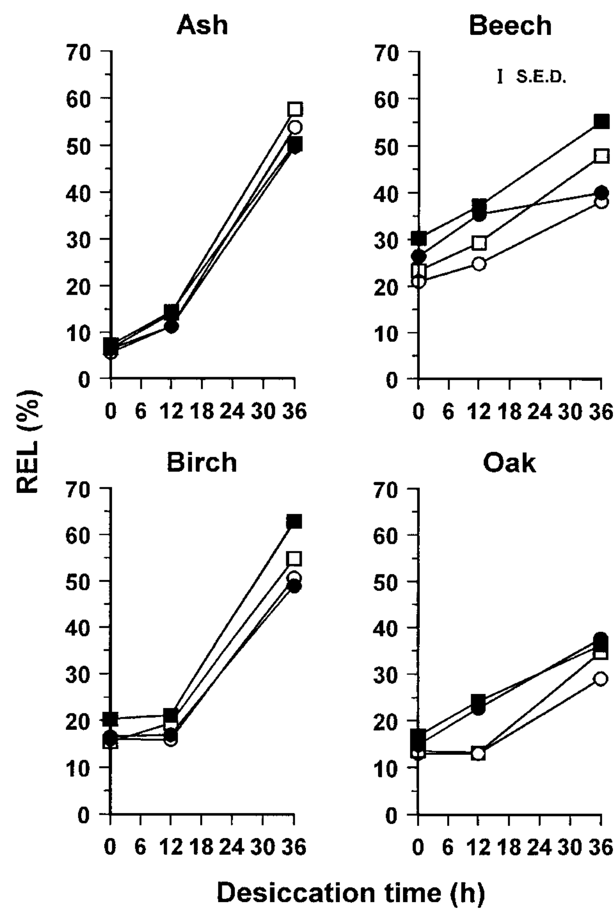

Figure 5. The effects of duration of desiccation and rough-handling on the moisture contents of the fine roots of uncut and undercut ash, beech, birch and oak seedlings. ●○ Uncut and undercut, carefully handled; ■□ uncut and undercut, roughly handled. REL: root electrolyte leakage.

3.4. Field performance

Survival of both ash and oak seedlings in all treatments was greater than 90 % (*figure 6*). However, 36 h desiccation greatly reduced survival of both beech and birch seedlings. In birch, desiccation for 36 h reduced survival of all seedlings to less than 10 %, while in beech seedlings which had been dried for 36 h, survival of undercut seedlings was about 30 % compared with only 5 % survival for uncut seedlings. Despite the high survival of ash seedlings, undercut ash produced little height increment after 0 and 12 h desiccation, and height of seedlings which received 36 h drying actually decreased (*figure 7*). In contrast, uncut ash seedlings increased in height after outplanting, and roughly handled seedlings were consistently shorter by the end of the first season. Both birch and beech also increased height after planting and again, carefully handled uncut beech and birch seedlings which had received 12 h desiccation were also taller than undried controls. Little growth occurred in oak, though carefully handled uncut seedlings tended to be taller. Results for stem diameter growth were similar to results for height growth (*figure 8*).

4. Discussion

4.1. The effect of undercutting

Despite the fact that undercutting of hardwoods was recommended as early as 1952 [42], there is still relatively little information specific to hardwoods (see [39]).

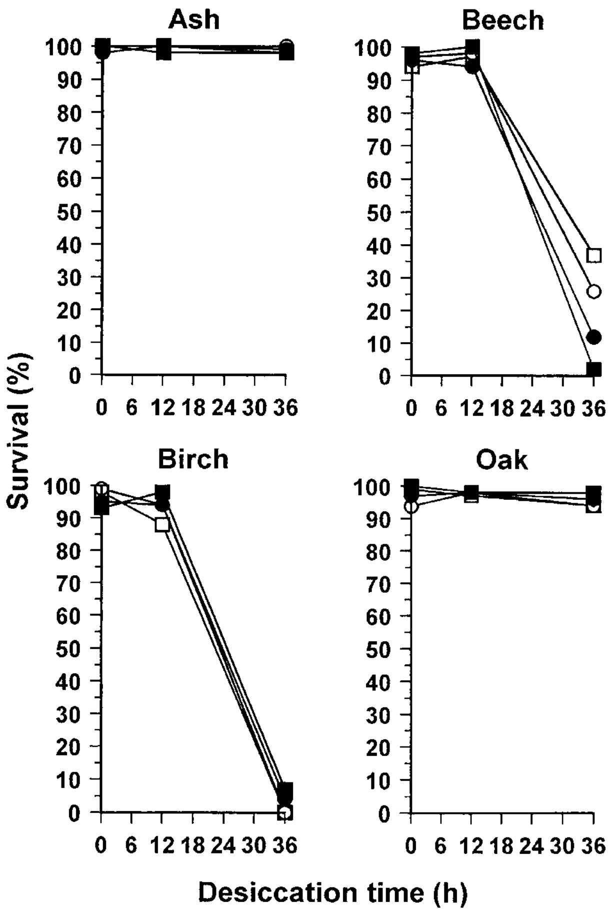

Figure 6. The effects of desiccation time and rough-handling on the percentage survival of uncut and undercut seedlings of ash, beech, birch and oak seedlings after the first season after outplanting. ●○ Uncut and undercut, carefully handled; ■□ uncut and undercut, roughly handled.

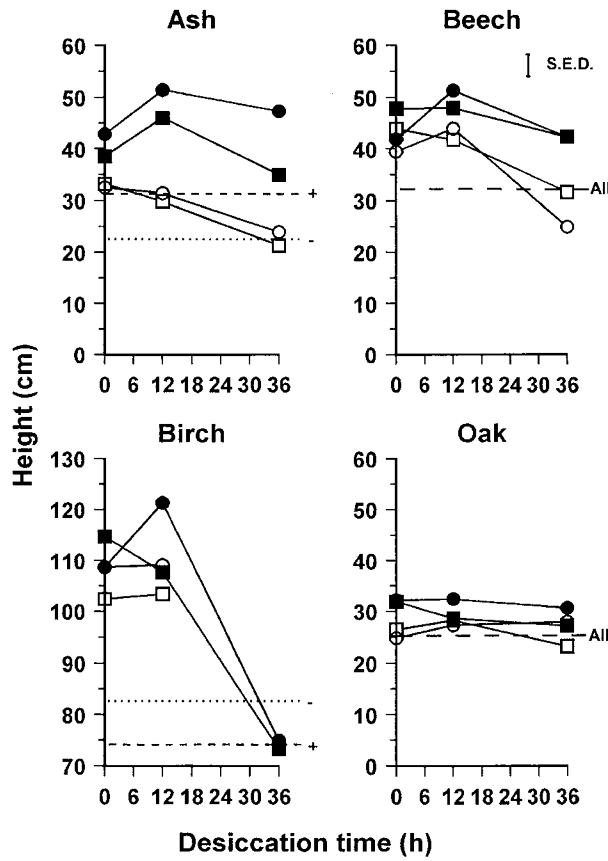

Figure 7. The effects of desiccation time and rough-handling on the height of uncut and undercut seedlings of ash, beech, birch and oak seedlings after the first season after outplanting. ●○ Uncut and undercut, carefully handled; ■□ uncut and undercut, roughly handled. If uncut (–) and undercut (+) heights differed significantly at the end of the nursery phase, both are shown as dotted or slashed horizontal lines; otherwise, the mean (All) of uncut and undercut heights at the end of the nursery phase is shown.

Nevertheless, broadleaves in general seem to respond to undercutting in the same way as conifers, i.e. height and stem weight are decreased, whereas root weight and the number of lateral roots are increased giving an increase in the R/S ratio [6, 8, 16, 19, 20, 24, 41]. In some studies, however, the total seedling dry weight was decreased [41]. In this study, stem weight was generally decreased by undercutting, but so too was root biomass, leading to a small but significant reduction in the R/S ratio.

The biomass and morphological changes induced by undercutting were species dependent. The effect of undercutting in limiting aboveground biomass was most marked in birch (height and weight were reduced) while effects on the root system were most significant for beech (total dry weight and tap root dry weight were decreased and the total number of laterals was increased). Ash deviated most from the general pattern reported by other workers; height and diameter were increased by undercutting. Our results on the effect of undercutting on biomass partitioning within *Q. robur* root systems corroborates those of Harmer and Walder [16] who reported no effect on total root weight, a minor negative effect on fine root weight but a large and significant increase in the biomass of laterals > 1 mm in diameter. Our results also agree with those of Hipps et al. [20], who found that undercutting had no significant effect on height growth of *Q. robur*. The observed responses of birch agree with those of Abod and Webster [1] who found that after removal of both old coarse and fine roots there

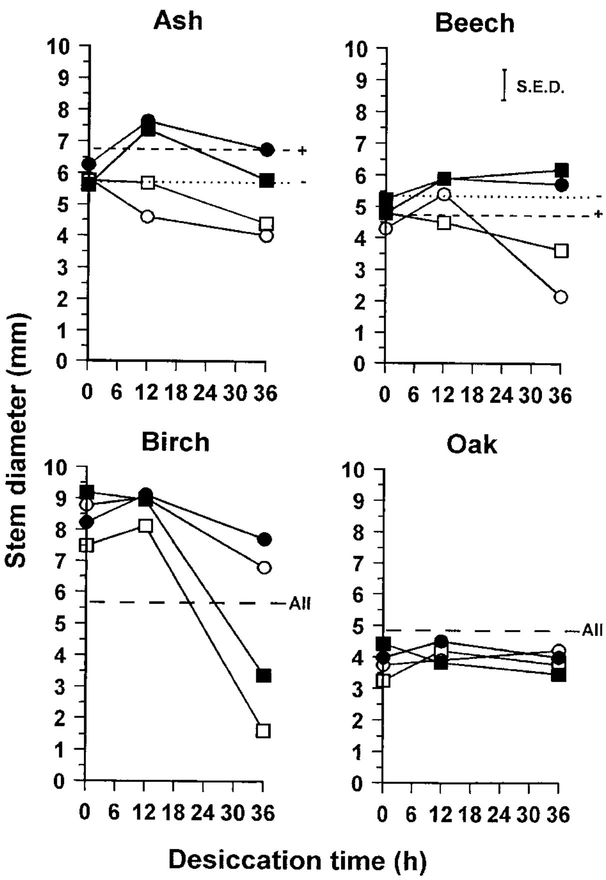

Figure 8. The effects of desiccation time and rough-handling on the stem diameters of uncut and undercut seedlings of ash, beech, birch and oak seedlings after the first season after out-planting. ●○ Uncut and undercut, carefully handled; ■□ uncut and undercut, roughly handled. If uncut (–) and undercut (+) diameters differed significantly at the end of the nursery phase, both are shown as dotted or slashed horizontal lines; otherwise, the mean (All) of uncut and undercut diameters at the end of the nursery phase is shown.

was no compensatory root production from the primary root and that shoot extension and diameter growth were totally inhibited.

Undercutting reduced the electrolyte leakage rate from fine roots of the undesiccated controls. A decrease in fine root leakage was previously observed for undercut and wrenched conifers by McKay and Mason [33]. The mechanism is unknown. Total plant moisture content of undesiccated seedlings was increased significantly by undercutting for birch and beech, although oak and ash were not significantly affected. Total plant moisture content was influenced mainly by the lateral and fine root components, suggesting that the greater moisture content of birch and beech might be caused by a reallocation of biomass to smaller diameter roots normally induced by undercutting. However, in this experiment undercutting did not influence the fine root biomass and there was no consistent pattern in the way undercutting affected lateral and fine root biomass of birch and beech on the one hand and oak and ash on the other. Thus, the reason for the increased total plant moisture content of undercut birch and beech is not clear.

The general negative effect of undercutting on the performance, particularly growth, of 1-year-old ash, birch and oak, seems to be related to its detrimental effect on root growth during the nursery phase, which apparently outweighed the small beneficial effect it had on moisture content and REL.

Undercutting, however, improved the survival of desiccated beech, which is surprising since it decreased total biomass, diameter and root biomass, in particular the tap root biomass, with a consequent decrease in the R/S ratio and quality index. There are, however, two possible reasons for the improved survival of beech but not the other species. Beech and ash undercuts had the greatest number of lateral roots (13.4 and 13.7, respectively) and beech had most from the undercutting point on the tap root (10.8). Kormanik [28] reported that the survival and regrowth of sweet gum (*Liquidamber styraciflua* L.) was related to the number of permanent lateral roots while Struve and Moser [48] found that pin oak (*Quercus palustris* L.), which is easy to transplant, had more first-, second- and third-order laterals than scarlet oak (*Quercus coccinea* Muench.), which is difficult to transplant. Survival of *Eucalyptus camaldulensis* Dehnh. was related to the number of large primary lateral roots [8]. In undercut beech, the lateral roots originating at the undercutting point may access more soil water because of their deeper penetration of the soil profile. A second possibility relates to the fact that undercutting was associated in beech with significantly lower electrolyte leakage of fine roots. Lower leakage rates have been associated with greater survival of conifers damaged both by cold storage [31, 33] and desiccation [34], although the exact mechanism is not fully understood.

4.2. The impact of desiccation and rough-handling

Initial moisture content of the stems was lower than that of the roots and, within the root system, moisture content increased as diameter decreased; similar gradients have been reported by Coutts [9] for Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Sucoff et al. [50] for red pine (*Pinus resinosa* Ait.) and white spruce (*Picea glauca* (Moench.) Voss.), and Insley and Buckley [23] for downy birch and narrow-leaved ash. In the present experiment, the rate of moisture loss was inversely related to initial moisture content and within the root systems in the present experiment, water loss was greater in roots of smaller diameter corroborating the findings of Coutts [9], Insley and Buckley [23] and Murakami et al. [36]. Differential water loss may be due to the greater surface area to volume of finer roots and their lack of secondary thickening and suberin. Insley and Buckley [23] also suggested that, since roots of birch and ash of similar diameters and initial moisture contents lost water at different rates in their experiments, physiological responses also determined the rate of water loss.

The desiccation treatments used here decreased plant moisture content and root membrane control but had no significant effect on the performance of ash and oak, and only the most severe treatment reduced the survival and growth of birch and beech. Compared to the desiccation treatments, dropping ten times from 1 m had a minor effect on membrane function and negligible effect on performance.

The effect of stress combinations has become a recent concern following examples, mainly from conifer studies, of particularly damaging interactions of stresses [11, 23, 37]; these often involve desiccation as one factor [32]. In the present experiment, there were some indications of a significant interaction between rough handling and desiccation: first, the increase in fine REL due to rough-handling was greater with increasing desiccation, and second, the decrease in stem diameter after one growing season of roughly handled birch was greatest in the seedlings desiccated for 36 h. In general, however, these interactions were limited and small by comparison with the effect of species in modifying the effect of desiccation and rough-handling.

4.3. Relationships between seedling condition at planting and early field performance

Undesiccated and carefully handled ash had a slightly but significantly better survival than oak. This may be explained by the fact that ash roots tend to regrow faster than oak. Root tips of green ash (*Fraxinus pennsylvanica* Bork.) elongated within 9 d and adventitious roots emerged within 17 d [5], whereas red oak (*Quercus rubra* L.) takes 10–50 d for root regeneration [15, 49]. The better survival of ash may also be due to its large fine root component which, judging by REL values, was in excellent condition. In Britain, ash is generally considered to be easy to establish [21, 27] and, in the United States, *Fraxinus pennsylvanica* is described as relatively easy to transplant [47].

Survival of beech and birch was decreased by desiccation, whereas oak and ash were unaffected. The two groups differed in a number of morphological respects: beech and birch had greater stem biomass and height, smaller roots (mainly because of the tap root component), smaller R/S ratio and poor sturdiness quotient and quality index. There was no clear difference between the two groups in root leakage rates or moisture contents. The link between R/S ratio and survival has been demonstrated most extensively with conifers (e.g. [14, 29, 40, 46]), but also with broadleaves [8, 53]. Poor performance after transplanting is most often associated with water stress [7, 30] and the ratio of R/S is an index of the potential of the root system to supply sufficient water for its shoot. In the present experiment, all species survived well when plants had not been desiccated, but survival of birch (with a R/S ratio of 0.5) began to decrease following 12 h desiccation, and following 36 h desiccation survival of beech (R/S ratio of 2.1) also declined. Even 36 h desiccation did not significantly affect the survival of ash and oak with R/S ratios of 2.8 and 3.7, respectively, even though their total moisture contents had fallen to 106 and 79 %. These species differences agree with Hipps [18], who reported that beech was more susceptible to desiccation than pedunculate oak, sycamore (*Acer pseudoplatanus* L.), wild cherry (*Prunus avium* L.) and maple (*Acer platanoides* L.).

Survival has often been related to the structure of the root system. For example, Struve [47] stated that species with fibrous root systems are easier to transplant than species with coarse root systems. However, in desiccating situations, Insley [22] found that thicker-rooted species (Norway maple and sessile oak) dried out more slowly and survived better than the finer-rooted *Nothofagus obliqua* (Mirbel) Blume. This study suggests that both fine- and coarse-rooted species can survive well, even when they have been severely desiccated, provided they have large R/S ratios, large tap roots and short stems. The relative importance of each of these three features cannot be evaluated in this study. This study also suggests that both beech, which had a small ratio of fine/tap root biomass, and birch, which had the greatest fine/tap root biomass, were severely affected by desiccation. The features characterising beech and birch were smaller R/S, larger stems, smaller roots, small tap roots and poor sturdiness quotients and quality index.

The differences in survival after desiccation of the two groups cannot be explained by differences in REL or rates of moisture loss. Within the desiccation-resistant group after 36 h desiccation, ash had the greatest moisture content in tap, lateral and fine roots and oak had the lowest moisture content while total plant moisture content of oak, beech and birch were not significantly different. It seems unlikely that the differences are related to the ability of the existing root system immediately after transplanting to take up water because beech and oak had approximately equal fine and lateral root weights yet oak had a much better survival. Although these two species differed in their tap root biomass, this is likely to have relatively little effect on their uptake capability because the specific surface area of tap roots is small and the tissue is highly suberised. The most likely explanation for the difference between the two groups is a difference in the root regenerating capacity; positive correlations between root growth capacity and early survival and growth have been reported in red oak [54] and sugar maple *Acer saccharum* Marsh [52]. We suggest that as damage to the original root system increases, root regeneration is likely to be adventitious and the vitality of the woody root as a source of adventitious roots becomes increasingly important. Ash and oak, having larger woody roots than beech and birch, are more likely to retain their capacity to produce adventitious roots following damage by desiccation or rough-handling.

In conclusion, both plant types of ash, beech, birch and oak with R/S ratios greater than 0.5, sturdiness quotients less than 14.0, tap root electrolyte leakages less than 17.0 and fine root moisture contents greater than 440 % had the potential for 90–100 % survival and positive height increments in their first growing season given recommended silvicultural practices [4, 10] and no adverse weather conditions. In such favourable conditions, ash had the best survival and this may be associated with the quantity and condition of its fine root system. Poor plant care, especially desiccation, compromised the survival and growth of beech and birch but not ash or oak. These differences among species seem to be related negatively to the height of the stem, positively to the R/S ratio, and positively to the absolute quantity of tap root rather than aspects of the fine or lateral roots. We suggest that these features reflect the seedlings' ability to produce adventitious roots and the balance between quantity of tissue responsible for water uptake and loss.

Acknowledgements: This study was funded by the Department of Environment. We wish to acknowledge the help of the staff at Headley Nursery, especially A. Dowell for growing and lifting the plants, staff at Alice Holt Technical Support Unit for planting out and assessing the stock, A. Hague for laboratory assistance, and G. Kerr, W. Mason and P. Freer-Smith for their helpful comments on the manuscript.

References

[1] Abod S.A., Webster A.D., The influence of root pruning on subsequent root and shoot growth of *Malus, Tilia,* and *Betula,* J. Hort. Sci. 66 (1991) 227–233.

[2] Anonymous, Review of the Arboricultural Advisory and Information Service, Department of Environment, Bristol, UK, 1991.

[3] Anonymous, Forestry Facts and Figures 1994–1995, Forestry Commission, Edinburgh, UK, 1995.

[4] Anonymous, Handling and Establishing Landscape Plants, The Horticultural Trades Association, Reading, Berks, UK, 1996, p. 21.

[5] Arnold M.A., Cupric carbonate modification of *Quercus rubra* and *Fraxinus pennsylvanica* root systems and implications for production and transplant, MS thesis, Ohio State University, Columbus, OH, 1987.

[6] Atterson J., Survival and growth of undercut seedlings in the nursery and forest, in: Report on Forest Research, 1963, HMSO, London, 1963.

[7] Burdett A.N., Physiological processes in plantation establishment and the development of specifications for forest planting stock, Can. J. For. Res. 20 (1990) 415–427.

[8] Chamshama S.A.O., Hall J.B., Effects of nursery treatments on *Eucalyptus camaldulensis* field establishment and early growth at Mafiga, Tanzania, For. Ecol. Manage. 21 (1987) 91–108.

[9] Coutts M.P., Effects of root or shoot exposure before planting on the water relations, growth and survival of Sitka spruce, Can. J. For. Res. 11 (1981) 703–709.

[10] Crowther R.E., Low A.J., Tabbush P.M., Establishment and tending, in: Hibbard B.G. (Ed.), Forestry Practice, Forestry Commission Handbook 6, Her Majesty's Stationery Office, London, 1991, p. 239.

[11] Deans J.D., Lundeberg C., Tabbush P.M., Cannell, M.G.R., Sheppard L.J., Murray M.B., The influence of desiccation, rough handling and cold storage on the quality and establishment of Sitka spruce planting stock, Forestry 63 (1990) 129–141.

[12] Dickson A., Leaf A.L., Hosner J.F., Quality appraisal of white spruce and white pine seedling stock in nurseries, For. Chron. 36 (1960) 10–13.

[13] Englert J.M., Warren K., Fuchigami L.H., Chen T.H.H., Antidesiccant compounds improve the survival of bare-root deciduous nursery trees, J. Am. Soc. Hort. Sci. 118 (1993) 228–235.

[14] Feret P.P., Kreh R.E., Seedling root growth potential as an indicator of loblolly pine field performance, For. Sci. 31 (1985) 1005–1011.

[15] Girard S., Clément A., Boulet-Gercourt B., Guehl J.M., Effects of exposure to air on planting stress in red oak seedlings, Ann. Sci. For. 54 (1997) 395–401.

[16] Harmer R., Walder K.E., The growth of shoots and lateral roots of *Quercus robur* L. seedlings following simulated undercutting, New For. 8 (1994) 351–362.

[17] Hermann R.K., Seasonal variation in the sensitivity of Douglas-fir seedlings to exposure of roots, For. Sci. 13 (1967) 140–149.

[18] Hipps N., Conditioning against transplant shock, Grower, 4 Jan. (1996) 19–21.

[19] Hipps N.A., Higgs K.H., Collard L.G., The effect of irrigation and root pruning on the growth of sycamore (*Acer pseudoplatanus*) seedlings in nursery beds and after transplanting, J. Hort. Sci. 71 (1996) 819–828.

[20] Hipps N.A., Higgs K.H., Collard L.G., Effects of root wrenching and irrigation rate on the growth and water relations of *Castanea sativa* and *Quercus robur* seedlings in the nursery and after outplanting, Can. J. For. Res. 27 (1997) 180–187.

[21] Hodge S.J., Amenity tree planting with bare-root stock, Arboriculture Research Note 97, 1991, 4 p.

[22] Insley H., Damage to broadleaved seedlings by desiccation, Arboriculture Research Note 8, 1979, 4 p.

[23] Insley H., Buckley G.P., The influence of desiccation and root pruning on the survival and growth of broadleaved seedlings, J. Hort. Sci. 60 (1985) 377–387.

[24] Johnson P.S., Undercutting alters root morphology and improves field performance of northern red oak, in: Worrall J., Loo-Dinkins J., Lester D.P. (Eds.), Proceedings of the 10th North American Forest Biology Workshop, 'Physiology and Genetics of Reforestation', 10–22 July 1988, Vancouver, British Columbia, 1988.

[25] Kalinin M.I., Yatsyuk, O.Z., (Effect of root trimming on the growth and development of red oak seedlings), Izv. Aviats. Tekh. + Lesnoi Zhurnal 2 (1988) 5–7.

[26] Kauppi P., Stress, strain and injury: Scots pine transplants from lifting to acclimation on the planting site, Acta. For. Fenn. 185 (1984) 1–49.

[27] Kerr G., Silviculture of ash in southern England, Forestry 68 (1995) 63–70.

[28] Kormanik P.P., Lateral root morphology as an expression of sweet gum seedling quality, For. Sci. 32 (1986) 595–604.

[29] Larsen H.S., South D.B., Boyer J.M., Root growth potential, seedling morphology and bud dormancy and survival of loblolly pine, Tree Physiol. 1 (1986) 253–263.

[30] Margolis H.A., Brand D.G., An ecophysiological basis of understanding plantation establishment, Can. J. For. Res. 20 (1990) 375–390.

[31] McKay H.M., Electrolyte leakage from fine roots of conifer seedlings: a rapid index of plant vitality following cold-storage, Can. J. For. Res. 22 (1992) 1371–1377.

[32] McKay H.M., A review of the effect of stresses between lifting and planting on nursery stock quality and performance, New For. 13 (1997) 369–399.

[33] McKay H.M., Mason W.L., Physiological indicators of tolerance to cold storage in Sitka spruce and Douglas-fir seedlings, Can. J. For. Res. 21 (1991) 890–901.

[34] McKay H.M., White I.M.S., Fine root electrolyte leakage and moisture content: indices of Sitka spruce and Douglas-fir seedling performance after desiccation, New For. 13 (1997) 139–162.

[35] McKay H.M., Gardiner B.A., Mason W.L., Nelson D.G., Hollingsworth M.K., The gravitational forces generated by dropping plants and the response of Sitka spruce seedlings to dropping, Can. J. For. Res. 23 (1993) 2443–2451.

[36] Murakami P., Chen T.H.H., Fuchigami L.H., Desiccation tolerance of deciduous plants during postharvest handling, J. Environ. Hort. 8 (1990) 22–25.

[37] Nelson D.G., Ray D., Establishment of Sitka spruce in relation to mound size, plant handling and soil temperature, Research Information Note 167, Forestry Commission, UK, 1990, 4 p.

[38] Palta J.P., Levitt J., Stadelmann E.J., Freezing injury in onion bulbs cells I. Evaluation of the conductivity method and analysis of ion and sugar efflux from injured cells, Plant Physiol. 60 (1977) 393–397.

[39] Racey J.E., Racey G.D., Undercutting and root wrenching of tree seedlings: an annotated bibliography, Ont. Min. Nat. Resour. For. Res. Rep. No. 121, 1988, 79 p.

[40] Ritchie G.A., Roden J.R., Kleyn N., Physiological quality of lodgepole pine and interior spruce seedlings: effect of lift date and duration of freezer storage, Can. J. For. Res. 15 (1985) 636–645.

[41] Röhrig E., Root pruning of oak seedlings, Forstarchiv. 48 (1977) 25–28.

[42] Rose A., Raising hardwood planting stocks by undercutting, J. For. Comm. 23 (1952-54) 52.

[43] Schultz R.C., Thompson J.R., Nursery practices that improve hardwood seedling root morphology, Tree Plant. Notes 41 (1990) 21–32.

[44] Sharpe A.L., Mason W.L., Howes R.E.J., Early forest performance of roughly handled Sitka spruce and Douglas-fir of different plant types, Scot. For. 44 (1990) 257–265.

[45] Silim S.N., Lavender D.P., Relationship between cold hardiness, stress resistance and bud dormancy in white spruce seedlings (*Picea glauca* (Moench.) Voss.), in: Proceedings of the 11th Annual Conference for the Forest Nursery Association of British Columbia, 1991, Prince George, BC, 1991.

[46] Simpson D.G., Thompson C.F., Sutherland C.D., Field performance potential of interior spruce seedlings: effect of stress treatments and prediction by root growth potential and needle conductance, Can. J. For. Res. 24 (1994) 576–586.

[47] Struve D.K., Root regeneration in transplanted deciduous nursery stock, Hort. Sci. 25 (1990) 266–270.

[48] Struve D.K., Moser B.C., Root system and root regeneration characteristics of pin and scarlet oak, Hort. Sci. 19 (1984) 123–125.

[49] Struve D.K., Rhodus W.T., Phenyl indole-3-thiobutryrate acid increases growth of transplanted 1–0 red oak, Can. J. For. Res. 18 (1988) 131–134.

[50] Sucoff E., Buschena C., Tamte P., Desiccation and water potentials in the roots, leaves, and shoots of bare-root red pine and white spruce, Can. J. For. Res. 15 (1985) 989–992.

[51] Tabbush P.M., Rough handling, soil temperature and root development in outplanted Sitka spruce and Douglas fir, Can. J. For. Res. 16 (1986) 1385–1388.

[52] von Althen F.W., Webb D.P., Effects of root regeneration and time of planting on sugar maple plantation establishment, in: Pope P.E. (Ed.), Central Hardwood Forest Conference II. Proceedings of a meeting held at Purdue University, West Lafayette, IN, 14–16 November 1978, 1978, pp. 401–411.

[53] Watson G.W., Sydnor T.D., The effect of root pruning on the root system of nursery trees, J. Arboricult. 13 (1987) 126–130.

[54] Webb D.P., von Althen F.W., Effects of various storage regimes and packaging methods on root regeneration and hardwood seedling quality, USDA For. Ser. Gen. Tech. Rep. NC-62, 1980, p. 16.

[55] Wilner J., Relative and absolute electrolyte conductance tests for frost hardiness of apple varieties, Can. J. Plant. Sci. 40 (1960) 630–637.