ORIGINAL ARTICLE

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Seedling growth strategies and seed size effects in fourteen oak species native to different soil moisture habitats

Abstract Seedling growth and morphology are thought to reflect evolutionary responses to habitat or influences of seed size. To test these hypotheses, we selected fourteen species of North American oaks differing in soil moisture habitat preference and seed size. Seedlings were grown for 1–2 years with abundant soil water and moderate soil nutrition in pots placed outdoors and in a common garden. Oak species native to xeric environments produced the smallest seedlings. Oaks from hydric soils had more shoot weight per unit of root weight and more height per unit of total plant weight than did mesic or xeric oaks. Essentially no differences in leaf area per unit of total plant weight were detected. Species with thinner and larger individual leaves tended to produce larger seedlings. Within species, seed size was generally unrelated to seedling growth, although results may have been complicated by uncontrolled genotypic variability. However, when species were compared, those with larger mean seed size produced larger seedlings. Root/shoot allometry, height growth and leaf thickness in the tested species may reflect evolutionary responses to soil moisture and flooding. Although seed size influenced seedling growth, no clear relationship between seed size and soil moisture habitat was found.

Key words *Quercus* · Carbon allocation · Allometry

Introduction

Plants adjust their allocation of carbon to shoots and roots in order to increase acquisition of limiting resources or survive periods of environmental stress. For example, shoot growth may increase if light is limiting, and root growth may be enhanced if water and nutrients are limiting. In woody plants, three mechanisms of adjusting carbon allocation are important: (1) short term plastic responses (Schulze 1982; Osunkoya et al. 1994); (2) ontogenetic changes (Evans 1972, Schulze 1982, 1983; Miller et al. 1990); and (3) evolution or ecotypic differentiation (Grime 1977). Evolutionary response is reflected in the distribution of plants across natural environmental gradients. For example, plants common to dry sites tend to allocate proportionally more carbon to roots than do plants from moist sites, even when both plant types are grown in similar environmental conditions (Immel et al. 1978; Bongarten and Teskey 1987; Matsuda et al. 1989; Miller et al. 1990). Evolved tendencies in shoot/root allometry have also been found for late versus early successional species (Monk 1966; Gleeson and Tilman 1990) and species from nutrient poor versus nutrient rich sites (Elberse and Berendse 1993).

In addition to shoot and root allometries, seed size may affect plant survival in stressful environments. Larger seeds may enhance flexibility in shoot/root allometry, speed of germination and overall growth (McComb 1934; Grime and Jeffrey 1965; Dunlap and Barnett 1982; Bonner 1987; Osunkoya et al. 1994; Reich et al. 1994). However, many studies have shown weak or no correlation between seed size and growth rate (Larson 1963; Weis 1980; Singh and Rai 1988; St. Clair and Adams 1991; Reich et al. 1994), and thus it is unclear if seed size influences are widespread or rare.

The relationship between leaf area and total plant weight may also influence total seedling growth and survival. Larger investment in leaf area per unit of total plant carbon enhances growth rate (Newhouse and Madgwick 1968; Farmer 1980; Reich et al. 1992), even more than an increase in photosynthetic rate does (Schulze 1983). Thus, plants that develop a high leaf area ratio (LAR, leaf area per unit of total plant weight) would also be expected to grow faster. Species that do not need a large root system for optimum growth (e. g., those native to moist sites or with an affinity for disturbed sites), may have the greatest capacity for high rates of leaf area production.

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Table 1 Ecological characteristics of oak species used in pot and field experiments. See Materials and methods for details of experiments; 8–16 plants harvested per species per experiment

Species	Natural environ-ment	Mean acorn fresh weight (g)	Species used					
			Pot exp.			Field exp.		
			1	2	3	1	2	3
Q. falcata Michaux	mesic	1.22	X	X	X			X
Q. hemisphaerica	mesic	1.20	X	X				
Bartram ex Willd.								
Q. laevis Walter	xeric	3.65		X				
Q. laurifolia Michaux	mesic	1.58	X	X		X	X	
Q. lyrata Walter	hydric	5.04	X	X		X	X	
Q. margaretta Ashe	xeric	2.29			X			
Q. marilandica	xeric	1.95	X	X				
Muenchh.								
Q. nigra L.	hydric	1.18	X	X	X			
Q. nuttallii Palmer	hydric	5.13			X			
Q. pagoda Raf.	hydric	1.68	X	X				
Q. rubra L.	mesic	5.99	X	X	X			X
Q. shumardii Buckley	mesic	5.21	X	X	X			
Q. stellata Wangenh.	mesic	1.64		X				
Q. velutina Lam.	mesic	2.89	X	X				

Species and authorities as in Brown and Kirkman (1990) except *Q. nuttallii* from Godfrey (1988)

Table 2 Soil characteristics for pots and field plots before fertilizer was added. (*NM*, not measured)

Variable	Pot	Field
pH	7.11	5.32
Cation Exchange Capacity (meq/100 g)	NM	3.73
Soluble salts (mg/g)	203.0	NM
Organic matter (%)	NM	0.72
Phosphorus (mg/g)	4.00	2.48
Potassium (mg/g)	8.00	9.19
Magnesium (mg/g)	14.00	55.99
Calcium (mg/g)	34.00	148.15
Total nitrogen (mg/g)	NM	0.40
Nitrate-nitrogen (mg/g)	14.16	NM

Many studies have failed to demonstrate that plant allometry reflects evolutionary responses to environmental stress (Abrahamson and Caswell 1982; Elberse and Berendse 1993). Such failures may mean that traits other than allometry (e.g., nutrient or water-use efficiency, or plant architecture) are the most critical for survival in particular environments (Abrahamson and Caswell 1982; Kolb and Steiner 1990; Gleeson and Tilman 1994; Kohyama and Grubb 1994). They may also reflect the failure of an experiment to control for ontogenetic drift or plastic responses (Evans 1972). A further problem in experimental design arises when plants of vastly different phylogeny are compared. If two taxa have very different anatomy, observed differences in allometry may simply reflect anatomical constraints on growth. To minimize problems with experimental design, investigations of plant allometry should: (1) compare plant growth in a common environment where plastic responses to environment are minimized; (2) compare plants at a common developmental state (i.e., common size) to control for ontogenetic effects; and (3) use congeneric species or conspecific varieties to reduce problems with phylogenetic constraints (Bongarten and Teskey 1987; Matsuda et al. 1989; Rice and Bazzaz 1989; Garnier 1992; Elberse and Berendse 1993).

The objectives of this study were to determine if patterns of seedling growth and allometry in a congeneric species group (*Quercus* spp.; oaks) reflect evolutionary responses to a soil moisture gradient or the influences of seed size. We hypothesized that: (1) species from drier sites, where soil water and nutrients are relatively scarce but light is often abundant, would tend to produce small shoot/root ratios and therefore small ratios of leaf area to total plant weight and slower growth; and (2) plants with larger seeds, regardless

of which environment they have evolved in, would produce larger seedlings both within and among species.

Materials and methods

Plant materials and study site

For our study, we chose fourteen oak species native to the south-eastern states of USA that have soil moisture preferences ranging from xeric to periodically flooded (Burns and Honkala 1990), and seed fresh weights differing by as much as 500% (Table 1; Young and Young 1992). For each species, acorns were collected from one to several (usually >2) trees growing in Alabama or Georgia. Seeds were collected in fall and stored overwinter in polyethelene bags at 2 °C and uniform moisture conditions (approx. 100% relative humidity). Prior to planting, the surface of each acorn was dried using a paper towel and fresh weight was measured. Within a species, acorns stored and weighed in this manner should have relatively similar moisture contents at the time of weighing; however, among species differences in moisture content may have been significant (Bonner and Vozzo 1987). Moisture contents of stored acorns tend to be greater for the white oak subgenus (40–55%) than for the red oak subgenus (30–40%); therefore, our estimates of moisture free seed reserves (i.e., dry mass) are probably biased.

Species were classified as hydric, mesic, and xeric based on habitat preference (Burns and Honkala 1990) and seed source (Table 1). For example. *Q. nigra* occurs across a broad range of soil moisture habitats, but we collected seeds from a floodplain forest and thus *Q. nigra* was classified as hydric. Overall results of the study were little affected if species of questionable habitat preference were reclassified and analyses were repeated.

Potted plant and field experiments were conducted at the Auburn University campus in east-central Alabama. The climate there is warm temperate with long, hot and humid summers. Vegetation was dominated by *Pinus taeda* L. and *P. palustris* Mill. for 50 years before clearing in 1986. Soils are predominantly Cowarts series, a Typic Kanhapludult that is moderately well drained and has a site index for *P. taeda* of 24 m (base age 50 years). Available nutrients and organic matter in the A horizon are typical for formerly cultivated Coastal Plain upland soils (Table 2).

Pot experiments

Three potted seedling experiments were conducted: two initiated in 1991 and harvested in either 1991 or 1992, and one initiated and harvested in 1992. In May 1991, acorns of 12 species were planted into 30 pots per species. Approximately half of the pots were harvested in fall 1991 (pot exp. 1) and half in fall 1992 (pot exp. 2), or all were harvested in fall 1992 if germination was poor (Table 1). In March 1992, acorns from six species, including two not used in 1991, were planted into 15 pots per species for harvest in fall 1992 (pot exp. 3). Two acorns were planted in each pot to insure that sufficient plant

material was available for harvest. In pots where both acorns germinated, the smallest or least healthy seedling was removed soon after both seedlings had emerged from the soil. Due primarily to insufficient germination, the actual number of plants harvested per species per experiment ranged between 8 and 16 (mean of 12).

Pots were 0.057 m³ in volume and filled with a nutrient poor 4 : 1 v/v mixture of washed medium grade mortar sand : vermiculite-based potting soil (Table 2). Potted plants were grown outdoors under neutral density shade with light levels 60% of ambient. Water was supplied by drip irrigation once every 48 h except during times of sufficient precipitation. Following recommendations from the USDA Forest Service Southern Hardwoods Research Laboratory (Stoneville, Miss.), we provided an intermediate level of soil fertility by applying 13.5 g/pot of 14-14-14 controlled release fertilizer at the beginning of the first and second growing seasons. In response to leaf chlorosis noted at the beginning of the second growing season (especially in *Quercus rubra*) we applied 18.9 grams of sulfur and 0.3 grams of a micro-nutrient fertilizer containing 14% sulfur, 1.35% boron, 3.2% copper 7.5% iron, 8.0% manganese, 0.04% molybdenum, and 4.5% zinc. Plant health improved rapidly after treatment.

Harvests were conducted 22–28 October 1991 and 16–28 September 1992. Prior to the removal of each seedling, numbers of flushes and leaves, and shoot height were recorded. Seedlings were then carefully lifted out of the pots with minimal loss of fine root material. At the end of the first growing season, roots were not restricted by pot size. However, after the second growing season, most plants had completely encircled the pot with lateral roots, and tap root extension was severely limited. After being lifted from pots, seedlings were brought to the lab and separated into component parts (roots, stems, foliage, and cotyledons). Total leaf area per seedling was measured using a portable leaf area meter (Model LI-3000; LI-COR Inc., Lincoln, Neb.), and fresh weight of the acorn remains (i.e., cotyledons) was measured. Finally, all plant parts were dried in ovens at 60 °C and weighed.

Field experiments

Three field experiments were used to determine if results from the three pot experiments were repeatable in a natural soil system. Soil was tilled to a depth of 10 cm and then planted with acorns at a 0.61 × 0.61 m spacing. Thirty acorns of each of six oak species were planted in May 1991 and harvested in 1991 (field exp. 1) or 1992 (field exp. 2). Due to insufficient germination in four of the species, only two, *Quercus lyrata* and *Q. laurifolia*, were harvested in both 1991 and 1992. Fifteen acorns for each of two additional species were planted in March 1992 and harvested in fall 1992 (field exp. 3). Mean number of plants harvested per species per field experiment was 12.

Field plants were grown in full sun. During the growing season, they were watered every 48 h except when sufficient natural precipitation occurred. To decrease nutrient limitations on plant growth, 13.5 g of 14-14-14 slow release fertilizer were spread uniformly in a 46 cm radius around each seedling at the beginning of the first and second growing seasons. Plots were maintained in a weed-free state by periodic hand weeding.

Field seedlings were harvested 29–30 October 1991 or 10–12 October 1992. Seedlings were lifted by excavating a circular trench 46 cm from the base of the stem followed by removal of the root ball. There was no observed lateral root extension beyond 46 cm. Soil was carefully washed from the ball to minimize fine root loss. Plants were then processed as described for potted seedlings.

Data analysis

Several morphology variables were computed from the harvest data including specific leaf area (SLA; leaf area per unit of leaf weight), LAR, shoot to root weight ratio, and mean size of individual leaves. Differences among habitat groups in total plant weight, seed weight, and other size and morphology variables were then assessed by analysis of variance (ANOVA) followed by Tukey's test (Sokal and Rohlf 1981). Separate analyses were conducted for each of three experiments where a sufficient number of species existed for a meaningful comparison; i.e., pot experiments 1, 2 and 3. Data from different experiments were not combined for these analyses because plant size was strongly affected by plant age at harvest (one versus two growing seasons, hereafter 1- and 2-year-olds), year of harvest (1991 versus 1992) and location of experiment (pot versus field).

Allometric differences among habitat groups were first explored by plotting shoot over root weight, leaf area over total plant weight (i.e., LAR), and many other two-variable relationships. By inspection we determined that logarithmic transformations were needed in some cases to linearize the data, a prerequisite for the analyses we used. To minimize the influence of ontogenetic effects and thereby focus on genetically based differences in allometry, we used analysis of covariance (ANCOVA) as outlined by Ledig et al. (1970) and Jones and Sharitz (1990). For each two-variable relationship tested, regression lines were computed for each of the three species groups (i.e., soil habitat classes). One variable was arbitrarily chosen as the response (e.g., shoot weight), the other was the covariate (e.g., root weight) and soil habitat class was the independent factor. Allometric differences among the three classes were indicated if ANCOVA identified significant differences in regression slope or intercept estimates.

As in the case for total plant size, allometric relationships could be affected by plant age, year of harvest and location. Because plants of different age were expected to have large differences in size, separate analyses were planned for 1- and 2-year-old seedlings. Within each age class, however, we hoped to combine data from different experiments. To identify which experiments could be combined, we selected species that were used in more than one experiment and then analyzed within-species to determine if experiments caused shifts in allometry, or if allometry was similar regardless of experiment. Data were combined if few or no within-species differences were found.

To test for seed size effects, acorn fresh weights were correlated with ten plant characteristics (height, leaf area, mean area of single leaf, LAR, total dry weight, shoot to root weight ratio, and dry weights of leaves, stems, shoots and roots). To test for within-species effects, separate coefficients were calculated for each unique combination of species, age, year of harvest, and location (i.e., the 34 contingencies listed in Table 1). Due to some missing data, only 300 of a possible 340 coefficients were calculated and tested for significance. To determine if relationships existed across species, means for each combination of species, age, year of harvest and location were calculated and then coefficients were computed using the means; however, separate analyses were used for 1-year-old and 2-year-old seedlings because we expected that seed size effects would weaken as seedlings grew older. Most statistics were calculated by SAS software (SAS 1988).

Results and discussion

Size and size variation

Xeric species had the slowest growth. In each potted seedling experiment, mesic and hydric species had significantly larger biomass than xeric species (ANOVA; numerator *df* 2, denominator *df* range 63 to 136; $P \leq 0.031$; Table 3). However, no significant differences were found between hydric and mesic species. In general, *Quercus nuttallii, Q. shumardii, Q. lyrata, Q. velutina* and *Q. rubra* grew most rapidly while *Q. stellata, Q. hemisphaerica, Q. laevis, Q. margaretta* and *Q. falcata* grew most slowly (Long 1993). Although results may have differed somewhat if plants were grown in a greater variety of environments, these findings agree with our anecdotal observations of seedling growth in natural forests, and with other oak seedling studies that have compared growth of species from different soil moisture habitats (Bourdeau

Table 3 Mean total plant dry weight at harvest and initial acorn fresh weight for potted oak seedlings in 14 species grouped by soil moisture habitat. Within seedling age/year of harvest groups, column means followed by different superscripts were significantly different ($P < 0.05$) according to Tukey's test

Seedling age/ year of harvest	Soil habitat group	No. seedlings harvested*	Total dry weight at harvest (g)	Specific leaf area (cm²/g)	Initial acorn fresh weight (g)
1-year-old/ 1991	hydric	48	5.34	120	2.39
	mesic	59	7.13	128	2.92
	xeric	12	3.96	104	1.88
1-year-old/ 1992	hydric	24	42.57	122	3.23
	mesic	36	32.50	122	5.92
	xeric	12	8.10	115	2.29
2-year-old/ 1992	hydric	54	96.45	120	2.06
	mesic	76	85.17	112	2.68
	xeric	19	33.76	94	2.92

* For some means within rows, number harvested was 0–21% smaller (but up to 48% in acorn weights) due to missing values

1954; Farmer 1980; Matsuda et al. 1989). Slow growth of xeric species may reflect evolution of a stress tolerance strategy which enhances survival when water or nutrients are scarce, but constrains growth when soil resources are relatively abundant (Grime 1977).

As expected, differences were also found between experiments (Long 1993). In general, 2-year-old seedlings were largest, 1-year-olds harvested in 1992 were intermediate in size, and 1-year-olds harvested in 1991 were smallest. Plant dimensions and size differences among species were similar to those reported in other studies of oak seedling growth (Bourdeau 1954; Ovington and MacRae 1960; Phares 1971; Immel et al. 1978; Farmer 1980; Kolb and Steiner 1989).

Variability in size and morphology was large, even for seedlings similar in age, year of harvest, location and species. Coefficients of variation (CV) within groups treated alike (i.e., seedlings of the same species, year of harvest, age and location of growth) averaged 43.8% with a range of 2.5 to 152.8%. This magnitude of variation is common not only in nature, but also in experiments where environmental conditions are relatively homogeneous (Evans 1972; Harper 1977; Miller and Weiner 1989).

Size and morphology variation may have been due to variability in the timing of germination and within species genetic variability. Within each species, the emergence of epicotyls was spread out over a several week period (dates not recorded for each seedling), and since growth initially increases at a geometric rate in most plants (Evans 1972), small differences in emergence time could have been magnified into large size differences. Some variation in size might also be expected due to within population genetic diversity (Bongarten and Teskey 1987). Kolb and Steiner (1989) found significant differences in both height and diameter growth of *Q. rubra* seedlings, not only within families, but also within clones. The large size variation observed within and among species underscores the need to correct for size differences when allometry is analyzed.

Without such corrections, species comparisons might partly reflect ontogenetic influences.

Seed size and leaf characteristics were less variable than other measures of growth and morphology. When coefficients of variation were calculated for each batch of seedlings treated alike (i.e., same species, age, location and year of harvest), the least variable parameters were initial seed weight (mean CV 14.0%), SLA (15.2%), number of flushes (25.4%), LAR (30.1%), height (40.1%), mean area of an individual leaf (44.8%), and shoot to root ratio (45.8%). All other size parameters had mean CVs between 60 and 80%. Low variability in initial seed weight was expected because the same has been demonstrated for many other plant species (Harper 1977). The low variability in SLA, LAR and height growth may reflect the relatively similar light regime experienced by all plants within each experiment. Leaf thickness, leaf area and height growth are strongly keyed to light environment (Phares 1971; Immel et al. 1978; Rice and Bazzaz 1989).

Allometry and native habitat

Data from some of the experiments were combined before allometric analyses were performed. For seedlings of the same species and same age, allometry was significantly affected by year of harvest (5 of 12 ANCOVA tests were significant; $P < 0.05$). Location of the experiment also affected within-species seedling responses in 2-year-old (5 of 6 tests significant), but not 1-year-old seedlings (2 of 12 tests). Based on these results, we divided the total data set into three subsets: 1-year-old seedlings harvested from pots and the field in 1991 (pot exp. 1 plus field exp. 1), the same but harvested in 1992 (pot and field exps. 3), and 2-year-old seedlings harvested from pots only (pot exp. 2). To determine if the combining of pot and field data led to spurious conclusions, we also performed statistical tests with just pot data. Results of statistical tests were essentially the same if field data were not included, except for the test of shoot to root allometry in the 1992 harvests where the significance of species group effects was $P = 0.005$ with field plants and $P = 0.082$ without. Hereafter, only results of the combined data sets will be discussed.

As hypothesized, shoot to root ratios were greater for wet than for dry site species. In all three data sets, significant habitat differences in shoot versus root weight were found (ANCOVA; *df* 2, 83 to 2,137; $P \leq 0.02$). Plots of the data showed that hydric species had slightly more shoot per unit of root weight than mesic and xeric species; however, differences between mesic and xeric species were very small (Fig. 1). Some individual species did not follow the general trend which resulted in overlap among habitat groups. The gap between hydric and the other groups was largest for the 1991 harvest where plants were generally small (Fig. 1). As seedlings grew larger and older, differences narrowed. These data suggest that allometric differences may be greatest for relatively young or small seedlings; however, because of the limits on tap root extension in the 2-year-old potted seedlings, our results may be
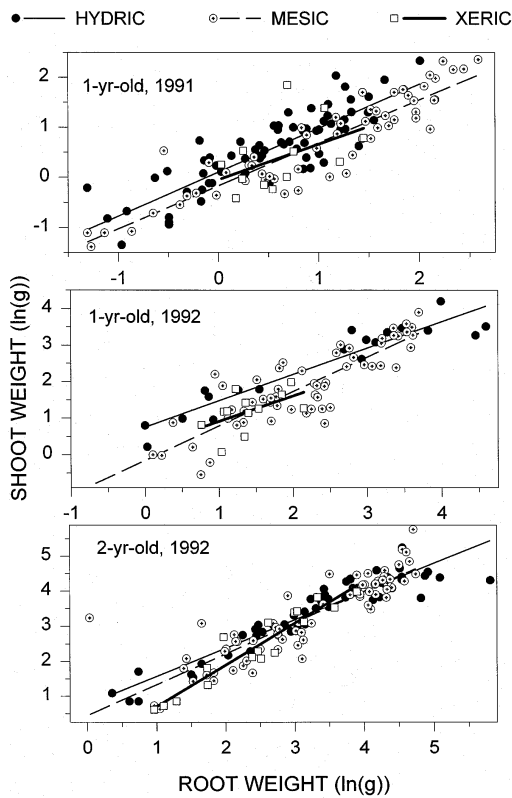
Fig. 1 Allometric relationship between shoot and root weight for three data sets differing in seedling age and year of harvest. Each data set includes 6–12 species grouped into one of three soil moisture habitat preferences; a regression line is shown for each habitat group
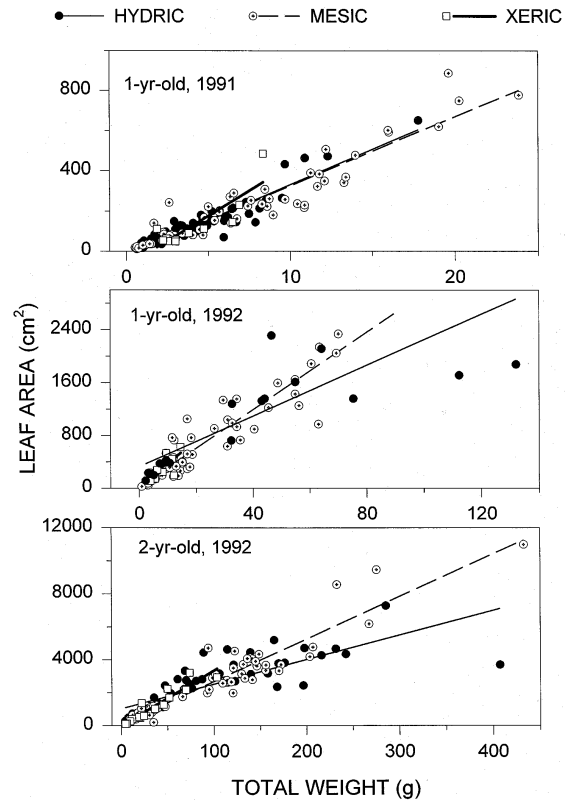
Fig. 2 Allometric relationship between leaf area and total weight for three data sets differing in seedling age and year of harvest. Each data set includes 6–12 species grouped into one of three soil moisture habitat preferences; a regression line is shown for each habitat group

biased. In nature, allometric differences may be maintained for larger seedlings.

Low rates of shoot growth relative to root growth have been found in other dry site woody species including oaks (Zimmer and Grose 1958; Immel et al. 1978; Matsuda et al. 1989). However, in one recent study of black spruce [*Picea mariana* (Mill.) B. S. P.], drought tolerant seed sources maintained a stable ratio of shoot to root growth under drought conditions while drought intolerant seed sources had reduced shoot growth and therefore developed smaller shoot to root ratios (Tan et al. 1995). Thus, the development of smaller shoot to root ratios is not necessarily a predictor of how a species or genotype will perform when soil resources are scarce.

Allocation to stems may have been the key to the trend in shoot/root allocation we observed in oak seedlings. When separate analyses were performed for leaf versus root weight and stem versus root weight, significant differences among habitat groups ($P < 0.05$) were found in all three tests for stem versus root but in only two of three tests for leaves. In all cases, however, hydric species had the greatest mean leaf weight and stem weight per unit of root weight.

In contrast with our hypothesis, the allometric relationship between leaf area and total plant weight (i.e., LAR) was similar across the three habitat groups (Fig. 2). For

1-year-old seedlings harvested in 1991, no significant leaf area to total weight differences were found among habitat groups (ANCOVA; *df* 2,137; $P = 0.125$). Significant differences were found in the other two tests (ANCOVA; *df* 2,83 to 2,133; $P \leq 0.002$). However, if the two largest seedlings (apparent outliers) were removed from each of the latter data sets, the test for 1-year-old seedlings harvested in 1992 was no longer significant ($P = 0.384$).

Since the three species groups had similar LARs, their different rates of growth might have been caused by differences in photosynthetic rates or leaf thickness (i.e., differences in their SLA). Our data were useful for exploring the leaf thickness idea. First, we calculated mean SLA and mean total plant weight for each combination of species and experiment (total of 34). Correlations were then calculated for all 1- and all 2-year-old data separately (i.e., $n = 20$ and 14, respectively). SLA was positively but not significantly correlated with mean total weight ($r = 0.19$ and 0.37 for 1- and 2-year-olds; $P > 0.19$). Next, we broke down the data into the three species groups and three experimental data sets (as in the analyses of allometry) and found that species from xeric sites had a tendency for both slower growth and smaller SLA (Table 3), although the SLA differences were significant in only one of the three data sets. These findings make sense in light of recent reviews of how leaf thickness, assimilation rate, nitrogen content,
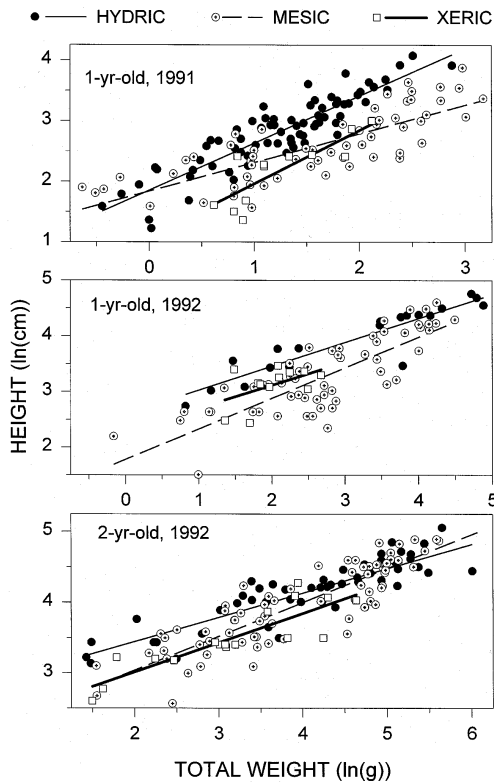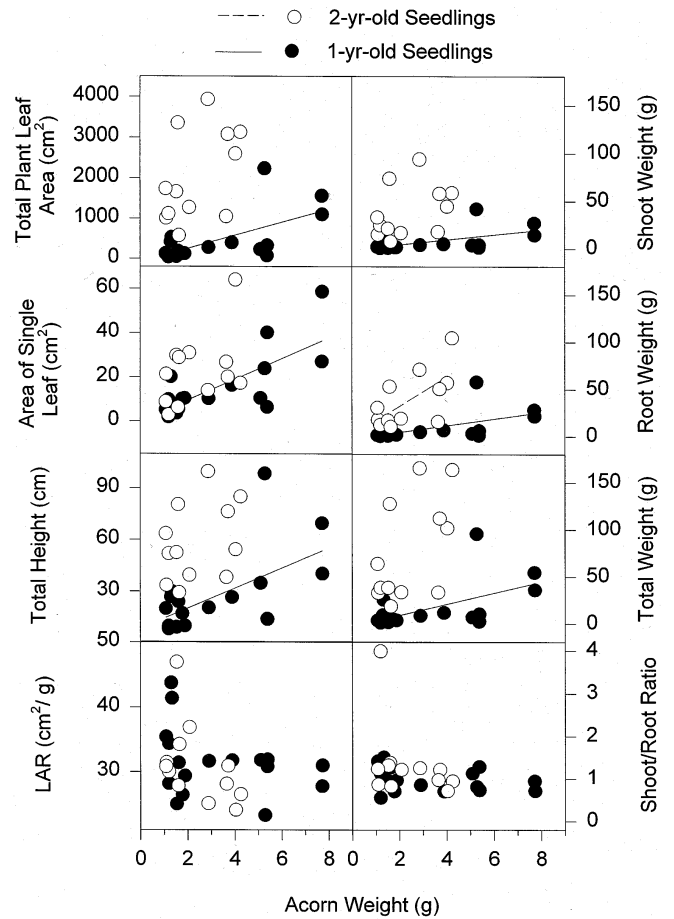
Fig. 3 Allometric relationship between height and total plant weight for three data sets differing in seedling age and year of harvest. Each data set includes 6–12 species grouped into one of three soil moisture habitat preferences; a regression line is shown for each habitat group

Fig. 4 Relationship between various plant size and morphology characteristics and initial acorn fresh weights for 1- and 2-year-old seedlings. Each symbol represents a mean for a single species harvested from one location (pot or field) during one year (1991 or 1992). Regression lines are plotted for significant ($P < 0.05$) correlations

lifespan and leaf area are related (Reich et al. 1992; Walters et al. 1993). Species with shorter leaf life spans tend to have thinner, more nitrogen rich leaves with greater assimilation rates per gram of leaf tissue.

One other allometric relationship was consistently significant ($P \leq 0.020$) in all three data sets. Hydric species had greater height per unit of total plant weight than did mesic and xeric species, although differences became very small for large and old seedlings (Fig. 3). Other studies have reported greater hight growth of wet site versus dry site woody species, but no adjustments for differences in plant size were made (Bourdeau 1954; Farmer 1980; Matsuda et al. 1989). In our study, the same trend was found even after correcting for differences in total plant weight.

Enhanced height growth in hydric species may reflect an evolutionary response to intense competition for light: a resource that is more limiting in nutrient and moisture rich floodplain forests than in uplands. Alternatively, this trait may be tied to avoidance of flooding stress. Seedlings of most woody plants, even those classified as flood tolerant, succumb to flooding if their leaves are completely submerged for more than a few days (Hosner 1958; Jones et al. 1989; Streng et al. 1989). Presumably, seedlings with rapid height growth, either by having greater growth rates or by allocating more carbon to shoot extension, would be more likely to survive flooding. Seedlings of some flood tolerant

species do indeed increase height growth rate when the soil is saturated, while height growth of intolerant plants decreases (Kozlowski 1984). However, the latter is a plastic response induced by specific environmental conditions. Our study is the first to suggest that flood tolerant species may have enhanced height growth compared with non-flood tolerant species even in the absence of stimulation by flooding. Although height may be important for flood avoidance, other traits may be more important in oak seedlings. For example, demographic data suggest that oaks in south-eastern USA floodplains avoid flood-induced mortality by germinating late in the growing season when flooding is less common (Streng et al. 1989). More tests are needed to determine if germination timing and height allometry influence flood tolerance in these species.

Seed size effects

Oak seedlings apparently receive the majority of energy obtained from the acorn in the first growing season. Approximately 70% (range of means = 65–76%) of

acorn fresh weight was lost during the first growing season. By the end of the second growing season, total weight loss had increased only slightly to 80% (range 73–84%) of initial weight. The small drop in acorn biomass from year 1 to year 2 probably represents decomposition and not further energy extraction for use by the seedling.

Within species, acorn weight was generally unrelated to plant size and morphology. Only 17 of the 300 correlations between initial acorn fresh weight and various plant characteristics were significant ($P < 0.05$), a rate of about 5.6% which would be expected on the basis of chance alone. In contrast to our results, McComb (1934) found a within-species relationship between seed size and plant growth in *Quercus prinus* L. (as *Q. montana* Willd.) and Kolb and Steiner (1989) found the same for *Q. rubra*. These apparent conflicts in results may reflect poor control over acorn moisture content (in our study and in others), or more likely, the influences of genotypic variation on seed size effects. Reich et al. (1994) found that seed size effects in *Pinus sylvestris* varied among local genotypes as well as across a latitudinal gradient. In our study, we did not strictly control for genotype nor did we include seed sources from multiple geographic areas.

Clearer relationships between acorn weight and seedling performance were found when more than one species was compared (Fig. 4). For 1-year-old seedlings, acorn weight was significantly correlated with one morphological characteristic (mean area of a single leaf) and with several size characteristics including total leaf area, height, leaf weight, stem weight, root weight and total weight ($r = 0.55–0.74$; $P < 0.05$). In 2-year-old seedlings, only the correlation with root weight was significant ($r = 0.65$). Correlations with LAR and shoot to root weight ratio were never significant ($r = –0.49$ to $–0.29$; $P > 0.05$); thus, our interpretations on allometric differences between hydric, mesic and xeric species groups were apparently not complicated by seed size effects.

The observed correlation between acorn weight and mean leaf size has been noted elsewhere (Farmer 1980). Apparently there is a tendency for larger seeded oaks to produce seedlings with large mean leaf size and rapid growth rates.

Although this study and others (McComb 1934; Kolb and Steiner 1989) suggest that acorn size influences seedling size, the relationship may be complicated by other evolutionary forces that affect seedling growth. Hydric, mesic and xeric species groups differed in mean initial acorn weight in two of three ANOVA tests (*df* range 2,64 to 2,116; *P* range $< 0.001–0.070$); however, trends in acorn mass did not correlate well with trends in total plant weight. For example, 2-year-old seedlings of xeric species had the lowest mean total plant weight and yet the greatest initial acorn weight (Table 3). Perhaps the influence of seed size on seedling growth holds only for mesic and hydric species, or alternatively, the positive influences of seed size can not overcome the inherently slow growth of xeric species. Since only a few xeric species were included in our study, more studies with a greater number of species are needed to test these ideas.

If size has an important influence on seedling survival, oaks growing where survival is poor (e.g., flooded and xeric sites) would have selective forces favoring larger seeds. Yet no correlations of environment and seed size were evident in our study (Table 3), nor can they be found when all North American oaks are considered (Young and Young 1990). It is likely that interpretation of oak seed size evolution is complicated by natural selection for pattern of dispersal, mechanism of pollination and seed production, and avoidance of predation (Westoby et al. 1992).

Results of this study show that oak species differ in basic seedling allometry, initial growth, and possibly in the relationship between seed size and initial growth. The fact that disparities were found among congeneric species growing in a common garden suggests that the differences are of evolutionary origin and not related to phylogenetic constraints or to short-term plastic responses. However, a more powerful test of hypothesized relationships would be afforded by reciprocal transplanting of hydric, mesic and xeric species into each of the three natural environments. Survival of the transplants should be monitored to determine if allocation and growth patterns are related to survival and competitive advantages in a natural environment.

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