



Relative Growth and Water Use of Seedlings from Three Italian *Quercus* Species

Daniel K. Struve, Francesco Ferrini, Alessio Fini, and Laura Pennati

Abstract. A species' water use characteristics and growth habits are important to urban foresters. Seedlings from three species (and two sources)—*Quercus cerris* L., *Q. pubescens* Willd., and *Q. robur* L.—were container-grown and subjected to a three day water use trial under nonlimiting soil moisture conditions. Water use varied among species and between sources within a species. Larger seedlings used more water than smaller seedlings; *Q. robur* seedlings were the tallest, 70.5 cm (27.8 in), and had the greatest water use seedling, 73.4 g (2.5 oz) water, while *Q. pubescens* and *Q. cerris* seedlings were shorter, 46 and 45 cm (18.1 and 17.7 in), and averaged 47.5 and 44.9 g (1.68 and 1.58 oz) water, respectively. *Quercus pubescens* seedlings had the highest water use cm² leaf area (0.111 g); *Q. cerris* seedlings had the highest height-adjusted water use (1.4 g water cm⁻¹ height). There were significant differences in water use between sources within species. Principal component analysis, using 20 variables, showed that seedlings of *Q. robur* and *Q. pubescens* sources clustered while seedlings of the two *Q. cerris* sources were separate from each other and the *Q. robur* and *Q. pubescens* sources. The clustering reflected the proportionally greater distribution of dry weight to shoot growth and correspondingly less to root growth of the *Q. robur* and *Q. pubescens* seedlings, than that for *Q. cerris* seedlings. The results are related to the species' relative value to nursery producers and to the potential value to urban forest managers and the potential for cultivar development.

Key Words. Drought Resistance; Dry Weight Partitioning; Seedling Growth; Water Use.

The urban environment is stressful. Tree growth and survival are limited by edaphic factors such as soil moisture, essential mineral nutrients, high pH and compaction, temperature extremes, light, airborne pollution, and mechanical injury (Fini and Ferrini 2007). A species' growth rate, drought resistance, and water use are important characteristics to urban forest managers. Oaks are adapted to various sites (from wet and humid floodplains to mesic uplands and xeric forests (Johnson et al. 2002) and thus are potential candidates for planting in the urban forest. Oaks (*Quercus* sp.) as a species are generally considered drought resistant (Abrams 1990), with drought resistance being conferred by a combination of drought avoidance and tolerance mechanisms (Abrams 1990). Three common Italian oak species—*Quercus cerris* L., *Q. robur* L., and *Q. pubescens* (Willd.)—are the subject of this study. *Quercus robur* has the greatest potential size, followed by *Q. cerris* and *Q. pubescens* (Krussman 1986).

In European forests, the genetic complex of *Quercus robur*, *Q. petraea*, and *Q. pubescens* occupy a continuum of mesic-to-xeric sites with *Q. cerris* occupying more xeric sites. The authors are unaware of any study that compares the relative drought resistance among these three species. However, *Q. robur* is considered the least and *Q. pubescens* the most drought resistant species (Fineschi et al. 2002). *Quercus pubescens* drought resistance is attributed to both drought avoidance and tolerance mechanisms. Under drought conditions, *Quercus pubescens* trees express drought avoidance traits such as: maintenance of hydraulic conductivity and high relative leaf moisture content, high assimilation rates and stomatal conductance, and low water use efficiency, attributed to a deep root system that allows access to subsurface soil moisture (Damesin and Rambal 1995; Damesin et al. 1997; Damesin et al. 1998; Nardini et al. 1998; Nardini

and Pitt 1999; Lo Gullo et al. 2003; Mediavilla and Escudero 2004; Fotelli et al. 2005; Poyatos et al. 2005; Zweifel et al. 2005; Zweifel et al. 2006). Under extreme drought, *Q. pubescens* trees close their stomata as predawn leaf moisture potentials decrease (Damesin and Rambal 1995; Tognetti et al. 1999), and can shed leaves and limit the current season's shoot growth to avoid desiccation (Nardini and Pitt 1999; Lo Gullo et al. 2003). *Quercus pubescens* also expresses drought tolerance by a rapidly increasing its leaf water potential and leaf conductance following drought relief (Tognetti et al. 1999; Galle et al. 2007). *Quercus robur* and *Q. petraea* also respond to drought using both drought avoidance and tolerance mechanisms. However, because of higher water use efficiency, *Q. petraea* seedlings are considered better adapted to xeric sites (Epron and Dreyer 1993). Under nonlimiting soil moisture conditions, *Q. robur* seedlings have a faster growth rate, but under drought they have lower rates of assimilation and stomatal conductance than *Q. petraea* seedlings (Steudle and Meshcheryakov 1996; Ponton et al. 2002; Gieger and Thomas 2005). Although *Q. robur* seedlings are not as drought resistant as *Q. petraea* seedlings, their quicker recovery from drought was considered an expression of greater drought tolerance.

Less studied is *Q. cerris*' physiological response to drought. It is considered a mesophile species (D'Alessandro et al. 2006). It expressed less stomatal control than the xeric-adapted *Fraxinus ornus* during a summer drought indicative of deep root access to subsurface soil moisture (D'Alessandro et al. 2006). One study compared *Q. cerris* and *Q. pubescens* seasonal water use (Valentini et al. 1992). Both species relied on ground water (as opposed to surface soil moisture) during a summer drought, with *Q. pubescens* being more water conserving than *Q. cerris*. Another study compared *Q. petraea* and *Q. cerris* sap flow and cavitation. *Quer-*

cus cerris trees had higher sap flow than *Q. petraea* in part due to higher water storage (Tognetti et al. 1996). Both species experienced progressive drought stress during the day, but recovered by night, demonstrating high degree of drought tolerance. Based on seasonal reductions in root hydraulic conductance relative to leaf area, leaf water potential, and leaf relative water content, *Q. cerris* was considered a drought tolerant species (Nardini et al. 1999).

No studies have compared the relative growth and drought resistance of *Q. cerris*, *Q. pubescens* and *Q. robur*, which is understandable as they are not sympatric species. However, in urban landscapes, these species are all candidates for planting and thus the relative growth rates and water use characteristics are concerns to both nursery producers and urban forest managers as they could be sympatric species in the context of the urban forest.

Oaks are genetically diverse. *Quercus robur*, *Q. petraea*, and *Q. pubescens* form a genetic complex (Bruschi et al. 2000) characterized by high genetic diversity (Dumolin-Lapegue et al. 1999; Kleinschmit 1993; Petit et al. 2002). Morphological characteristics of fruits, leaves, and twigs indicated that *Q. robur* and *Q. pubescens* are divergent species, while *Q. petraea* and *Q. pubescens* form a continuum of intermediate types (Dupouey and Badeau 1993). In contrast, genetic analysis indicated that *Quercus robur* and *Q. petraea* are less differentiated from each other than they are from *Q. pubescens* (Dumolin-Lapegue 1999). Genetic diversity is greater among individuals in mixed stands than among individuals from pure stands (Dumolin-Lapegue 1999). Recent hybridization and introgression maintain the high degree of genetic diversity found within these species (Dumolin-Lapegue 1999; Bruschi et al. 2000). Italy served as one refugium during the glaciation of Northern Europe (Kremer et al. 2002; Petit et al. 2002). Genetic analysis indicates that current Italian oak populations originated in Sicilian and Balkan refugia (Fineschi et al. 2002). Genetic analysis showed that *Quercus cerris* and *Q. suber* are clearly divergent from the other sections of the white oak complex (Petit et al., 2002; Curtu et al. 2004).

This study was conducted to determine the inter- and intra-species variation in the growth rate, dry weight partitioning, and water use of seedlings from two sources from each of three Italian oak species in order to assess the relative fitness for nursery production, and survival and growth in the urban forest.

MATERIALS AND METHODS

Acorns were collected in fall 2006 from two sources from each of three species (Table 1) and sown the following February in 0.9 L (0.23 gal), 12 cm (4.7 in) tall, square black plastic containers. In March, acorns were sown one per container in a 3:1 (by vol) peatmoss:pumice substrate supplemented with 3 kg m⁻³ (4.9 lb yd⁻³) 15N-2.9P-K7.12 controlled release fertilizer (15-7-12 eight to nine month release, Osmocote, Scotts Miracle-Gro, Marysville, OH). The seedlings were spaced container-to-container and grown under 40% neutral shade cloth (black woven polypropylene fabric, Boscato Reti, Vicenza, Italy) at the University of Florence's Polo Scientifico campus, Sesto Fiorentino. In July, they were repotted into 2.1 L (0.55 gal) containers [18 cm tall, 10 cm square (7.1 and 3.9 in, respectively) black plastic] filled with the same substrate as before. They were spaced container-to-container and returned to the shade house.

In September, 40 seedlings were randomly selected from each of the six sources—a total of 240 seedlings. The seedlings were moved to a glasshouse under 50% neutral shade. The plants were spaced at twice the container diameter in a randomized complete block design with one replication on each of two greenhouse benches.

Air temperature, relative humidity and photosynthetically active radiation (PAR, 400 to 700 nm) were recorded every half hour using air temperature and relative humidity HD 9008TR (Delta Ohm, Padova, Italy) and PAR sensor LP PAR01, with sensors placed at mid-canopy height.

Daily water use was calculated by first watering the substrate to capacity, allowing the substrate to drain for one hour and weighting the individual seedling-substrate-container units. The seedlings were re-weighed approximately 24 hours later. The seedlings were then re-watered and the weighing schedule repeated for the following two days. The differences in daily weights were attributed to transpiration. The daily differences in weights were averaged to derive the average daily water use values for individual seedling during the three-day water use period.

At the end of the three-day water use period, all but four seedlings from each source (these seedlings were used in another study) were destructively harvested and the following data collected: plant height (cm), leaf number and area (cm²), and leaf, stem, and fine and coarse (root diameters of < 2 and ≥ 2 mm, respec-

Table 1. Description of *Quercus* species used in the experiment.

Species	Source No.	Provenance	Description
<i>Q. cerris</i>	1	Vivai Gubbio, Pupaggi di Sellano	bulked seed lot collected from selected mother trees in single-species stands and purchased from a commercial forestry nursery Latitude 42°53' 25".36 N; Longitude 12°55' 43"51 E; elevation: 547 m (1,777 ft).
	2	Vivaio Camaldoli, zona Cerreta	bulked seed lot collected from selected mother trees in single-species stands and purchased from a commercial forestry nursery Cerreta Latitude 43° 49' 23".55 N; Longitude 11°49' 09"07 E; elevation: 500 m (1,625 ft)
<i>Q. pubescens</i>	5	Vivaio Gubbio, Bazzano Inferiore	bulked seed lot collected from selected mother trees in mixed-species stands and purchased from a commercial forestry nursery Bazzano Latitude 42°46' 45".71 N; Longitude 12°47' 08.41 E; elevation: 384 m (1,248 ft)
	6	Vivaio Camaldoli, zona Cerreta	bulked seed lot collected from selected mother trees in mixed-species stands and purchased from a commercial forestry nursery Amiata Latitude 42°54' 00".00 N; Longitude 11°37' 48 E; elevation: 604 m (1963 ft)
<i>Q. robur</i>	7	Vivaio Gubbio, Pineta St. Vitale	bulked seed lot collected from selected mother trees in mixed-species stands and purchased from a commercial forestry nursery Pineta Latitude 44°29' 38".62 N; Longitude 12°16' 43"80 E; elevation: 3 m (10 ft).
	8	Parco cascine, Firenze	seed collected from a single tree in urban park surrounded by <i>Q. robur</i> trees Cascine Latitude 43°47' 07".61; N Longitude 11°12'50"39 E; elevation: 47 m (153 ft)

tively) root dry weights (g). Leaf area and number were estimated by scanning a subsample of the leaves (Mustek Scan Express A3 USB) and with image analysis software (Image Tool, U. of Texas Health Services Center, San Antonio, TX), also using the proportion of the subsample weight-to-total leaf weight to estimate total leaf number and area. From this data, the following variables were calculated: total shoot dry weight (leaves + shoot dry weights), total root dry weight (fine + coarse root dry weight), total plant dry weight (total shoot + total root dry weight), percent of total plant dry weight in leaves, roots, stems, fine and coarse roots, shoot-to-root dry weight ratio (total shoot dry weight/total root dry weight), water transpiring-to-absorbing ratio [leaf surface area/ fine root dry weight ($\text{cm}^2 \text{g}^{-1}$)], specific leaf weight ($\text{cm}^2 \text{g}^{-1}$) and average height adjusted water use ($\text{g cm}^{-2} \text{seedling height day}^{-1}$).

Data were subject to multivariate analysis of variance using the general linear model procedure (SPSS, Version 12.0) as a fixed effects model with two replications with 20 seedlings per replication and seed source. Means were separated using the Student-Neuman-Kuels test at the $\alpha \leq 0.05$ level of significance. The data were also subjected to principal component analysis (SPSS, Version 12.0) by seed source using the 20 variables described above.

RESULTS AND DISCUSSION

Substrate bulk density averaged 0.43 g cm^{-3} (Table 2). The substrate had 63.7% total pore space and 46.8% water-filled pore space at field capacity (Table 2). The 2.1 L substrate volume contained an estimated $0.98 \pm 0.04 \text{ L}$ ($0.25 \text{ gal} \pm 0.01$) of water. Maximum water loss in any one day during the three day trial was $< 0.145 \text{ L}$ (0.04 gal), thus, the plants were not under substrate moisture stress during the three day water use period. Average PAR between sunrise and sunset ranged from 160 to $180 \mu\text{moles m}^{-2} \text{ s}^{-1}$; daily average relative humidity ranged from 47% to 51% and average daily temperature ranged from 19 to 21°C (67 to 70°F). The greenhouse was cooled by convection through a combination of side wall and roof vents.

Table 2. Physical properties of the 3:1 peatmoss:pumice (by vol) substrate in 18 cm tall, 2.1 L volume container.

Variable	Mean	Standard deviation
Bulk density (g cm^{-3})	0.43 ²	0.05
Total pore space (%)	63.7	2.3
Water-filled pore space	46.8	2.0
Air-filled pore space	16.5	4.2

² Each value is the mean of five containers.

Water Use

Seedlings of *Quercus robur* were the tallest and had the greatest water use per seedling, but had lower height-adjusted water use than *Q. cerris* sources (Table 3). However, water use per cm^2 leaf surface was lower than *Q. pubescens* sources. Within each species, there were differences between the sources in seedling height, water use per cm^2 leaf area and height-adjusted water use, except between the *Q. robur* sources for water use per seedling and between the *Q. cerris* sources for height-adjusted water use (Table 4). Among all the sources, water use per seedling varied by almost 200% (*Q. cerris* Amiata and *Q. pubescens* Cerreta sources versus both *Q. robur* sources, 36.0 and 32.6 g versus 72.1 and $74.7 \text{ g seedling}^{-1} \text{ day}^{-1}$, respectively) (Table 4). The *Q. robur* Cascine source had lower water use per cm^2 leaf

area than the Pineta source, which was higher than the *Q. cerris* Sellano source, and similar to the Amiata source, and lower than both *Q. pubescens* sources (Table 4). Height-adjusted water use varied by 80% among all the sources [*Q. robur* Cascine versus *Q. pubescens* Cerreta (1.2 versus $1.5 \text{ g cm}^{-2} \text{ height day}^{-1}$)]. Thus, the basis for the differences in water use among the sources was complex. Some of the differences in water use per seedling can be attributed to differences in seedling size; larger seedlings, relative to shorter seedlings, tended to have greater leaf area and greater water use per seedling (Figure 1). However, the correlations between seedling height and water use per seedling were low; R^2 values for individual sources were < 0.05 , except for the *Q. pubescens* Cerreta source where it was 0.21. Also, there were low correlations between water use per seedling and height-adjusted water use (Figure 2). The relationship between height-adjusted water use and seedling height of the six seed sources used in this study was markedly different from that of six Eastern North American *Quercus* species. For the Eastern North American species, when the individual seedling heights within a 1/2-sib family were plotted against height-adjusted water use, a graph similar to an exponential decay curve was seen (Struve et al. 2006). No such pattern was seen within the Italian seed sources.

As a summary example, the seedlings in the tallest source, *Q. robur* Cascine, used the highest water seedling⁻¹, but had the lowest water use per cm^2 leaf area and the lowest height-adjusted water use. In contrast, the seedlings in the shortest source, *Q. pubescens* Cerreta, used the least water per seedling, but had the greatest water use per cm^2 leaf area and the highest height-adjusted water use. Further, Figures 1 and 2 reveal significant variation within source variation in water use characteristics. Thus, basing a species' water use characteristics on a single water use parameter or on a single seed source can be misleading. The great variation in water use characteristics between species, sources and within sources presents an opportunity for genetic improve-

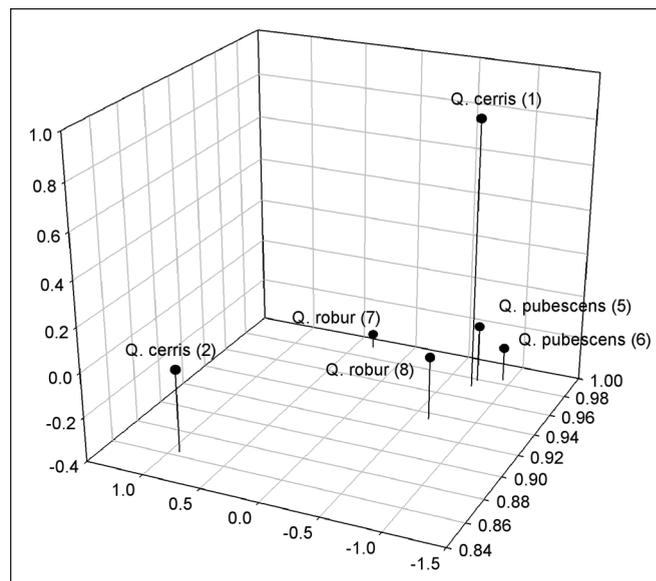


Figure 1. The relationship among seed sources, two sources from each of three Quercus species (cerris, pubescens, and robur). Total shoot length, total plant dry weights and leaf area-to-fine root dry weight were plotted against the first, second and third (respectively) principal component axes. The numbers in parenthesis refer to the seed source numbers in Table 1.

Table 3. Water use of three *Quercus* species over three days under greenhouse conditions.

Species	Height (cm)	seedling-1	Average daily water use (g day ⁻¹)	
			leaf area (cm ²)	Height-adjusted (cm ⁻¹) ^z
<i>Q. cerris</i>	45.3A ^y	47.5A	0.091A	1.4B
<i>Q. pubescens</i>	46.0A	44.9A	0.111B	1.3A
<i>Q. robur</i>	70.5B	73.4B	0.084A	1.3A

^z Height-adjusted water use was calculated by dividing the average daily water use by seedling height.

^y Means within a column followed by different letters are significantly different from each other at the $\alpha = 0.05$ level using the Student-Neuman-Kuels test. Each value is the mean of 72 plants.

Table 4. Water use of two sources from three *Quercus* species over three days under greenhouse conditions.

Species	Source	Height (cm)	Average daily water use (g day ⁻¹)		
			seedling ⁻¹	leaf area (cm ²)	Height-adjusted (cm ⁻¹) ^z
<i>Q. cerris</i>	Sellano	54.2 C ^y	58.9B	0.087B	1.4B
	Amiata	36.3AB	36.0A	0.094C	1.3AB
<i>Q. pubescens</i>	Bazzano	62.2D	57.2B	0.104D	1.2A
	Cerreta	29.7A	32.6A	0.118E	1.5BC
<i>Q. robur</i>	Pineta	67.1D	72.1C	0.098CD	1.4B
	Cascine	73.9E	74.7C	0.070A	1.2A

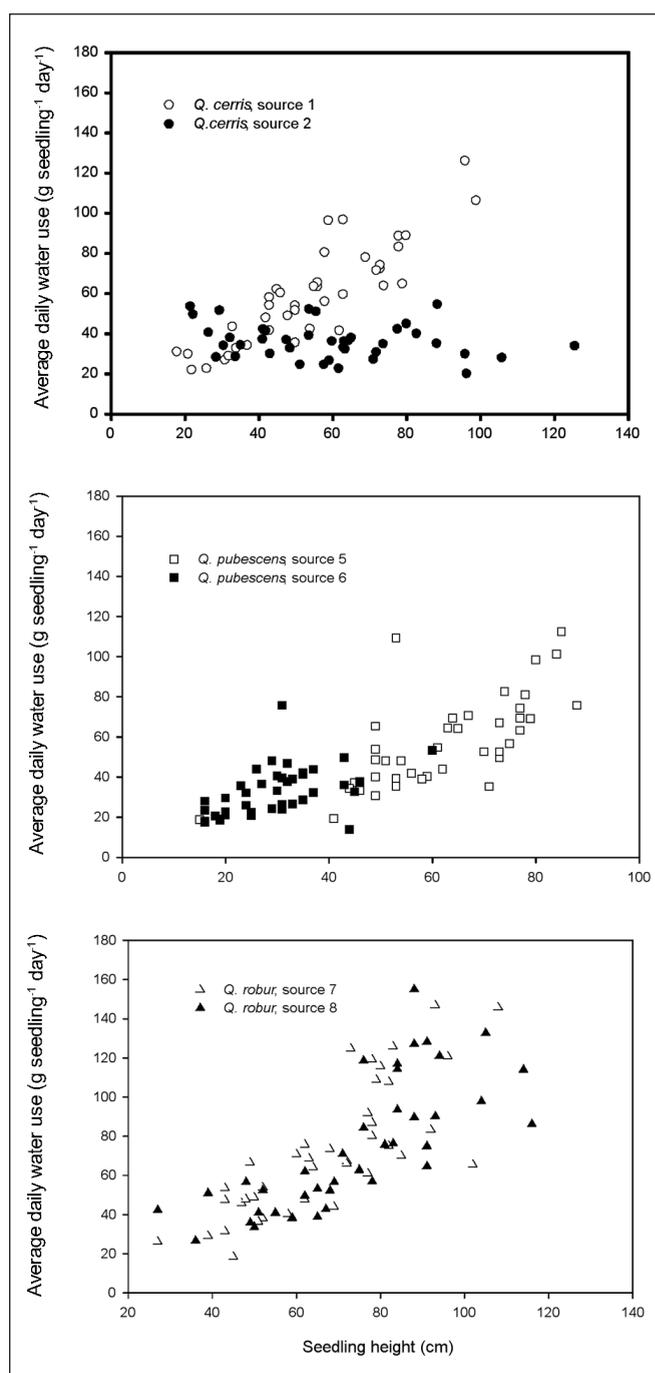
^z Height-adjusted water use was calculated by dividing the average daily water use by seedling height.

^y Means within a column followed by different letters are significantly different from each other at the $\alpha = 0.05$ level using the Student-Neuman-Kuels test. Each value is the mean of 36 plants.

ment through sexual or asexual methods. For instance, tall seedlings with either high or low height-adjusted water use could be identified within each seed source. Undetermined is whether the differences in an individual seedling's height-adjusted water use are related to adaptive features such as drought resistance, that would confer increased fitness to the urban forest environment.

Growth

For the two *Q. cerris* sources, three components in a principal component analysis that used 20 variables, extracted 79% and 74% (sources 1 and 2, respectively) of the total variation. Three components extracted 80% and 77% (sources 5 and 6) and 83% and 79% (sources 7 and 8) of the total variation for *Q. pubescens* and *Q. robur* sources, respectively. In the first component, factors associated with aboveground growth and dry weight (height, leaf number and area, total shoot dry weight, and shoot-root dry weight ratio) were highly correlated (> 0.80) and loaded positively on the first principal component axis, while root system associated factors (percent of root dry weight and percent coarse root dry weight) and water use cm⁻² leaf surface area, loaded negatively. In the second component, root-associated variables such as total, fine, and coarse root dry weight loaded positively while shoot factors as shoot-to-root dry weight ratio and percent shoot dry loaded negatively. In the third component, percent leaf area and leaf area-to-fine root dry weight ratio loaded positively while percent fine root and total shoot dry weight loaded negatively. Plotting total shoot length, total plant dry weight, and leaf area-to-fine root dry weight on the first, second, and third component axes, respectively, showed that sources 5, 6, 7, and 8 (*Q. pubes-*

**Figure 2. Water use per seedlings plotted against seedling height for two sources from each of three *Quercus* species.**

ens and *Q. robur*) clustered together while the two *Q. cerris* sources were separated from each other and the other species (Figure 3).

Quercus robur seedlings had greater leaf number and leaf area, greater leaf, stem and total plant dry weights and a larger shoot-to-root dry weight ratio than *Q. cerris* and *Q. pubescens* seedlings (Table 5). *Quercus robur* seedlings had similar coarse and total root dry weights as *Q. pubescens* seedlings, which was lower than that for *Q. cerris* seedlings. *Quercus robur* seedlings had greater specific leaf area than *Q. pubescens* seedlings, but lower than *Q. cerris* seedlings. As with the seedling height and water use data,

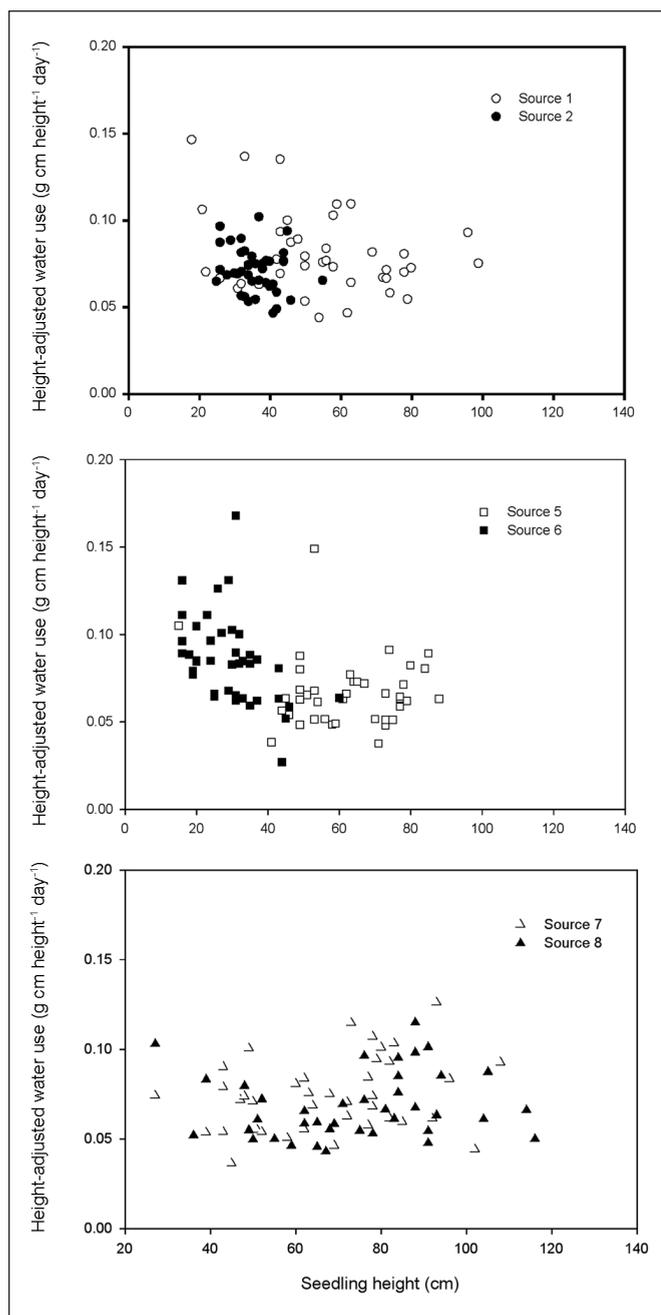


Figure 3. Height-adjusted water use (g water per cm seedling height per day) for two sources from each of three *Quercus* species.

there were significant differences between the sources within a species (Table 6). The extremes among the sources were *Quercus robur* seedlings from the Cascine source which had the greatest leaf area and dry weights, except for coarse and total root dry weights which were greatest in seedlings from the *Q. cerris* Amiata source.

Quercus robur seedlings had a similar percentage of total plant weight in leaf tissue as *Q. pubescens* seedlings, but the highest percentage of total plant dry weight in stem tissue, the greatest leaf area-to-fine root dry weight ratio and the lowest percentage of total plant dry weight in total, fine and coarse root dry weights (Table 7). *Quercus cerris* seedlings had the greatest

percentage of total plant dry weight in total root, fine, and coarse root dry weights and the greatest leaf area ratio (Table 7). There were significant differences among the sources in percentage of total plant dry weight in leaves, stems and root tissue, leaf area-to-fine root dry weight ratio and leaf area ratio (Table 8). One of the most striking differences among the sources was the range in the leaf area-to-fine root (the water transpiring-to-water absorbing) ratios. The greatest difference among the sources exceeded 250%, 321.3 versus 128.3 cm² g⁻¹, for the *Q. robur* Cascine versus *Q. cerris* Amiata, respectively. Almost as great was the difference in the leaf area-to-fine root dry weight ratio between the two *Q. cerris* sources, 340.5 versus 128.3 cm² g⁻¹, a 265% difference. It is not known whether these differences reflect differences in root system water absorbing efficiency or in leaf water use efficiency.

Quercus robur seedlings had a resource allocation pattern of a species capable of rapid growth: a greater investment in aboveground biomass at the expense of belowground biomass: more leaves of smaller size, a greater percentage of plant dry weight in stem and leaf tissues and larger shoot-to-root ratio. As a consequence of the relatively high investment in aboveground biomass, it had the greatest water use per seedling, but had the compensating adaptive traits of relatively lower water use cm⁻² leaf area and high leaf area-to-fine root dry weight ratio. *Quercus pubescens* seedlings, relative to *Q. robur* seedlings, had a lower investment in aboveground biomass and a relatively greater investment in root tissue. They also had the highest water use per leaf area and lowest leaf area-to-fine root dry weight ratio. *Quercus cerris* seedlings had a higher investment root biomass than *Q. pubescens* and *Q. robur* seedlings. However, there were significant differences among the sources in their growth habits and water use characteristics; the Bazzano, Cerreta, Cascine and Pineta (*Q. pubescens* and *Q. robur*, respectively) had similar growth and water use characteristics while the Sellano and Amiata (*Q. cerris*) sources had different growth habits and water use characteristics. The results illustrate the remarkable degree of variation between and within these seed sources and the great potential for genetic improvement to address a changing world climate and the harsh environmental conditions associated with urban forests. The great degree of variation occurred whether the seeds were collected from an individual tree (*Q. robur* Cascine), mixed-species stands (both *Q. pubescens* sources) or single-species stands (both *Q. cerris* sources).

From a nursery production aspect, where crop value is determined by the rate of height and caliper growth, *Q. robur* is the most desired species, but the species with the highest water use per seedling. The *Q. pubescens* Bazzano source is a possible alternative to the two *Q. robur* sources. Those seedlings grew nearly as tall, but the seedlings of this source used 30% less water per seedling than the Cascine seedlings. The Bazzano source seedlings also had a more efficient root system than the Cascine seedlings absorbing 0.00038 and 0.00017g water day⁻¹ g⁻¹ fine root dry weight, respectively. Seedlings of the *Q. pubescens* Cerreta source had the most efficient root system, 0.00065 g water per day per g fine root dry weight. As a species, *Q. pubescens* can maintain high rates of hydraulic conductance during drought which was attributed to a deep rooting habit (Naraini et al. 1998; Nardini and Pitt 1999; Lo Gullo et al. 2003; Poyatos et al. 2005; Zweifel et al. 2006). The apparent water absorbing efficiency of

Table 5. Leaf number and area and dry weights of plants from three *Quercus* species.

Species	no.	Leaf area (cm ²)	leaf	shoot	Dry weight (g)			total plant	Shoot to root dry weight ratio	Specific leaf area (cm ² g)
					Root type ^z		total			
					fine	coarse				
<i>Q. cerris</i>	22.9A ^z	532.9B	3.3A	3.6A	2.5AB	6.6B	9.1B	15.9A	0.8A	161.5C
<i>Q. pubescens</i>	34.3B	414.0A	31.2B	23.4B	2.2A	3.8A	6.0A	60.6B	9.8B	13.2A
<i>Q. robur</i>	56.2C	898.5C	59.1C	53.4C	2.9B	4.0A	6.9A	119.4C	18.2C	15.4B

Means within a column followed by different letters are significantly different from each other at the $\alpha = 0.05$ level using the Student-Neuman-Kuels test. Each value is the mean of 72 plants.

^z Fine roots were < 2 mm in diameter; coarse roots were ≥ 2 mm diameter.

Table 6. Leaf number and area and dry weights of plants from two *Quercus* sources from each of three species.

Species	Source	no.	Leaf area (cm ²)	leaf	shoot	Dry weight (g)			Total plant	Shoot to root dry weight ratio	Specific leaf area (cm ² g)
						Root type ^z		total			
						fine	coarse				
<i>Q. cerris</i>	Sellano	28.9AB ^y	680.9BC	3.8A	4.1A	2.0A	5.1B	7.1A	15.0A	0.6A	179.2D
	Amiata	16.8A	385.0A	2.7A	3.1A	3.0BC	8.0C	11.0B	16.8A	0.3A	142.6C
<i>Q. pubescens</i>	Bazzano	39.2B	552.4B	42.2C	32.7B	2.3AB	3.2A	5.5A	80.5C	5.9C	13.1A
	Cerreta	9.3AB	275.6A	20.5B	14.3A	2.1A	4.3AB	6.4A	41.1B	2.2B	13.4A
<i>Q. robur</i>	Pineta	32.7AB	736.6C	48.5C	50.8CB	2.6BC	3.8A	6.4A	105.7D	7.6D	15.2B
	Cascine	79.7C	1060.4D	69.7D	60.8C	3.3C	4.1AB	7.4A	133.0E	9.4E	15.2B

^z Fine roots were < 2 mm in diameter; coarse roots were ≥ 2 mm diameter.

^y Means within a column followed by different letters are significantly different from each other at the $\alpha = 0.05$ level using the Student-Neuman-Kuels test. Each value is the mean of 36 plants.

Table 7. Percentage of total plant dry weight in leaves, roots and stems, the leaf area-to-fine root dry weight sand leaf area ratios of seedlings from three *Quercus* species.

Species	Total plant dry weight (%)					Leaf area to fine root dry weight (cm ² g ⁻¹)	Leaf area ratio (cm ² g)
	leaves	stems	Root type ^z				
			fine	coarse	total		
<i>Q. cerris</i>	20.6A ^y	22.5A	15.6C	41.3B	56.9B	213.2A	33.3B
<i>Q. pubescens</i>	51.5B	38.6B	3.6B	6.3A	9.9A	188.2A	6.8A
<i>Q. robur</i>	49.5B	44.7C	2.4A	8.4A	5.8A	309.8B	7.6A

Means within a column followed by different letters are significantly different from each other at the $\alpha = 0.05$ level using the Student-Neuman-Kuels test. Each value is the mean of 72 plants.

^z Fine roots were < 2 mm in diameter; coarse roots were ≥ 2 mm diameter.

Table 8. Percentage of total plant dry weight in leaves, roots and stems, the leaf area-to-fine root dry weight sand leaf area ratios of seedlings from two provenances of three *Quercus* species.

Species	Source	Total plant dry weight (%)					Leaf area to fine root dry weight (cm ² g)	Leaf area ratio (cm ² g)
		leaves	stems	Root type ^z				
				total	fine	coarse		
<i>Q. cerris</i>	Sellano	25.3B ^y	27.4B	47.3B	13.3C	34.0C	340.5C	45.3D
	Amiata	16.0A	18.5A	65.5C	17.9D	47.6D	128.3AB	22.9C
<i>Q. pubescens</i>	Bazzano	52.5D	40.7D	6.8A	2.8A	4.0A	240.2B	6.9A
	Cerreta	34.1C	23.8C	42.1B	34.9B	7.2B	13.1A	6.7A
<i>Q. robur</i>	Pineta	45.8C	48.1E	6.1A	2.6A	3.5A	283.3BC	7.2AB
	Cascine	50.5D	44.2D	5.4A	2.4A	3.0A	321.3C	8.0B

^z Fine roots were < 2 mm in diameter; coarse roots were ≥ 2 mm diameter.

^y Means within a column followed by different letters are significantly different from each other at the $\alpha = 0.05$ level using the Student-Neuman-Kuels test. Each value is the mean of 36 plants.

the root system, g water day⁻¹ g⁻¹ fine root dry weight, was another contributing factor to maintenance of hydraulic conductivity. The Bazzano source seedlings had lower total plant dry weight than the Cascine seedlings, but part of the lower dry weight was attributed to lower leaf weight, which is not a factor in total plant dry weight after fall defoliation. Also, as a species, *Q. pubescens* is considered more drought resistant than *Q. robur* making it putatively better adapted to those urban environments where drought

is the main constraint to growth and survival. Interestingly, the Bazzano source had similar dry weight distribution as the *Q. robur* seedling suggesting that it had a similar growth habit—one that is associated with more rapid growth, a positive factor for nursery managers. Because of the relatively slower growth (the result of its greater biomass allocation to the root system) of the seedlings from the two *Q. cerris* sources, there is apparently no compelling reason for a nursery manager to produce *Q. cerris*

plants for urban greening purposes. However, the Amiata source, the slowest growing source, had the second highest root system efficiency, $0.00060 \text{ g water g}^{-1} \text{ fine root dry weight day}^{-1}$ and the conservative growth habit of the Amiata and Cerreta sources are of interest to urban foresters. The findings of this study show the great variation between and within species in economically and physiologically important traits to the nursery producers and urban foresters. More studies are needed to find other potentially better adapted sources for nursery production and the urban forest environment in a rapidly changing world climate.

There was significant variation in growth and water use characteristics among the seedlings from the six seed sources (two seed source of each of three species) tested. Average seedling height differed by 229% among the seed sources. The *Q. robur* sources, and to a lesser degree the *Q. cerris* Sellano and the *Q. pubescens* Bazzano sources, had a resource allocation pattern of a species capable of rapid growth: a greater investment in above-ground biomass at the expense of belowground biomass. In part, because of greater seedling size, *Q. robur* Cascine seedlings used the most water seedling⁻¹ day⁻¹, but had the lowest water use cm⁻² leaf area and highest leaf area-to-fine root dry weight ratio. *Q. pubescens* seedlings had the highest water use cm⁻² leaf area and seedlings of the *Q. pubescens* Cerreta source, which was the shortest source, had the highest height-adjusted water use (g water day⁻¹ cm⁻² seedling height). There were low correlations between seedling height and height-adjusted water use, which would allow for the selection of any plant height and height-adjusted water use combination. Thus, seedlings with rapid growth and a conservative water use habit (fast growing seedling with low height-adjusted water use) could be selected. There is great variation between and within these three oak species in economically and ecologically important traits from which to select and develop individuals or populations better adapted to stressful urban forest sites and to a changing global climate. Additional studies, preferably conducted with clonal material, are needed to determine if the seedling growth and water use characteristics described here are also expressed in larger sized plants.

These species are not commonly available in North American nurseries. However, they may be candidates for North American urban forests. These Apennine seed sources are found on limestone-derived shallow soils (www.soilmaps.it/download/csi-brochure_se.a4.pdf). Thus, they have evolved in soil conditions not unlike those typical of the urban forests. The seed sources were collected from European Plant Hardiness Zones 8 to 9 [-12 to -1°C (10 to 30°F), www.uk.gardenweb.com/forums/zones/hx-eleg.gif]. However, the species are found in colder climates [Zone 6; (-23 to -18°C or -10 to 0°F); forest.jrc.it/forest_and_climate/forest_trends/spdistribution]. There are specimens of *Quercus cerris*, *Q. pubescens*, and *Q. robur* at Dawes Arboretum, USDA Plant Hardiness Zone 5b/6a, so the species' potential adaptive range is great. Further research is needed to determine the adaptive potential of these species to urban forests of North America.

LITERATURE CITED

- Abrams, M.D. 1990. Adaptation and responses to drought in *Quercus* species of North America. *Tree Physiology* 7:227–238.
- Bruschi, P.G.G., Vendramin, F., Bussotti, and P. Grossoni. 2000. Morphological and molecular differentiation between *Q. petraea* (Matt.) Liebl. and *Quercus pubescens* Willd. (Fagaceae) in Northern and Central Italy. *Annals of Botany* 85:325–333.
- Curtu, A.L., R. Finkeldey, and O. Gailing. 2004. Comparative sequencing of a microsatellite locus reveals size homoplasy within and between European oak species (*Quercus* spp.). *Plant Molecular Biology* 22:339–346.
- D'Alessandro, A., Saracino, and M. Borghetti. 2006. Thinning affects water use efficiency of hardwood saplings naturally recruited in a *Pinus radiata* D. Don plantation. *Forest Ecology and Management* 222:116–122.
- Damesin, C., and S. Rambal. 1995. Field study of leaf photosynthetic performance by a Mediterranean deciduous oak tree (*Quercus pubescens*) during a severe summer drought. *New Phytologist* 131:159–167.
- Damesin, C., S. Rambal, and R. Joffre. 1997. Between-tree variations in leaf $\delta^{13}\text{C}$ of *Quercus pubescens* and *Quercus ilex* among Mediterranean habitats with different water availability. *Oecologia* 111:26–35.
- Damesin, C., S. Rambal, and R. Joffre. 1998. Seasonal and annual changes in leaf $\delta^{13}\text{C}$ in two co-occurring Mediterranean oaks: relations to leaf growth and drought progression. *Functional Ecology* 12:778–785.
- Dumolin, S., A. Kremer, and R.J. Petit. 1999. Are chloroplast and mitochondrial DNA variation species independent in oaks? *Evolution* 53(5):1406–1413.
- Dupouey, L.L., and V. Badeau. 1993. Morphological variability of oaks [*Quercus robur* L., *Quercus petraea* (Matt.) Liebl., *Quercus pubescens* Willd.] in northeastern France: preliminary results. *Annals of Forest Science* 50, Suppl. 1. 35s–40s.
- Epron, D., and E. Dreyer. 1993. Long-term effects of drought on photosynthesis of adult oak trees [*Quercus petraea* (Matt.) Liebl. and *Q. robur* L.] in a natural stand. *New Phytologist* 125:381–389.
- Fineschi, S., D. Turchini, P. Grossoni, R.J. Petit, and G.G. Vendramin. 2002. Chloroplast DNA variation of white oaks in Italy. *Forest Ecology and Management* 156:103–114.
- Fini A., F. Ferrini. 2007. Influenza dell'ambiente urbano sulla fisiologia e la sulla crescita degli alberi. *Italus Hortus* 14(1):9–24.
- Fotelli, M., K. Radoglou, and H. Constantinidou. 2005. Water stress responses of seedlings of four Mediterranean oak species. *Tree Physiology* 20:1065–1075.
- Galle, A., P. Haldimann, and U. Feller. 2007. Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. *New Phytologist* 174:799–810.
- Gieger, T., and F. Thomas. 2005. Differential response of two Central-European oak species to single and combined stress factors. *Trees* 19:607–618.
- Johnson, P.J., S.R. Shifley, and R. Rogers. 2002. Oak-dominated ecosystems. In: *The Ecology and Silviculture of Oaks*. CABI Publishing, N.Y. pp. 8–53.
- Kleinschmit, J. 1993. Intraspecific variation of growth and adaptive traits in European oak species. *Annals of Forest Science* 50, Suppl. 1. 166s–185s.
- Kremer, A., J. Kleinschmit, J. Cottrell, E.P. Cundall, J.D. Deans, A. Ducouso, A.O. Konig, A.J. Lowe, R.C. Munro, R.J. Petit, and B.R. Stephan. 2002. Is there a correlation between chloroplastic and nuclear divergence, or what are the roles of history and selection on genetic diversity in European oaks. *Forest Ecology and Management* 156:75–87.
- Krussman, G. 1986. *Manual of Cultivated Broad-Leaved Trees & Shrubs*. Bol. II, Prov.-Z. Epp Translator. Timber Press, Portland, OR.
- Lo Gullo, M.A., S. Salleo, R. Rosso & Trifilo. 2003. Drought resistance of 2-year-old saplings of Mediterranean forest trees in the field: relations between water relations, hydraulics and productivity. *Plant and Soil* 250:259–272.

- Mediavilla, S., and A. Escudero. 2004. Stomatal responses to drought of mature trees and seedlings of two co-occurring Mediterranean oaks. *Forest Ecology and Management*, 187:281–294.
- Nardini, A., M. Lo Gullo, and S. Salleo. 1999. Competitive strategies for water availability in two Mediterranean *Quercus* species. *Plant, Cell and Environment* 22:109–116.
- Nardini, A., M.A. Lo Gullo, and S. Salleo. 1998. Seasonal changes of root hydraulic conductance (KRL) in four forest trees: an ecological interpretation. *Plant Ecology* 139:81–90.
- Nardini, A., and F. Pitt. 1999. Drought resistance of *Quercus pubescens* as a function of root hydraulic conductance, xylem embolism and hydraulic architecture. *New Phytologist* 143:485–493.
- Petit, R.J., U.M. Csaikl, S. Bordacs, K. Burg, E. Coart, J. Cottrell, B. Van Dam, J.D. Deans, S. Cumolin-Lapegue, S. Fineschi, R. Finkeldey, A. Gillies, I. Glaz, P.G. Goicoechea, J.S. Jensen, A.O. König, A.J. Lowe, S.F. Madsen, G. Matyas, R.C. Munro, M. Olalde, M. Pemonge, F. Popescu, D. Slade, H. Tabbener, D. Turchini, S.G. M. De Vries, B. Ziegenhagen, and A. Kremer. 2002. Chloroplast DNA variation in European white oak Phylogeography and patterns of diversity based on data from over 2600 populations. *Forest Ecology and Management* 156:5–26.
- Ponton, S., J. Dupouey, N. Breda, and E. Dreyer. 2002. Comparison of water-use efficiency of seedlings from two sympatric oak species: genotype x environment interactions. *Tree Physiology* 22: 413–422.
- Poyatos, R., P. Llorens, and F. Gallart. 2005. Transpiration of montane *Pinus sylvestris* L. and *Q. pubescens* Willd. Forest stands measured with sap flow sensors in NE Spain. *Hydrology and Earth System Sciences* 9:493–505.
- Steudle, E., and A. Meshcheryakov. 1996. Hydraulic and osmotic properties of oak roots. *Journal of Experimental Botany* 47:387–401.
- Struve, D.K., P. Sternberg, N. Drunasky, K. Bresko, and R. Gonzalez. 2006. Growth and water use characteristics of six eastern North American oak (*Quercus*) species and the implications of urban forestry. *Arboriculture & Urban Forestry* 32:202–213.
- Tognetti, R., A. Raschi, C. Beres, A. Fenyvesi, and H. Ridder. 1996. Comparison of sap flow, cavitation and water status of *Quercus petraea* and *Quercus cerris* trees with special reference to computer tomography. *Plant, Cell and Environment* 19:928–938.
- Tognetti, R., A. Longobucco, F. Miglietta, and A. Raschi. 1999. Water relations, stomatal response and transpiration of *Quercus pubescens* trees during summer in a Mediterranean carbon dioxide spring. *Tree Physiology* 19:261–270.
- Valentini, R., G.E. Scarascia Mugnozza, and J. Ehleringer. 1992. Hydrogen and carbon isotope ratios of selected species of a Mediterranean Macchia ecosystems. *Functional Ecology* 6:627–631.
- Zweifel, R., L. Zimmermann, and D.M. Newbery. 2005. Modeling tree water deficit from microclimate: and approach to quantifying drought stress. *Tree Physiology* 25:147–156.
- Zweifel, R., L. Zimmerman, F. Zeugin, and D. Newbery. 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *Journal of Experimental Botany* 57:1445–1459.

Daniel K. Struve (corresponding author)
Ohio State University
Department of Horticulture and Crop Science
241B Howlett Hall 2001 Fyffe Ct.
Columbus, OH 43210, U.S.

Francesco Ferrini
Universita degli Studi di Firenze
Dipartimento di Ortoflorofrutticoltura
Firenze, Italy

Alessio Fini
Universita degli Studi di Firenze
Dipartimento di Ortoflorofrutticoltura
Firenze, Italy

Laura Pennati
Universita degli Studi di Firenze
Dipartimento di Ortoflorofrutticoltura
Firenze, Italy

Résumé. Les caractéristiques relatives aux besoins en eau d'une espèce ainsi que ses caractéristiques de croissance sont des aspects importants pour les forestiers urbains. Des semis de trois espèces (en provenance de deux sources) – *Quercus cerris* L., *Q. pubescens* Willd. et *Q. robur* L. – ont été produits en contenant et soumis à un essai de trois jours quant aux besoins en eau, et ce sous des conditions non limitées d'humidité de sol. Le besoin en eau variait entre les espèces et entre les sources d'une même espèce. Les semis plus gros avaient des besoins en eau plus élevés que les semis plus petits; les semis de *Q. robur* étaient les plus gros (70,5 cm) et avaient les plus grands besoins en eau (73,4 g d'eau), tandis que ceux de *Q. pubescens* et *Q. cerris* étaient plus petits (46 et 45 cm) et avaient des besoins moyens en eau de 47,5 et de 44,9 g d'eau respectivement. Les semis de *Q. pubescens* avaient les plus grands besoins en eau par centimètre carré de surface foliaire (0,11 g); les semis de *Q. cerris* avaient les hauteurs ajustées en eau les plus élevées (1,4 g d'eau par centimètre de hauteur). Il n'y avait pas de différence significative dans les besoins en eau entre les différentes sources au sein d'une même espèce. La principale composante d'analyse, faite au moyen de 20 variables, a montré que les sources de semis de *Q. robur* et de *Q. pubescens* étaient groupés alors que les deux sources de *Q. cerris* étaient séparées l'une de l'autre tout comme de celles de *Q. robur* et de *Q. pubescens*. Les grappes reflètent la plus grande distribution proportionnelle de la masse sèche de la croissance des pousses et de la correspondance moindre pour la croissance des racines chez les semis de *Q. robur* et *Q. pubescens*, et ce par rapport aux semis de *Q. cerris*. Les résultats sont mis en relation avec les valeurs relatives chez les pépiniéristes, la valeur potentielle pour les gestionnaires de forêts urbaines et le potentiel de développement de cultivars.

Zusammenfassung. Für einen Forstmann sind die Wasseransprüche und Wachstumseigenschaften einer Baumart wichtig. Es wurden Sämlinge von drei Arten (und zwei Quellen) – *Quercus cerris* L., *Q. pubescens* Willd., und *Q. robur* L. – in Containern gezogen und einem dreitägigen Bewässerungsversuch mit unbegrenztem Wasserangebot unterzogen. Der Wasserverbrauch variierte unter den Arten und innerhalb der Art entsprechend der Herkunft. *Q. robur*-Sämlinge waren die größten (70,5 cm) und hatten auch den Sämling mit dem größten Wasserverbrauch (73,4 g), während *Q. pubescens* und *Q. cerris*-Sämlinge kürzer (46 und 45 cm) waren und entsprechend weniger Wasser verbrauchten (47,5 und 44,9

g). *Q. pubescens*-Sämlinge hatten den größten Wasserverbrauch pro cm² Blattfläche (0,111 g), *Q. cerris* hatte den höchsten Wasserverbrauch im Höhenwachstum (1,4 g/cm-1 Höhe). Es gab signifikante Unterschiede innerhalb der Art bei den unterschiedlichen Herkünften. Eine grundsätzliche Komponentenanalyse mit 20 Variablen zeigte, dass Sämlinge von *Q. robur* und *Q. pubescens* Quellen Cluster bildeten, während die zwei *Q. cerris*-Quellen separat voneinander und den anderen blieben. Der Cluster-Effekt verdeutlicht die proportional größere Verteilung des Trockengewichts von Triebwachstum und korrespondierend weniger Wurzelwachstum bei *Q. robur* und *pubescens* Sämlingen als bei *Q. cerris*-Sämlingen. Die Resultate werden in Beziehung gestellt zum relativen Wert der Art für den Baumschulproduzenten und zum potentiellen Wert für urbane Forstwirtschaft und potentielle Kultivar-Entwicklung.

Resumen. Las características del uso del agua por las especies y los hábitos de crecimiento son importantes para los forestales urbanos. Brinzales de tres especies (y dos orígenes)—*Quercus cerris* L., *Q. pubescens* Willd., y *Q. robur* L.—crecieron en contenedor y fueron sometidas a un ensayo de uso del agua de tres días bajo condiciones de humedad del suelo no limitantes. El uso del agua varió entre especies y entre orígenes dentro de las especies. Los brinzales más grandes usaron más agua que los más pequeños; los brinzales de *Q. robur* fueron los más altos, 70.5 cm (27.8 pulg), y tuvieron el uso de agua mayor, 73.4 g (2.5 onz), mientras que los brinzales de *Q. pubescens* y *Q. cerris* fueron los más pequeños, 46 y 45 cm (18.1 y 17.7 pulg), y promediaron 47.5 y 44.9 g (1.68 y 1.58 onz) de agua, respectivamente. Los brinzales de *Quercus pubescens* tuvieron el más alto uso del agua cm-2 de área foliar (0.111 g); *Q. cerris* tuvo el uso de agua más alto (1.4 g de agua cm-1 de altura). Hubo diferencias significativas en uso de agua entre orígenes dentro de las especies. El análisis principal de componentes, usando 20 variables, mostró que los brinzales de *Q. robur* y *Q. pubescens* se agruparon mientras que los brinzales de dos fuentes de *Q. cerris* resultaron separados uno y otro de *Q. robur* y *Q. pubescens*. El análisis de aglomerados reflejó las distribuciones más grandes de proporcionalidad de peso seco a crecimiento de brotes y por tanto menor al crecimiento de raíz de los brinzales de *Q. robur* y *Q. pubescens*, que para *Q. cerris*. Los resultados son comparados al valor relativo de las especies para los viveristas y el valor potencial para los manejadores de bosques urbanos y el potencial para el desarrollo de cultivares.