Root characteristics and growth potential of container and bare-root seedlings of red oak (*Quercus rubra* L.) in Ontario, Canada

Edward R. Wilson · Kristjan C. Vitols · Andrew Park

Received: 10 May 2006/Accepted: 22 February 2007 © Springer Science+Business Media B.V. 2007

Abstract Root characteristics and field performance of container and bare-root seedlings of red oak (Ouercus rubra L.) were compared during the first growing season after planting. Sixty seedlings of each stock type were planted on a clearfell and weed-free site near Restoule, Ontario. Twenty-four additional seedlings from each stock type were compared at the start of the study in terms of shoot and root parameters. Measurement of root and shoot parameters were repeated at three dates during the first growing season in the field. The root systems of container stock had a larger number of first order lateral long roots and were significantly more fibrous than bare-root stock. These differences were sustained throughout the first growing season. In terms of field performance, container seedlings had 100% survival and achieved significant increases in both biomass and shoot extension. Bare-root seedlings suffered 25% mortality, significant shoot dieback and more variable growth. The mean relative growth rate (RGR) of container seedlings increased throughout the study period to a maximum of 30 mg/g/day, whereas the mean RGR of bare-root stock remained close to or below zero. Overall, the container seedlings proved less prone to transplanting shock than the bare-root seedlings, most likely due to favourable root architecture and the pattern of root development. Further work may be warranted in container design, growing regimes and root architecture to

E. R. Wilson

National School of Forestry, Newton Rigg, Penrith, Cumbria CA11 0AH, England, UK

K. C. Vitols

E. R. Wilson (⊠) 11 Howard Street, Penrith, Cumbria CA11 9DN, England, UK e-mail: ted.wilson@yahoo.co.uk

Urban Forestry Branch, Parks, Forestry and Recreation Division, City of Toronto, 18 Dyas Road, Main Floor, Toronto, ON, Canada M3B 1V5

A. Park Department of Biology, The University of Winnipeg, 515 Portage Avenue, Winnipeg, MB, Canada R3B 2E9

fully realise the potential of container systems for the production of high quality red oak seedlings across a range of site conditions.

Keywords Root regeneration · Root architecture · Seedling quality · Planting stock types · Field performance

Introduction

Red oak (*Quercus rubra* L.) is among the most important hardwood species in southern and central Ontario (Anderson et al. 1990; OMNR 2000), and is widely planted on oldfield and cutover sites. It has traditionally been grown in bare-root nurseries, where the objective has been to produce tall seedlings with a large root mass (Harris et al. 1971; Johnson et al. 1996). Studies of field performance support the view that red oak seedlings with a large root collar diameter and extensive root systems are most effective in competing with weedy vegetation (Dey and Parker 1997). Bare-root seedlings are usually produced over two growing seasons using a variety of undercutting and pruning regimes to stimulate lateral root development (Jacobs et al. 2003). The roots of bare-root seedlings are, however, sensitive to desiccation and damage during handling, storage, and transport from the nursery to the field (Fort et al. 1997; Girard et al. 1997; Garriou et al. 2000), which can lead to poor post-planting performance and high rates of mortality (e.g. Stroempl 1985).

In recent decades, container seedling production systems have come to dominate the tree nursery industry in Ontario (OMNR 2001). Advantages of container systems include better environmental control of the growing regime, shorter production cycles, increased stock uniformity and frequently superior field performance on poor quality sites (Brisette et al. 1991; Johnson et al. 1996). Most research and development work on container systems has focused on conifer species. By contrast, relatively little attention has been paid to container production of temperate hardwoods, such as red oak. A major reason for this is the higher cost of producing hardwoods in containers compared to bare-root plants (Johnson et al. 1996). However, where cost is not the critical factor, there is evidence that container-grown red oak can perform as well or better than a variety of bare-root stock types, due in large part to protection of root systems in soil media up to the time of planting (Johnson et al. 1996). Zaczek et al. (1997) compared field performance of a variety of stock types 6 years after planting in a clear-felled mixed oak stand. Seedlings grown from 2year-old containerised stock were tallest (averaging 3.3 m) and had excellent survival, while bare-root seedlings performed less well in terms of either height increment and/or survival.

Root regeneration is of critical importance to establishment of planted seedlings. New root growth enables the seedling to establish a functional connection with the soil and thereby overcome the moisture stress imposed by transplanting (Burdett 1990; Krasowski 2003; Grossnickle 2005). For this reason, a great deal of seedling quality research has been undertaken on root morphology and related physiological processes (Ritchie and Dunlap 1980; Davis and Jacobs 2005). However, as most of this work has focused on conifer species (e.g. Dominguez-Lerena et al. 2006), there is an increasing need to develop protocols and standards that recognize different patterns of root development and

seedling growth in hardwoods (Wilson and Jacobs 2006). Among the commonly assessed root system attributes of hardwood seedlings are the number of primary first order lateral roots (FOLRs) and root system fibrosity (Davis and Jacobs 2005). These parameters are broadly indicative of the structural framework (i.e. mainly involved in support and transport functions) and the fine root component (i.e. mainly involved in water and mineral nutrient uptake) of a seedling root system, respectively. A large number of FOLRs is linked to rapid early establishment, improved growth rates and survival of oak seedlings (e.g. Ruelhe and Kormanik 1986; Schultz and Thompson 1997). Root fibrosity is a relative index of root branchiness. A fibrous root system has a relatively high root surface area with a large number of root apices. Cultural treatments and growing regimes in either bare-root or container stock production systems that modify the number of FOLRs, fibrosity or any other root system attribute, therefore, have the potential to improve seedling quality.

The objectives of this study were to (1) compare measures of seedling growth and allocation during the first growing season after planting and (2) compare initial root architecture and patterns of root regeneration of container and bare-root red oak seedlings. The work was undertaken in conjunction with an operational trial to assess the potential of container-grown red oak seedlings on a reforestation site in central Ontario.

Materials and methods

Planting stock

Container-grown and bare-root seedlings were produced at two commercial nurseries, Webb's Greenhouse, North Bay, Ontario and W. Richardson Farms, Pontypool, Ontario, respectively. The container stock was produced using Jiffy 5090 Forestry Pellets" (Jiffy Products (N.B.) Ltd., Shippegan, New Brunswick, Canada). These comprised individual pellets of compressed peat enclosed in a fine plastic mesh. When moistened and fully expanded, each pellet had a diameter of 55 mm, depth of 90 mm and volume of 225 ml. Individual pellets were grown at a density of 288 plants/m². Seed was stratified in a peat substrate from November 1996 to March 1997 before being sown on 1 April 1997. Single acorns were placed into each pellet and seedlings were grown for 6 months in a greenhouse and then hardened outdoors prior to shipping to the planting site. The bare-root stock was produced as 2-year undercut stock. Seed was collected in autumn 1995 and immediately planted in open beds at the nursery. Root systems were undercut to arrest taproot development at a depth of between 8 cm and 12 cm in July of the second growing season. Seedlings were lifted only after they had become fully dormant in early November 1997. Seed for both stock types was collected from natural forest stands in central Ontario.

Each nursery supplied 150 plants of each stock type, which were graded in terms of height, stem form, bud development and root architecture (bare-root only) according to operational guidelines developed by Stroempl (1985). The 84 most uniform seedlings from each stock type were selected for the study. Twenty-four seedlings per stock type were used in initial laboratory analysis. Twelve of these seedlings were selected at random for morphological measurements (with a sub-sample of six seedlings being used for carbo-hydrate analysis) and 12 seedlings were assigned for determination of root growth potential (RGP). The remaining 60 seedlings per stock type were planted in the field.

Site conditions

The field site was located at Restoule, Ontario $(46^{\circ}07' \text{ N}, 79^{\circ}45' \text{ W})$. The elevation is 250 m above sea level and the general topography is undulating. Soils are well-drained sandy loams. The site had been clear-felled during winter 1996–97 and scarified with a disk trencher in the summer of 1997, several months before planting. Seedlings were outplanted in two experimental blocks that were located 200 m apart as a precaution against the possibility of browse damage by white tailed deer. Thirty seedlings of each stock type were randomly assigned to each block and planted in six rows of 10 seedlings, with spacing between seedlings of 0.5×0.5 m, on 6 November 1997 (day 1 of the study). The blocks were hand weeded prior to and during the study.

Measurements

Return visits to the field sites were made on three separate dates after planting: (1) Day 183 (7 May 1998), to coincide with leaf flush in the spring; (2) Day 245 (8 July 1998), at the conclusion of terminal shoot extension; and (3) Day 345 (16 October 1998), at the conclusion of the first growing season. Six live seedlings of each stock type were harvested from each block (i.e. 12 seedlings total per stock type) on each date. Care was taken to minimise damage to seedling root systems. Mortality was determined from the 18 remaining seedlings of each stock type in each block prior to the final harvest (Day 345). Measurements included total height from the root collar to the highest live shoot, total extension of lateral and terminal shoots (1998 growing season) and root collar diameter. Biomass was determined separately for the lateral roots, the taproot, the shoot system and foliage (where present); all plant tissue was oven dried at 80°C for 48 h prior to weighing. Mean periodic relative growth rate (RGR) for each stock type was calculated as outlined by Hunt (2002). Leaf biomass was included in the determination of RGR on days 183 and 245, but not days 1 and 345, due to the absence of live foliage at the beginning and end of the study.

Root architecture of excavated seedlings was defined by the number of FOLRs greater than 1 mm diameter (primary FOLR) originating along the length of the taproot and at the base of the taproot (i.e. at the point of undercutting in bare-root stock or air pruning in container stock). A root fibrosity index was devised to provide a relative measure of structural and fine root branching (Table 1). Individual seedling root systems were assigned a fibrosity class on a 1–5 scale, with five being the most fibrous. The scale was developed

		-
Rating	Fibrosity class	Description of root system appearance
1	Very low	No 2nd order long roots; zero or few short roots present
2	Low	1-3 2nd order long roots; low density of higher order long and short roots
3	Moderate	3-5 2nd order long roots; moderate density of higher order long and short roots
4	High	>5 2nd order long roots; moderate density of higher order long and short roots
5	Very high	>5 2nd order long roots; high density of higher order long and short roots

 Table 1
 Rating system for root fibrosity

The rating is based on visual assessment of the approximate number and type of high order lateral roots per 10 cm segment of primary first order lateral roots (i.e. those with a diameter >1 mm, branching from the taproot). Long roots are >5 mm and are likely to contain branches of the next highest order. Short roots are <5 mm; they do not support roots of higher order

from a fibrosity index devised by Hatchell and Muse (1990). Kinking, circling and other evidence of root deformation due to nursery practices were assessed using a root form index, modified from Harris et al. (1971) (Table 2). A 1–4 scale was used to assess root form, with a score of 1 for a root system free of deformation. The form of the taproot and lateral roots was assessed independently, generating two scores for each seedling. A three-point scale was devised for root orientation; a score of 1 indicating an even spread of lateral roots radiating in all directions from the plug (Table 3).

Starch, soluble sugar and total non-structural carbohydrate concentration (mg/g) were determined for lateral root, taproot and stem components on six seedlings per stock type at the time of planting. Starch was determined colorimetrically on finely ground freeze-dried material using the iodine method (Allen 1989). Soluble sugars were determined colorimetrically on finely ground freeze-dried material using the anthrone (0.2 g/100 ml concentrated H₂SO₄) method (Yemm and Willis 1954; Allen 1989). Twelve seedlings of each stock type were planted in small pots of potting mixture and placed in a growth cabinet for 14 days (16 h light:8 h dark; 16°C). RGP was determined by counting the number of new roots \geq 10 mm (see Ritchie and Dunlap 1980).

Statistical analysis

The original division of the planting effort into two separate blocks was done to buffer the seedling population against the possible effects of browsing by white tailed deer. Because seedling growth might have been affected by local environmental heterogeneity between blocks, we tested each stock type (container and bare-root) for between-block differences in total dry weight, the dry weights of shoots, roots, tap roots and lateral roots, seedling height, and root:shoot ratio. Differences were explored using *t*-tests with 10° of freedom assuming equal variances between blocks.

Forty-two exploratory tests were conducted (7 tests \times 3 harvests \times 2 root types). In a large majority of cases, the null hypothesis (H_0) of no mean difference between blocks was accepted (*P*-values between 0.12 and 0.97). Two tests returned *P*-values that indicated a borderline acceptance of the H_0 . One test, root:shoot ratio for bare-root stock in harvest 1, returned a marginally significant statistic, while the root:shoot ratio for container stock in harvest 3 showed a strongly significant difference between blocks. However, based on these tests, we concluded that overall between-block heterogeneity induced very few differences within either container or bare-root stock types. Therefore, pooling data across blocks for subsequent analyses of between root stock developmental differences is justified.

Rating	Description of root form
1	No kinking or circling roots
2	Acceptable root form but with some kinking and/or circling of roots
3	Moderate kinking and/or circling of roots, potential to impede future tree growth
4	Severe kinking and/or circling of roots, highly likely to impede future tree growth

 Table 2 Root form index (modified from Harris et al. 1971)

Taproot and primary first order lateral roots were assessed independently. A rating of 1 is considered to be most advantageous in terms of seedling quality

Table 5 Index of factor for themation						
Rating	Description of lateral root orientation					
1	Good lateral root spread, radiating in all directions from the root plug					
2	Lateral roots predominantly oriented in one direction; little radial spread, J-rooting					
3	Lateral roots showing evidence of spiralling or knotting in the root plug					

Table 2 Index of lateral root orientation

A value of 1 represents the most desirable orientation in terms of seedling quality

Differences between dry weight and the various ratio-based variables were tested using Welch's two-sample *t*-test, which assumes unequal variances and calculates approximate degrees of freedom based on sample variances. Ranked and ordinal data were tested using the Wilcoxon rank sum test. All tests were conducted in S-Plus for Windows (version 4.0, Mathsoft Inc., Seattle, Washington).

Results

Initial comparison between stock types

Carbohydrate concentrations at the start of the study were similar in each stock type (P > 0.05). Concentrations of starch and soluble sugars were approximately 210 mg/g and 60 mg/g, respectively, in each of the stem, taproot and lateral root segments. Overall, the total non-structural carbohydrates accounted for approximately 27% of total biomass in both stock types, with approximately 75% of total non-structural carbohydrates being located in the taproot. These findings are consistent with optimum values reported elsewhere (Wargo 1976) and eliminate carbohydrate concentration as a possible reason for differences in field performance of the two stock types. RGP was zero for all container and bare-root seedlings, indicating that both stock types were dormant at the time of planting.

In terms of biomass and morphology, container seedlings were significantly smaller in many growth parameters than the bare-root stock at the start of the study (Table 4). For example, the mean root collar diameter was 4.7 mm compared with 6.5 mm and the

Variable	Initial values	(Day 1)	Final Harvest (Day 345)			
	Container	Bare-root	P-value	Container	Bare-root	P-value
Seedling dry weight (g)	5.12 (0.69)	14.55 (1.88)	0.000	12.03 (1.43)	15.28 (4.44)	0.195
Shoot dry weight (g)	1.48 (0.21)	4.81 (0.72)	0.000	2.71 (0.22)	4.68 (1.14)	0.006
Root dry weight (g)	3.63 (0.53)	9.73 (1.37)	0.000	9.32 (1.38)	10.6 (3.59)	0.525
Root:Shoot ratio (g/g)	2.50 (0.31)	2.12 (0.34)	0.111	3.49 (0.54)	2.39 (0.65)	0.019
Root collar diameter (mm)	4.65 (0.27)	6.48 (0.62)	0.001	5.26 (0.20)	5.84 (0.78)	0.181
Seedling height (cm)	26.40 (2.64)	41.11 (2.70)	0.000	26.40 (2.94)	29.92 (6.46)	0.346

Table 4 Differences in dry weights, weight ratios and shoot morphology between container and bare-root stock types on day 1 (7 November 1997) and day 345 (16 October 1998) of the study

Values reported are the mean of 12 seedlings per stock type (±95% confidence interval)

average seedling height was 26.4 cm compared with 41.1 cm, for container and bare-root stock, respectively. Although mean total biomass of container seedlings was approximately one third less than that of bare-root seedlings, root:shoot ratio were similar for both stock types (P = 0.111). Lateral root biomass and lateral root: total root biomass ratio were both significantly higher in container seedlings than in bare-root stock (P = 0.013 and P = 0.000, respectively).

Field performance

The container stock generally performed better than the bare-root stock over the course of the growing season (Table 4). Initial differences between stock types largely disappeared as container seedlings increased in biomass and size relative to the bare-root stock. By day 345, seedling height, root collar diameter, total seedling dry weight and root dry weight were similar in container and bare-root seedlings. The contrasting patterns of root and shoot biomass allocation were highlighted by a significantly higher root:shoot ratio in the container stock compared to the bare-root stock. The increase in both taproot and lateral root biomass in container seedlings was evident from early in the growing season (from Day 183) (Fig. 1a, b). Shoot extension in container seedlings was not significantly different (P = 0.058) at day 345 (Fig. 2a).

There was a widening difference in mean periodic RGRs during the growing season between stock types (Fig. 2b). In the final growth period (Day 245–345) the mean RGR of container seedlings increased to 30 mg/g/day, compared with approximately zero in bareroot stock. The relative decline in many bare-root plants was confirmed by observation of terminal shoot dieback and premature leaf senescence from the middle of the growing season. At the conclusion of the first growing season (Day 345) there was 100% survival of container seedlings and 75% survival of bare root seedlings.



Fig. 1 Mean root growth parameters for container and bare-root seedlings of red oak over one growing season (6 November 1997 to 16 October 1998). (a) taproot biomass; (b) lateral root biomass; (c) lateral root:total root biomass ratio. Values are the means (\pm 95% confidence intervals) of 12 seedlings per stock type



Fig. 2 (a) Mean total shoot extension and (b) mean periodic relative growth rates for container and bareroot stock types during the 1998 growing season. Day 183 = 7 May; day 245 = 8 July; day 345 = 16 October. Values for each date are the mean of 12 seedlings per stock type. 95% confidence intervals are shown in (a)



Fig. 3 Schematic diagrams of the structural root system of container and bare-root seedlings at the time of planting (Day 1) and after one year in the field (Day 345). The numbers of first order lateral roots are based on mean values of 12 seedlings per stock type at each date. Diagrams are not to scale and do not attempt to accurately illustrate root lengths, deformity or orientation

Root growth and architecture

There were significant differences in the structural architecture of seedling root systems between the container and bare-root stock types (Table 5). At the beginning of the study, container seedlings had approximately 10 FOLRs, originating along the length and at the base of the taproot. In contrast, bare-root stock had an average of only three FOLRs originating above the point of root undercutting. The root system of bare-root stock was

Variable	Initial values (Day 1)				Final harvest (Day 345)			
	Medians				Medians			
	Container	Bare- root	Z- score	P- value	Container	Bare- root	Z- score	<i>P</i> -value
Root architecture								
Total No. FOLR	9.0	3.5	2.82	0.005	14.0	8.0	-3.02	0.003
No. FOLR origin along tap root	5.5	3.5	-1.05	0.292	8.0	1.5	2.99	0.003
No. FOLR origin at base of tap root	5.0	0.0	3.00	0.003	5.0	6.0	-0.34	0.740
No. replacement taproots	0.0	4.0	-3.06	0.002	0.0	3.5	-3.86	0.000
Root system form								
Tap root form	2.0	1.5	-1.72	0.085	2.5	2.0	2.95	0.003
Lateral root form	2.0	1.0	1.64	0.100	1.8	1.0	3.09	0.002
Lateral root orientation	1.0	2.0	-3.32	0.001	1.0	1.0	0.64	0.541

 Table 5
 Initial (day 1) and final (day 345) root system attributes for container and bare-root stock types of red oak seedlings

Values reported are the medians of 12 seedlings per stock type at each harvest date

dominated by replacement taproots, which were generally thicker and woodier than typical lateral roots; this morphology resulted from earlier root undercutting in the nursery. No lateral roots were found at the base of the taproot on bare-root stock. Diagrams of structural root architecture illustrate the general differences between stock types (Fig. 3).

Differences in structural root architecture between stock types were sustained throughout the duration of the study (Fig. 4). By the final harvest, container seedlings had 14 primary FOLR, almost twice as many as bare-root seedlings. In the container seedlings, the increase in the number of primary FOLRs took place along the taproot as a result of secondary thickening of existing FOLRs. The increase in number was evident from early in the growing season. In contrast, most primary FOLR development in bare-root seedlings was in the form of new roots from the base of the taproot(s), at the point of undercutting in the nursery. These FOLRs were recorded from the July measurement (Day 245).

Initially there was no significant difference (P = 0.085) between stock types in the taproot form; little evidence of kinking or deformation was found that might impede future seedling growth. By the end of the growing season, however, differences were evident between the stock types (P = 0.003) due to a higher incidence of kinking and circling in the taproots of container seedlings. Kinking in the taproot was most obvious at the interface between the base of the container and the soil. In terms of lateral root form, there was initially no significant difference between stock types (P = 0.100) and little evidence of kinking and circling of lateral roots, either in the container or root plug. Although the lateral roots of container seedlings at the conclusion of the growing season were more likely to circle or be kinked than those in bare-root stock (P = 0.002), this difference was not considered to be critical to future field performance. In both stock types, lateral roots were found to radiate in all directions from the plug and there was no evidence of J-rooting or other restrictions in root system development.

Root fibrosity remained high in container seedlings and low in bare-root stock, throughout the duration of the study (Table 6). Only at the final harvest was there evidence



Fig. 4 Mean number of primary first order lateral roots along the length of the taproot and at the base of the taproot in (a) container and (b) bare-root seedlings. n = 12 seedlings per stock type. The 95% confidence interval corresponds to the mean total number of FOLRs on seedlings of each stock type at each date

	Initial values (Day 1)	Harvest 1 (Day 183)	Harvest 2 (Day 245)	Harvest 3 (Day 345)
Container Stock	3.75	3.75	3.50	3.50
Bare-root Stock	1.50	1.50	1.50	2.00
Z-score	2.99	4.06	4.21	2.98
P-value	0.005	0.000	0.000	0.003

 Table 6
 Comparison of root fibrosity scores at each harvest date for container and bare-root stock types of red oak

Values reported are the medians of 12 seedlings per stock type at each harvest date. Data were analyzed using the Wilcoxon rank sum test

of an increase in high-order root branchiness on bare-root seedlings. This result is supported by differences in the lateral:total root biomass ratio, which increased from 15% to 36% in container seedlings, while in bare-root stock it only increased by 4–13% (Fig. 1c).

Discussion

Contrasting patterns of root development may explain the differences in first growing season field performance of the container and bare-root stock types in this study. The container seedlings had a larger number of primary FOLRs, high root fibrosity, and a higher proportion of lateral root biomass than bare-root stock (Table 5). The root system of bare-root seedlings, on the other hand, was largely composed of woody taproots, had very few FOLRs and had very low root fibrosity, despite a much larger initial seedling biomass. Many researchers have noted that a high number of FOLRs and a fibrous root system are

important attributes in high quality red oak planting stock (Ruehle and Kormanik 1986; Thompson and Schultz 1995). Such modifications in root architecture are linked to increased rates of root regeneration and reductions in water stress in the period immediately after out-planting. Schultz and Thompson (1997) found that red oak seedlings with five or more FOLRs had better fifth-year survival and growth than those with fewer roots. An increase in the number of FOLRs in red oak bare-root stock can be attained by arresting the development of the taproot (Carpenter and Guard 1954; Johnson,1979; Tinus 1979). Undercutting and wrenching during the growing season (usually at a depth of 15–25 cm) causes bare-root seedlings to produce new roots in the upper soil zone to compensate for those that are lost. The effectiveness of these treatments is dependent on timing of operations and growing conditions, with practices varying widely between nurseries (Jacobs 2003). Considerable variation in the form of bare-root seedling root systems is likely unless close control is maintained over root regeneration processes.

Although, plant water relations were not assessed, it is likely that the largely woody roots of bare-root seedlings were less effective in meeting the moisture demand of the shoot system than the relatively fibrous roots of the container planting stock. Struve and Joly (1992) found that a reduction in leaf area, shoot dieback, and reduced growth were symptomatic of adjustments in photosynthate allocation to mediate the effects of transplanting moisture stress. The dramatic difference in periodic RGR reported in our study is evidence that container-grown plants acclimated more rapidly by establishing functional root-to-soil contact than did the bare-root stock. This finding is supported by the slower rate of shoot extension and higher mortality in bare-root stock.

Several important differences were evident in the structural root architecture of each stock type in this study. In container seedlings, a relatively large number of primary FOLRs developed both along the length of the taproot and at the base of the taproot, similar to earlier findings by Tinus (1979). The early air pruning of the taproot (at a depth of 10 cm) in container seedlings appears to be the major factor stimulating strong lateral root development. Johnson (1979) noted that a higher number of root initials on container seedlings, compared with bare-root stock, contributed to a greater average total length of unsuberized roots in the 10 weeks after establishment. This facilitated water absorption as soon as environmental conditions were suitable for growth in the spring, and was, therefore, a major factor in minimizing moisture stress. In our bare-root seedlings, a prolonged period of moisture stress is likely in response to a smaller number of lateral roots combined with a slow rate of initiation and regeneration of new roots after planting.

Despite the superior performance of container seedlings in this study, further improvements in planting stock quality in red oak may be possible. The pellets used in this study allowed for a taproot depth of approximately 10 cm, with a rooting volume of 250 ml. Given that red oak has a strong, woody taproot, it may be desirable to use larger containers than are commonly used for conifer stock. Jacobs et al. (2005) found that multiple-variable models, incorporating FOLR, root volume, root collar diameter and seedling height, were most effective predictors of seedling performance one and two years after out-planting. Tinus (1979) recommended a container volume of 400 ml to allow for more extensive root development in hardwood planting stock. Large containers also allow for the production of seedlings with larger and sturdier shoot systems (Hanson et al. 1987). As seedling biomass and RGR are positively correlated, the use of larger container stock may promote better out-planting performance of red oak (Tinus 1979; Zaczek et al. 1997). This is especially important on relatively nutrient-rich sites, such as former agricultural fields, where weed competition is often the most critical limiting factor in initial seedling

performance. To fully evaluate this will require more detailed research both under controlled and field conditions.

Root form is an important consideration in both container and bare-root seedlings. Under ideal conditions the lateral roots extend evenly in all directions away from the root plug. This maximises exploitation of soil resources for early seedling growth, and also ensure that the seedling develops a stable root plate. Where rooting is limited either by inappropriate stock production or planting methods, such as when J-rooting occurs, there is risk that stand stability and stem form will be compromised (Lindström and Rune 1999). Our results found little evidence for significant post-planting problems in root form or orientation in either stock type. However, we did note slightly higher levels of root kinking and circling in the container seedlings. The cause for this is not entirely clear, but could include constriction of roots due to the persistence of the net material around the Jiffy pellet, factors of planting or root restrictions due to physical soil impediments. Relatively few studies have been undertaken on seedling architecture in oak planting stock. Riedacker and Belgrand (1983), for example, studied root systems in seedlings of Quercus robur L., and found that geotropism in roots is under control of the taproot tip. When extension of the taproot is arrested, either by air pruning or undercutting, primary FOLRs that normally extend in an approximately horizontal orientation away from the taproot assume a more vertical orientation. Similar work on root regeneration and orientation may be of value as part of the continuing development and application of container technology in hardwood production systems.

Application of findings

This study confirms that many recognised advantages of container-grown nursery stock appear to hold true for the production of high quality red oak seedlings. The container stock had greater uniformity, more rapid early growth, higher root fibrosity, and a higher rate of survival relative to the bare-root seedlings. The favourable root architecture and fibrosity resulting from container design is especially noteworthy. Nevertheless, further research is warranted to realise the full benefits of container production systems for red oak. Apart from the economic issues, this work should include underlying processes that influence root initiation and branching, orientation of regenerating roots, and optimum cell volumes in relation to seedling size and field performance.

Acknowledgements We would like to thank Don Willis (Jiffy Products), Terry Blake, Vera Borsos-Matovina and John McCarron (University of Toronto), and Eva Casson-du Mont (University of Central Lancashire) for technical assistance and contributions to the research. The Ontario Industrial Research Assistance Program and the Ontario Forest Renewal Co-op provided funding and technical support for the project. The Royal Society, London provided funds for completion and presentation of this paper. We thank Doug Jacobs (Purdue University), Andrée Morneault (Ontario Ministry of Natural Resources) and two anonymous reviewers for their constructive comments on earlier versions of the manuscript.

References

Allen SE (1989) Chemical analysis of ecological materials, 2nd edn. Blackwell Scientific Publications, Oxford 368 pp

Anderson HW, Batchelor BD, Corbett CM, Corlett AS, Deugo DT, Husk CF, Wilson WR (1990) A silvicultural guide for the tolerant hardwoods working group in Ontario. Science and Technology Series, vol 7. Ontario Ministry of Natural Resources, Forest Resources Group, Sault Ste. Marie, Ontario, Toronto, 178 pp

- Brisette JC, Barnett JP, Landis TD (1991) Container seedlings. In: Duryea ML, Dougherty PM (eds) Forest regeneration manual. Kluwer Academic Publishers, Dordrecht, pp 117–141
- Burdett AN (1990) Physiological processes in plantation establishment and the development of specifications for forest planting stock. Can J For Res 20:415–427
- Carpenter IW, Guard AT (1954) Anatomy and morphology of the seedling roots of four species of the genus *Quercus.* J For 52(4):269–274
- Davis AS, Jacobs DF (2005) Quantifying root system quality of nursery seedlings and relationship to outplanting performance. New Forests 30(2/3):295–311
- Dey DC, Parker WC (1997) Morphological indicators of stock quality and field performance of red oak (*Quercus rubra* L.) seedlings underplanted in a central Ontario shelterwood. New Forests 14(2): 145–156
- Dominguez-Lerena S, Herrero Sierra N, Carrasco Manzano I, Ocaña Bueno L, Peñuelas Rubira JL, Mexal JG (2006) Container characteristics influence *Pinus pinea* seedling development in the nursery and field. For Ecol Man 221:63–71
- Fort C, Fauveau ML, Muller F, Label P, Grainier A, Dreyer E (1997) Stomatal conductance, growth and root signalling in young oak seedlings subjected to partial soil drying. Tree Physiol 17:281–289
- Garriou D, Girard S, Guehl JM, Généré B (2000) Effect of desiccation during cold storage on planting stock quality and field performance in forest species. Ann For Sci 57:101–111
- Girard S, Clément A, Boulet-Gercourt B, Guehl JM (1997) Effects of exposure to air on planting stress in red oak seedlings. Ann Sci For 54(4):395–401
- Grossnickle SC (2005) The importance of root growth in overcoming planting stress. New Forests 30(2/3):273–294
- Hanson PJ, Dixon RK, Dickson RE (1987) Effect of container size and shape on the growth of northern red oak seedlings. HortScience 22:1293–1295
- Harris RW, Dais WB, Stice NW, Long D (1971) Root pruning improves nursery tree quality. J Amer Soc Hort Sci 96(1):105–108
- Hatchell GE, Muse HD (1990) Nursery cultural practices and morphological attributes of longleaf pine bareroot stock as indicators of early field performance. Research Paper SE-277. USDA Forest Service, Asheville, NC, 34 pp
- Hunt R, Causton DR, Shipley B, Askew AP (2002) A modern tool for classical plant growth analysis. Ann Bot 90:485–488
- Jacobs DF (2003) Nursery production of hardwood seedlings. Extension Report FNR-212. Hardwood Tree Improvement and Regeneration Center, Purdue University, Indiana, 8 pp
- Jacobs DF, Salifu KF, Seifert JR (2005) Growth and nutritional response of hardwood seedlings to controlled-release fertilization at outplanting. For Ecol Man 214(1–3):28–39
- Johnson F, Paterson J, Leeder G, Mansfield C, Pinto F, Watson S (1996) Artificial regeneration of Ontario's forests: species and stock selection manual. Forest Research Information Paper 131. Ontario Ministry of Natural Resources, Ontario Forest Research Institute, Sault Ste. Marie, Ontario, 58 pp
- Johnson PS (1979) Growth potential and field performance of planted oaks. In: Holt HA, Fisher BC (eds) Proceedings: Regenerating oaks in upland hardwood forests. The 1979 John S Wright Forestry Conference. Purdue University, Indianna, pp 113–119
- Krasowski MJ (2003) Root system modifications by nursery culture reflect on post-planting growth and development of coniferous seedlings. For Chron 79(5):882–891
- Lindström A, Rune G (1999) Root deformation in plantations of container-grown Scots pine trees: effects on root growth, tree stability and stem straightness. Plant Soil 217(1–2):29–37
- Ontario Ministry of Natural Resources (OMNR) (2000) A silvicultural guide to managing southern Ontario forests, version 1.1. Ontario Ministry of Natural Resources. Queens Printer for Ontario, Toronto, 648 pp
- Ontario Ministry of Natural Resource (OMNR) (2001) A review of current and potential seedling production in Ontario for afforestation. Ontario Ministry of Natural Resources, Toronto, 32 pp
- Riedacker A, Belgrand M (1983) Morphogénèse des système racinaires des semis et boutures de chêne pédoncule. Plant Soil 71:131–146
- Ritchie GA, Dunlap JR (1980) Root growth potential: its development and expression in forest tree seedlings. N Z J For Res 10:218–248
- Ruehle JL, Kormanik PP (1986) Lateral root morphology: a potential indicator of seedling quality in northern red oak. Southeasten Forest Experiment Station. USDA Forest Service. Research Note SE-344. 6 pp
- Schultz RC, Thompson JR (1997) Effect of density control and undercutting on root morphology of 1 + 0 bareroot hardwood seedlings: five-year field performance of root-graded stock in the central USA. New Forests 13(1–3):301–314

Stroempl G (1985) Grading northern red oak planting stock. Tree Plant Notes 36(1):15–18

- Struve DK, Joly RJ (1992) Transplanted red oak seedlings mediate transplant shock by reducing leaf surface area and altering carbon allocation. Can J For Res 22:1441–1448
- Thompson JR, Schultz RC (1995) Root system morphology of *Quercus rubra* L. planting stock and 3-year field performance in Iowa. New Forests 9:225–236
- Tinus RW (1979) Use of container-grown hardwoods for reforestation. In: Holt HA, Fisher BC (eds) Proceedings: Regenerating oaks in upland hardwood forests. The 1979 John S Wright Forestry Conference. Purdue University, Indianna, pp 120–125
- Wargo PM (1976) Variation of starch content among and within roots of red and white oak trees. For Sci 22:468–471
- Wilson BC, Jacobs DF (2006) Quality assessment of temperate zone hardwood seedlings. New Forests 31:417-433
- Yemm EW, Willis AJ (1954) The estimation of carbohydrates in plant extracts by anthrone. Biochem J 57:508
- Zaczek JJ, Steiner KC, Bowersox TW (1997) Northern red oak planting stock: 6-year results. New Forests 13(1-3):177-191