Ecological Monographs, 74(4), 2004, pp. 635–662

MULTIPLE TRAIT ASSOCIATIONS IN RELATION TO HABITAT DIFFERENTIATION AMONG 17 FLORIDIAN OAK SPECIES

JEANNINE CAVENDER-BARES,[1,2,3,5] KAORU KITAJIMA,[4] AND F. A. BAZZAZ[3]

[1]*Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Drive,*
St. Paul, Minnesota 55108 USA
[2]*Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037 USA*
[3]*Department of Organismic and Evolutionary Biology, 16 Divinity Avenue, Harvard University,*
Cambridge, Massachusetts 02138 USA
[4]*Department of Botany, 220 Bartram Hall, University of Florida, Gainesville, Florida 32611 USA*

Abstract. Differentiation of species distributions along environmental gradients and phenotypic specialization help explain the co-presence of 17 oak species that might otherwise be expected to competitively exclude one another. In an effort to understand the role of niche differentiation in the co-presence of these congeneric species in north-central Florida, we examined the community structure of oak-dominated forests in this region in relation to environmental variables and a suite of life history and physiological traits. Landscape distribution patterns of oaks and other woody species were determined from randomly established plots in three state parks. Soil moisture, nutrient availability, and fire regime were found to be critical factors influencing community structure, and the distribution of oak species was strongly correlated with these gradients. Detrended correspondence analysis of species' distributions supported the grouping of oak species into three major community types: (1) hammock, (2) sandhill, and (3) scrub. Principal components of multiple traits also supported differentiation of oak species into these three groups.

There is clear evidence for ecological sorting among the oaks in these forests as species partition environmental gradients more than expected by chance, and most functional traits of species correspond to species distributions as predicted based on a priori understanding of trait function. Across phylogenetic lineages, species showed evolutionary convergence in function and habitat preference. In contrast, leaf-level traits were conserved within phylogenetic lineages and were not well correlated with local habitat factors, but rather with the broader geographic distributions and northern range limits of species. The cumulative results reported here provide strong evidence that oak species specialize for particular niches via trade-offs in functional traits, and such niche partitioning contributes to the high diversity of oak species at the landscape level. At smaller spatial scales, phylogenetic diversity among the oaks is likely to be important in promoting their coexistence through other mechanisms.

Key words: detrended correspondence analysis; fire regime; functional traits; leaf life span; phylogenetic lineage; Quercus; *soil moisture; soil nutrients.*

INTRODUCTION

A critical issue in ecology is understanding the forces that maintain biological diversity, both taxonomic and functional. Central to this question has been a quest to explain the patterns of species distributions and abundance across the landscape (Huston 1994) and to determine whether species specialize to partition the environment or whether distributions are the result of predominantly stochastic processes (Diamond and Case 1986, Brokaw and Busing 2000, Hubbell 2001). Although a number of mechanisms, including density dependent mortality, are important in regulating relative abundance and diversity of species in both tropical (Wills et al. 1997, Wright 2002) and temperate systems (HilleRisLambers et al. 2002), such mechanisms do not explain the association of functional traits with habitat and resource regimes as niche theory does (McKane et al. 2002). Indeed, a central goal of many ecological studies has been to explain patterns of species distributions in relation to life history and functional traits (Monk 1966, Chabot and Hicks 1982, Hollinger 1992, Mulkey and Kitajima 1995, Reich et al. 1999, Ackerly et al. 2002).

North Central Florida is at the confluence of the northern temperate flora and the southern subtropical flora, providing a rich regional pool of species. Seventeen species of oaks are dominant or codominant with pines in forest communities across the landscape. Due to the potential for close relatives to competitively exclude one another, the coexistence of multiple congeners in this region is challenging to explain, particularly given the lack of major elevational gradients that occur in other regions of high oak diversity (Whittaker

---

Manuscript received 10 January 2003; revised 30 October 2003; accepted 15 November 2003; final version received 5 January 2004. Correponding Editor: M. J. Lechowicz.

[5] E-mail: cavender@umn.edu

TABLE 1. A list of oak species in the study.

Species	Code	Clade	General habitat type	Fire frequency ranking‡	Canopy habit
Q. falcata Michaux	FA	red	sandhill/hammock	2	deciduous
Q. hemispherica W. Bartram ex Willd.	HE	red	hammock	3	evergreen
Q. incana Bartram	IN	red	sandhill	1	brevideciduous
Q. laevis Walter	LV	red	sandhill	1	deciduous
Q. laurifolia Michaux	LA	red	hammock	5	brevideciduous
Q. myrtifolia Willd.	MY	red	scrub		evergreen
Q. nigra L.	NI	red	hammock	5	brevideciduous
Q. pumila Ashe	PM	red	scrub		brevideciduous
Q. shumardii Buckley	SH	red	hammock†	4	deciduous
Q. austrina Small	AU	white	hammock§	3	deciduous
Q. chapmanii Sargent	CH	white	scrub		brevideciduous
Q. margaretta Ashe	MA	white	sandhill	1	deciduous
Q. michauxii Nuttall	MX	white	hammock	5	deciduous
Q. stellata Wangenheim	ST	white	hammock‖	2	deciduous
Q. geminata Small	GE	live	scrub		evergreen
Q. minima (Sargent) Small	MN	live	scrub¶		evergreen
Q. virginiana Miller	VI	live	hammock	5	evergreen

Notes: Authorities are shown to the right of the species, along with a two-letter code and the major lineage to which it belongs. General habitat type, fire-frequency ranking (Jackson et al. 1999), and canopy habit are given. Definitions of general habitat type are as follows: sandhill = high pineland, open woodland, deep sands, high fire frequency (1–15 yr) with low severity; scrub = dense thicket, sandy soil, infrequent fire (15–50 yr) with high severity; hammock = mesic or hydric temperate hardwood forests with low or unpredictable fire frequency. Habitat descriptions are from Myers (1990), Platt and Schwartz (1990), Ewel (1990), and Kurz and Godfrey (1962).

† Soils underlain by limestone.

‡ Ranking is from a model based on habitat types, excluding scrub habitats, as follows: (1) park-like forest/savanna; (2) dry upland forest; (3) intermediate dry upland forest; (4) moist upland forest; (5) infrequently flooded bottomland forest (Jackson et al. 1999).

§ Often found on limestone bluffs.

‖ Upland soils frequently underlain by clay or marl.

¶ Seepage areas of sandy-clay upland; restricted to sites subject to burning.

1956, Platt and Schwartz 1990). One possibility is that oaks specialize into different niches, thus allowing them to partition the landscape and maintain their diversity. Here, we test the concept of the *n*-dimensional niche, (as defined by Bazzaz [1987], based on earlier conceptions of the niche by Hutchinson [1957] and Whittaker [1975]) using the distribution of oak species across critical environmental gradients. We refer to the physical gradients of the environment as habitat factors and the observed location of species across these gradients as habitats or realized niches.

While these oak species occur in close proximity, floristic studies have described them to be associated with distinct communities (hammock, sandhill, and scrub; Table 1), which vary markedly in soil water availability, fertility, and fire regime (Kurz and Godfrey 1962, Ewel 1990, Myers 1990, Long and Jones 1996). Oak species in this region also show significant variation in phenology and traits related to water use (Cavender-Bares et al. 1999, Cavender-Bares and Holbrook 2001), as found in other systems of high oak diversity (Knops and Koenig 1994, Villar-Salvador et al. 1997, Damesin et al. 1998).

The overarching impetus for the study was to understand factors that may help explain the maintenance of high oak diversity at the landscape level (1–100-ha scale) in north-central Florida. We first ask whether species are nonrandomly distributed across environmental gradients. This allows us to investigate whether distinct community affiliations of north Florida oaks described in the literature are supported by quantitative spatial analysis of species distributions relative to the abiotic environment. Second, if species are partitioning environmental gradients, what are the mechanisms, or functional traits, that allow them to do so? For example, do suites of leaf-level traits known to be associated with contrasting nutrient and water use strategies across a wide range of plant groups (e.g., Reich et al. 1997) allow oak species to specialize for particular resource regimes? In an effort to answer these questions, we sought to (1) quantify distributions of 17 sympatric oak species with respect to each other and other woody species; (2) analyze the distributions of species with respect to critical environmental factors; (3) determine whether species are partitioning their environment more than expected by chance using null models; and (4) determine whether and how functional traits of species correspond to their spatial distribution, their community affiliation, and to abiotic features of their habitats.

As a result of the typical geological features in north-central Florida, namely sand deposition on a clay layer or limestone bedrock, even minor topographic changes within a few meters of elevation cause marked changes

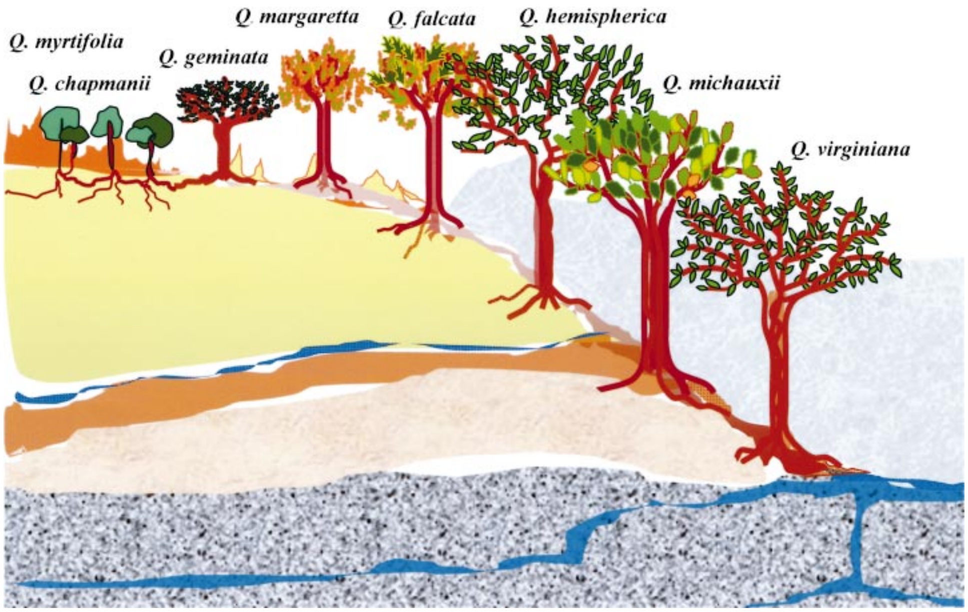

FIG. 1. Schematic diagram showing environmental heterogeneity in woodlands of north-central Florida. The presence of several important gradients, including water availability, soil fertility, and fire frequency and severity suggests the hypothesis that oak species partition these gradients, allowing many species to coexist.

in soil hydrology, and consequently nutrient availability and fire regime (Fig. 1) (Myers and Ewel 1990). In general, the wetter the site, the higher the productivity and nutrient availability and the lower the fire frequency. As fire frequency decreases, the fuel load and the fire intensity tend to increase (Jackson et al. 1999). However, in Florida, high temperatures combined with high humidity and soil moisture give rise to rapid decomposition; hence, fuel loading is not necessarily related to time since last fire, as in other systems. As a result, the more mesic and often lower elevation sites, dominated by hammocks of deciduous and evergreen broadleaf trees, are considered to have high productivity and high soil nutrient availability, as well as rare and unpredictable fire frequency (fire interval >100 yr with variable fire severity [Ewel 1990]). The higher elevation sites on thick sand deposits are xeric and infertile and, in the absence of fire suppression, are likely to harbor either sandhill or scrub communities. Although soil water and nutrient availability appear to vary little between sandhills dominated by longleaf pine (*Pinus palustris*) and scrub communities dominated by *Quercus* spp. or sand pine (*P. clausa*), they differ markedly in fire regimes (Myers 1985, 1990). The fire regime in scrub communities has been characterized as having a relatively frequent and predictable frequency (on the order of every 50 yr), but also as being quite severe with crown fires that destroy most of the aboveground biomass (Myers 1985, Myers 1990). The sandhill fire regime has been described as both frequent and predictable (1–15 yr) but consists largely of low-intensity surface fires that seldom extend into the crown (Myers 1990, Glitzenstein et al. 1995). These contrasting fire regimes are thought to be facilitated, at least in part, by the vegetation itself (Webber 1935, Menges and Hawkes 1998, Carrington 1999). Frequent fires in the sandhill communities are encouraged by grasses in the open understory and relatively flammable litter of longleaf pine in the sandhill communities while a dense layer of evergreen shrubs decreases fire frequency in scrub communities (Abrahamson and Hartnett 1990, Menges and Hawkes 1998). Unfortunately, precise records of fire frequency are lacking in most sites, but woody species composition of the community itself is considered as a good indicator of fire frequency and intensity (Jackson et al. 1999).

Based on theoretical considerations and prior empirical studies on the role of functional traits, we expected species occurring in communities prone to fire to have mechanisms of fire resistance (e.g., thick bark [Vines 1968, Jackson et al. 1999]) or post-fire recovery (e.g., clonal spreading and rhizome resprouting [Menges and Kohfeldt 1995, Carrington 1999]), and species' traits related to growth and competitive ability to be positively correlated with soil resource availability (Tilman 1984, 1988, Goldberg 1997). Differences in stature, wood density, and seed size were also analyzed as important aspects of life history strategies that influence species distributions in other systems (Westoby et al. 1992, Baker et al. 2003, Meinzer 2003, Reich et al. 2003). Based on previous studies linking leaf longevity and specific leaf area to nutrient availability (Monk et al. 1989, Kikuzawa 1995, Reich et al. 1997, 1999, Givnish 2002) or water availability (Wright et al. 2001, Westoby et al. 2002), we expected leaf level traits, including leaf life span and period of canopy foliation, to be negatively correlated with soil fertility, and we expected specific leaf area to be positively correlated with soil moisture and soil fertility. We also examined interspecific variation in species traits with respect to both community affiliation and phylogenetic lineage to determine whether traits tend to show similarity within communities, within lineages or both.

The combination of quantitative data on spatial distribution and community structure, species' distributions with respect to environmental factors, and species' functional traits both in situ and in a common garden provide us with a rare opportunity to examine whether niche differentiation is an important factor maintaining diversity among oaks of North Central Florida.

METHODS

Quantification of species spatial associations and environmental distributions

Study sites and field sampling.—Quantitative data on vegetation and soil variables were collected from randomly established 0.10-ha plots in three state parks in north-central Florida. The parks included San Felasco Hammock State Preserve, a 2803-ha park in Alachua County with major sinkhole formations including Sanchez Prairie and Church Swamp (31 plots); Ichetucknee Spring State Park, a 921-ha park bridging Columbia and Suwanee counties and bisected by the Ichetucknee river (20 plots); and Manatee Springs State Park, a 960-ha park abutting the Suwanee River in Levy County (21 plots). Parks were chosen that have had minimal disturbance in the last century, including large tracts of old growth, and in which attempts have been made to restore the fire regimes. Random plots were established in each park by dropping pine needles on a topographic map and marking where the tips fell. We then located the approximate coordinates of the marks on the ground and recorded UTM (Universal Transverse Mercator) coordinates using a hand-held GPS instrument (GPS 12, Garmin International, Inc., Olathe, Kansas, USA). Roads and park boundaries were excluded, as was the northern recent addition of San Felasco, which has experienced recent logging and agricultural disturbance. Two additional plots were established at Payne's Prairie State Preserve and Morning Side Nature Center in Alachua County to increase the sampling of less common scrub species. Seventy-four plots were established in total. Based on visual inspection of their physiognomies, 48 plots were in hammock, 18 plots were in sandhill, and 8 plots were in scrub communities.

At each location, 20 × 50 m plots were established in an arbitrary orientation following the North Carolina Vegetation Survey Protocol (Peet et al. 1996). Within each plot, the dbh of each oak tree over 1.3 m height was measured for calculation of basal area and the species recorded. The presence/absence of other woody species was also recorded for each of the plots (Appendix A).

Detrended correspondence analysis of species distributions.—We used detrended correspondence analysis (DCA), an indirect method of gradient analysis, to compute ordinations of plots and species using (1) presence/absence data for all woody species, including oaks; (2) presence/absence of oaks only; and (3) relative basal area of oaks only. DCA was performed using the method of Hill (1979) with the DECORANA option in PC-ORD (McCune and Mefford 1997). We specifically used indirect gradient analysis because we wanted to describe community structure and examine species associations independently of environmental variables before we determined whether environmental variables were correlated with the community structure. Despite known limitations to DCA (e.g., Minchin 1987), it is generally the most widely used and cited ordination technique in the ecological literature and has advantages for our application in that plots and species are ordinated simultaneously.

We then tested whether values for soil variables, measured within each plot (see *Soil nutrient and moisture measurements*), were correlated with the plots scores from the vegetation data for the first two axes of ordination. We also tested whether species traits, including fire frequency classification (see *Species niche overlap*), were correlated with species scores on the first two axes of ordination.

Soil nutrient and moisture measurements.—Soil cores were collected in December 1998 from the top 10 cm of the soil, excluding undecomposed litter, in four subplots within each plot for a total of 296 individual samples. Subplot samples were used to calculate a plot mean for each soil variable after analysis. Soil samples were dried at 45°C for several days and passed through a 3-mm mesh sieve. Samples were analyzed for content of organic matter, calcium, nitrate N, ammonium N, labile phosphorus, potassium, and magnesium, as well as pH, at the soil testing laboratory of at the University of Florida. Dried soil samples were extracted with Mehlich I extractant (0.05 moles/L HCl and 0.05 moles/L H_2SO_4) and the filtrate analyzed by inductively coupled argon plasma (ICAP) spectroscopy. Organic matter content, reported as a percentage of total weight, was analyzed by a modified Walkley-Black dichromate procedure for samples below 5% organic matter or by loss on ignition for samples above 5% organic matter. Nitrate N and ammonium N were extracted with KCl and analyzed colorimetrically with a lower detection limit of 0.2 μg/g. Ca, P, NH_4-N and NO_3-N are reported in units of mg/kg of soil.

Resin bags were also used to determine relative concentrations of exchangeable phosphorus. These were made from nylon hose filled with 14 g of anion and cation exchange resins (Ionac R NM-60, Sybron Chemicals, Inc., Birmingham, New Jersey, USA) and sealed with hot glue. They were initially soaked in 2 moles/L

KCl solution, rinsed with distilled water, and air dried following procedures adapted from Binkley and Matson (1983). Bags were inserted into the soil in four subplots within each plot to a depth of 5 cm in June 1999 within 2 to 3 d during which no rainfall events occurred. They were tied to markers with fishing line so that they could be easily retrieved. Bags were left in the ground for three months and removed at the end of summer within a 2–3-d period during which there was no precipitation. Resins were extracted with 2 moles/L KCl and filtrate was measured for P colorimetrically, reported in units of mg/kg of resin beads.

Soil water content integrated over 1 m depth was measured within four subplots of each plot using time domain reflectometry (TDR) and calibrated for two soil types (sandy soil with $<5\%$ organic matter and sandy soil with $>5\%$ organic matter). Five sets of measurements taken during all seasons over a 14-mo period between June 1998 and August 1999 were averaged for each plot. Calibration of the TDR measurements is described in Cavender-Bares and Holbrook (2001). Average plot values of soil moisture and nutrients were analyzed in relation to plot scores from the ordination analysis.

One limitation of our study is that, for practical reasons, we measured soil water content rather than soil water potential, which is more relevant to the physiological function of plants than soil water content. Due to the variation of soil moisture release curves not only across soil types, but also with soil depth, we did not have a reliable way to convert soil moisture to soil water potential. However, when we did estimate soil water potential using soil moisture release curves for Arredondo Fine Sand (Carlisle et al. 1988), the most appropriate match for most plots, it did not significantly change the results. Using soil water potential changes the shapes of the distributions across the water gradient, with higher resolution at drier sites and lower resolution at wetter sites. Nevertheless, the relative order of species along the spectrum from xeric to hydric soils does not change. The shapes of the relationships between species traits and the soil moisture regime also change depending on whether soil moisture or water potential is used. However, the association of traits with soil water regime is clear in either case. Hence, none of the major conclusions reached in the study are altered by this limitation.

Species niche overlap.—Pianka's species overlap index (Pianka 1973) was computed for all pairwise combinations of oak species across seven resource levels for each of six soil factors. Overlaps were calculated based on relative basal area of species within plots using the following equation:

$$O_{jk} = O_{kj} = \frac{\sum_{i}^{n} E_{ij}E_{ik}}{\sqrt{\sum_{i}^{n} (E_{ij}^2) \sum_{i}^{n} (E_{ik}^2)}}$$

where O_{jk} is the overlap of species j on species k, i is the resource level, n is the number of resource levels ($n = 7$), and E_{ij} is the proportion of basal area of species j in resource level i divided by the number of plots that fall within resource level i (Lawlor 1980). Bin width and number can influence the outcome of such analyses. We chose the smallest number of bins that gave good resolution of species niche structure while minimizing the number of empty bins. A sensitivity analysis showed that results were robust to bin width and that whether first and last bins were open or closed did not matter. Overlap values of species pairs were tested against a null model in which we randomized the raw data matrix by shuffling plot level values of relative basal area across plots. Each randomization procedure was run 1000 times and the significance of observed mean overlaps was tested against the distribution of the 1000 means of the random communities, as described above. This procedure was carried out by a program written in Visual Basic following methods similar to those described by Gotelli and Graves (1996), but it allowed us to randomize the raw data matrix rather than the derived values of proportion of basal area per resource level.

Testing for diversity–resource availability relationships.—The number of woody species and number of oak species per 0.10-ha plot were compared to mean soil fertility (nitrate N plus ammonium N) within plots to determine whether diversity was related to soil fertility. Plots were rank ordered by their soil fertility and divided into seven consecutive groups of 10 plots. The number of woody species, the number of oak species and the soil fertility was then averaged for each of the groups of plots.

Species, habitat preferences, range limits, and phenotypic traits

Species classification.—One issue that arises when studying promiscuous species, such as the oaks, is whether species are actually distinct entities. In this study region, species are phenotypically distinct (Kurz and Godfrey 1962), despite the tendency within the genus for introgression to occur. In a separate study, genetic data showed little relevant intraspecific variation and species monophyly was not strongly contradicted (Cavender-Bares et al. 2004), in contrast to previous studies in other regions (e.g., Whittemore and Schaal 1991). In southern latitudes where the growing season is long, including north-central Florida, temporal separation in flowering is thought to be an important prezygotic isolating mechanism preventing hybridization (Nixon 1985, 1997). Farther north, as the length of the growing season is reduced, such isolating mechanisms may no longer be possible and hybridization events may increase in frequency, reducing the distinctiveness of species. In this study region, however, oak species appear to adhere well to the ecological species concept (VanValen 1976, Mishler and Donoghue 1982, Daghlian and Crepet 1983) and are treated as distinct entities, following the taxonomic treatment of Kurz and Godfrey (1962).

Species habitat preferences.—We calculated species habitat preferences for several soil resources as the mean weighted soil moisture or nutrient value for each species according to the following equation:

$$\mu^* = \frac{y_1x_1 + y_2x_2 + \cdots + y_nx_n}{y_1 + y_2 + \cdots + y_n}$$

where μ^* is the habitat preference (weighted mean); $y_1, y_2, \ldots y_n$ are the basal area of the species within plots 1, 2, . . . n; and $x_1, x_2, \ldots x_n$ are the mean values of the environmental variable within plots 1, 2, . . . n (terBraak and Looman 1995).

Fire frequency classification.—Species were classified into categories of increasing fire frequency based on predictive models developed by Jackson et al. (1999) that link the following habitat types to fire regimes (see Table 1): (1) frequently flooded bottomland forest, (2) infrequently flooded bottomland forest, (3) moist upland forest, (4) intermediate dry, (5) dry upland forest, and (6) park-like forest/savanna (sandhill). Species were placed in these categories and assigned the corresponding rank. No rank was given to the five scrub species: *Quercus chapmanii*, *Q. pumila*, *Q. minima*, *Q. myrtifolia*, and *Q. geminata*.

Geographic distributions of species.—Northern range limits of species were determined from distribution maps from Nixon (1997) and Burns and Honkala (1990), as described in Cavender-Bares and Holbrook (2001). Temperature and season length covary with latitude and range limit can effectively serve as a proxy for season length.

Physiological and morphological measurements of leaves of mature trees.—Measurement of several leaf-level traits were carried out on six to 10 individuals of each species at San Felasco Hammock State Preserve or Payne's Prairie State Preserve. Traits measured include gas exchange rates (leaf area and mass basis), laminar leaf area, specific leaf area, leaf nitrogen, and leaf chlorophyll content (data shown in Appendix B). All measurements were carried out on leaves of sun branches in order to control for light level, which has been shown to affect leaf life span and related leaf traits significantly (Williams et al. 1989, Reich et al. 1991, Ackerly 1996). Canopies of trees too tall to reach were accessed with the use of aerial lifts or scaffolding towers. Five such towers were erected in steep ravine areas not accessible with an aerial lift, allowing canopies of 15 trees to be reached in this manner. All measurements of gas exchange, SLA, total leaf N percent, and chlorophyll content were made during June on leaves of the first flush of the season. Carbon assimilation, stomatal conductance, and transpiration were measured with a portable gas exchange system (LI-6400, Li-Cor, Inc., Lincoln, Nebraska, USA) under saturating light (2000 μmol·m^{-2}·s^{-1}) using the red–blue LED attachment of the Li-6400. Leaf temperature was controlled at 30°C. All gas exchange measurements were conducted in the morning between 08:00 and 11:00 hours on clear days in an effort to avoid stomatal depression with declining leaf water potential following methods of Cavender-Bares and Bazzaz (2000). Five leaves of each individual were measured. The leaves were removed for measurement of laminar leaf area (leaf size), determined by measuring fresh leaf area with the petiole removed using a LI-3000 portable leaf area machine (Li-Cor, Inc., Lincoln, Nebraska, USA). Leaves were oven dried for one week at 65°C and weighed to calculate specific leaf area (SLA; cm^2/g) and photosynthesis on a mass basis (A_{mass}). Percent total leaf nitrogen (%N) was determined for three leaves of each tree measured. Dried leaf tissue was ground, and ~200 μg was used to determine %N using a Europa Elemental Analyzer (model ANCA-sl) attached to a Europa model 20–20 Stable Isotope Analyzer via a capillary interface (Europa Instruments, Crewe, UK).

Relative chlorophyll content of leaves was measured with a SPAD-502 chlorophyll meter (Minolta, Tokyo, Japan) on leaves at the time of leaf removal from the tree. A previous study of chlorophyll in oak leaves found a linear relationship between relative SPAD units and chlorophyll content on an area basis within the range of values found in the current study. SPAD units were converted to chlorophyll content following methods described in Cavender-Bares et al. (2000) using the following equation:

$$y = 5.53x - 62.9$$

where y = chlorophyll content (mg/m^2) and x = SPAD absorbance (relative).

Leaf life span and period of canopy foliation.—Leaf life span—the number of days a leaf survives—was calculated for six to 10 mature trees of each species from leaf birth and death dates monitored on three branches per tree. Only four, three, and three individuals were measured for *Q. shumardii*, *Q. laurifolia*, and *Q. stellata*, respectively, because of the difficulty in accessing their canopies. Prior to leaf emergence, branches were flagged. After flushing occurred, the leaves were numbered with permanent ink on the tip of the leaf, and the birth date of each leaf was recorded. Each branch and each flush on each branch was color coded so that leaves could be counted with a spotting scope from the ground. Monthly surveys were conducted for a 14-mo period to determine the timing of new flushing events, to record the number of new leaves produced and record the numbers of leaves still present from each flush. By subtracting the number of remaining leaves from the number of leaves originally marked, survival time for each cohort of leaves was determined and recorded. The monthly surveys provided a 15-d resolution for each measurement. Every several months, new flushes were flagged and new leaves numbered. Flushing and leaf-fall dates were also monitored over a second year, and were similar to the first year; hence, only data from the first year are reported. We used two measures of leaf life span: (1) the mean leaf life span of the first cohort of leaves flushing in spring and (2) leaf life span averaged across all leaf cohorts. Species means for these two methods were highly correlated ($r = 0.89$). However, the first method was more consistent between the two years because it was less dependent on the timing of the onset of cold weather. Subsequent flushes tended to get truncated by chilling events, skewing the average. The first method is also better correlated with seedling leaf life span measured in a common environment without a cold period ($r^2 = 0.92$ vs. $r^2 = 0.85$). All analyses were done with both measures, and the results were very similar. For brevity, we report only the first method.

Period of canopy foliation was averaged for six to 10 individuals per species over a 2-yr period based on monthly surveys. The period of canopy foliation was calculated as the number of days per year that a tree maintained 50% or greater of its foliage relative to maximum summer foliage. Canopy habit was defined by period of canopy foliation as follows: deciduous <300 d; brevideciduous ≥ 300 d and <365 d; evergreen $= 365$ d (Table 1).

Whole-plant traits of mature trees.—Whole-plant traits, including asymptotic height, sapling outer bark thickness, maximum hydraulic conductance normalized by sapwood area (maximum K_s), whole-shoot transpiration normalized by sapwood area, Huber value (ratio of sapwood area to supported leaf area), native percent loss of conductivity (PLC, native embolism), wood density, radial growth rate, rhizome resprouting potential, and seed mass, unless otherwise indicated, were measured for six to 10 mature trees across the range of their distributions at San Felasco or Payne's Prairie. Data are shown in Table 1 and Appendix C. Methods for determining maximum K_s, whole shoot transpiration, Huber value, and native PLC are described in Cavender-Bares and Holbrook (2001).

Seed size.—Size of acorns was determined both by volume and mass. Volume was calculated from radius (r) and height (h) of the fresh acorn assuming an ellipsoid shape using the equation: $4/3\pi r^2(h/2)$. Acorns were dried at 70°C for 3 d and weighed with and without the seed coat. Weights were only recorded for undamaged acorns. A minimum of 30 acorns were weighed per species, although volume was measured for 30–100 acorns per species. For 480 acorns from 16 species, an empirical relationship was determined between acorn volume (V) and acorn mass with seed coat removed (M): $M = 0.6363V - 0.1213$, $R^2 = 0.97$. Using this equation, seed mass for *Q. stellata* was determined from data collected from the U.S. Forest Service (Burns and Honkala 1990). We report seed mass without the seed coat as we assume that it is the most critical measure of seed size (Bazzaz 1997).

Asymptotic height and rhizome resprouting potential.—Asymptotic tree height was estimated by measuring height and dbh of 50–100 individuals of all sizes for each species and fitting an exponential function to the data as described by Thomas and Bazzaz (1999). We found our data to be in accord with data from the U.S. Forest Service and other published sources (Burns and Honkala 1990, Nixon 1997, Greenberg and Simons 1999). We used height information from Nixon (1997) for *Q. minima* and *Q. pumila*. For rhizome resprouting potential and clonal spreading (RhResprPot), a rank was assigned to each species based on seedling experiments, observations in the field, and published sources (Webber 1935, Kurz and Godfrey 1962, Burns and Honkala 1990, Guerin 1993, Menges and Kohfeldt 1995, Nixon 1997, Greenberg and Simons 1999) according to the following criteria: (1) no resprouting from rhizomes or roots, (2) resprouting from rhizomes possible but rare, (3) occasional vegetative reproduction from rhizomes and clonal spreading in small patches, (4) considerable sprouting from roots and underground runners almost always present, including clonal spreading and dome formation.

Outer bark thickness.—We adapted methods described by Jackson et al. (1999) and Adams and Jackson (1995) to measure outer bark (rhytidome) thickness of saplings. Log-log regression equations of outer bark thickness vs. stem diameter were used to estimate outer bark thickness at stem diameters representing approximately one-quarter of the asymptotic tree height, based on relationships between stem diameter and height. Outer bark thickness of the short-statured runner oaks, *Q. pumila* and *Q. minima*, was estimated at 2 cm stem diameter, which corresponds to a stem height that is close to their maximum. We collected data for ~20 individuals per species for *Q. myrtifolia*, *Q. hemispherica*, *Q. pumila*, *Q. nigra*, *Q. minima*, *Q. chapmanii*, *Q. austrina*, *Q. falcata*, *Q. laevis*, *Q. margaretta*, *Q. incana*, and *Q. geminata*. Data for remaining species was taken from Jackson et al. (1999).

Radial growth increment.—Radial growth increment (mm/yr), a measure of absolute growth rate, was calculated from tree ring widths from tree cores of mature trees for 17 species. Cores were taken only from trees with straight trunks and fully exposed canopies. Cores were sanded until polished and viewed under a dissecting scope (Wild M3Z, Heerbrugg, Switzerland). Tree rings were measured to the nearest 0.01 mm using a Velmex Unislide tree ring measuring system (Velmex Company, New York, New York, USA) and software designed specifically for collecting tree ring data (Measure J2X version 2.2.6, Voortech Consulting, Holderness, New Jersey, USA; tree ring data bank).[6] Annual growth increments vary with stem diameter, age, life history stage and growth conditions (Clark and Clark

---

[6] ⟨http://www.voortech.com/projectj2x/measureJ2XInfo.html⟩

1999). Moreover, stem diameters and age at maturity vary greatly among these oak species, making comparison of growth rates difficult. In an effort to account for these factors, we averaged 10 consecutive growth increments for each individual during its maximum growth phase after reaching reproductive age. Reproductive ages for each species were based on data from Burns and Honkala (1990) and Kurz and Godfrey (1962). For the runner oaks (*Q. pumila* and *Q. minima*), which are reproductive after only a few years, the last five annual growth increments were used.

Wood density.—Density of sapwood was determined from tree cores or small segments for six to 10 individuals of the same species as explained for radial growth. Volume was determined for fresh samples from radius and length measurements of the cores or by volume displacement in distilled water. Dry wood mass was determined by weighing oven-dried samples.

Seedling traits from a glasshouse experiment

Because species differences in phenotypes expressed in their native habitats reflect both genetic and environmental differences, in situ field measurements of individuals alone do not allow clear assessment of evolutionary divergence. Therefore, it is important to examine the association of species traits expressed under common garden conditions with habitat preferences determined in the field. Hence, in addition to leaf and whole-plant traits of adult trees in situ, seedling traits were determined in a glasshouse for a subset of species included in the analysis.

Growth conditions.—Plants were grown in glasshouse facilities at Harvard University. Acorns were collected in the fall of 1996 in north-central Florida for the nine species: *Q. falcata*, *Q. geminata*, *Q. hemispherica*, *Q. laevis*, *Q. margaretta*, *Q. michauxii*, *Q. myrtifolia*, *Q. nigra*, and *Q. myrtifolia*. *Q. alba*, considered a hammock species, whose range begins just north of the field study area, was also included in the common garden study although it was not represented in the field study. Acorns were stored in a cold room at 5°C after collection and planted in 60 × 35 × 20 cm tubs with Promix potting soil (Premier Horticulture, Dorval, Quebec, Canada) in the spring of 1997. Germination took ~1–2 mo. Germinants were transplanted into individual 12-L tree pots within 1–2 wk after emergence. The soil in these pots included a 2-cm layer of gravel and 2 cm of Turfus (Profile Products, Buffalo Grove, Illinois, USA) at the bottom of the pot. Pots were then filled to the surface with sand and a small amount of peat and field soil. At the time of transplanting, the date was recorded, and initial measurements were made on stem height, root and stem diameter, number of leaves, and length of the longest leaf. Approximately 40 plants were transplanted per species, depending on germination rates and viability of acorns. At least 30 additional plants per species were measured, dried, and weighed to determine allometric relationships between measured variables and biomass. Temperature was maintained at circa 28°C during the day and 20°C at night.

Seedling growth rates.—Absolute and relative growth rates were measured on all species in the experiment. Absolute growth rate (AGR, g/yr) was determined from dry biomass. Relative growth rate (RGR, $\mathrm{g \cdot g^{-1} \cdot d^{-1}}$) was calculated as follows:

$$\mathrm{RGR} = \frac{\mathrm{Log}_e(M_{\mathrm{final}}) - \mathrm{Log}_e(M_{\mathrm{initial}})}{T_{\mathrm{final}} - T_{\mathrm{initial}}} \qquad (1)$$

where M_{final} and M_{initial} are biomass at the time of harvest (T_{final}) and the time of transplanting (T_{initial}) (Hunt 1982). Allometric equations were developed relating plant parameters—including stem height, stem diameter, leaf number, and length of longest leaf—to dry biomass based on separate harvests of at least 30 seedlings per species (Appendix D). These equations were used to estimate M_{initial} from nondestructive measurements on the common garden plants

Leaf-level traits.—Leaf life span was determined by recording birth and death dates of leaves from apical shoots on ~15 individuals per species. Leaves were surveyed weekly for a 16-mo period, providing high resolution for these data. Gas exchange was measured on 10–15 individuals per species in late July, controlling light level (1500 $\mu\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) using a LI-6400 portable photosynthesis system (Li-Cor, Lincoln, Nebraska, USA). After photosynthesis was measured, a leaf disk of known area was removed in the same area on the leaf where gas exchange was measured. Large primary and secondary veins were avoided. The disk was weighed with a microbalance for calculation of A_{mass}. Leaf laminar area (leaf size), and specific leaf area (SLA) were measured for multiple leaves per individual at the time of harvest in the same manner as described for mature trees. Whole plant transpiration rates were calculated by multiplying mean maximum transpiration rates per species by the average leaf surface area per species.

Linking functional traits, habitat variables, and community affiliations

Independent contrast correlations.—Using hypotheses about phylogenetic relationships between species, determined in a separate study (Cavender-Bares et al. 2004), we examined the direction and magnitude of evolutionary change in particular traits in relation to other traits or habitat preferences, following the method originally proposed by Felsenstein (1985) and standardized by branch lengths (Garland et al. 1992). By reconstructing ancestral states of traits, this method allowed us to examine evolutionary trade-offs and patterns of correlated evolution among traits and habitat preferences. Analyses were carried out using four equally likely tree topologies in the program CACTUS (Schwilk and Ackerly 2001).[7]

---

[7] ⟨http://www.pricklysoft.net/software/cactus.html⟩

Principal components analysis.—PCA for traits of mature trees and for traits of seedlings in the common garden were carried out using Data Desk v. 6.0 (Data Description, Inc., Ithaca, New York, USA) to determine whether functional traits of species group by the three community types—hammock, sandhill, and scrub. Traits included in the mature tree PCA were rhizome resprouting potential, wood density, Huber value, maximum leaf life span, radial growth rate, asymptotic height, seed mass, native PLC, maximum K_s, A_{mass}, laminar leaf area, whole-shoot transpiration, and SLA. Traits included in the seedling PCA were SLA, seed mass, laminar size, absolute growth rate, relative growth rate, whole plant transpiration, A_{mass}, and leaf life span.

Testing for species similarity within communities and lineages.—Multiple analysis of variance (MANOVA) was used to determine whether variation among species in (1) spatial distribution (axis scores from the DCA analyses) and (2) habitat preferences (weighted mean values of each soil factors for each species) could be explained either by the preassigned community affiliations, treated as a fixed effect with three levels, or by phylogenetic lineage, treated as a fixed effect with three levels. For the ordination data, first- and second-axes scores were included as dependent variables in the MANOVA, but separate tests were run for the two different DCA analyses. For habitat preferences, species mean, weighted values for soil moisture, soil pH, soil nitrate N plus ammonium N, soil calcium, and organic matter content were treated as dependent variables. We also used univariate ANOVAs to determine whether community affiliation or lineage explained interspecific variation in functional traits. All analyses were carried out in Data Desk v. 6.0.

RESULTS

Quantification of species distributions

Indirect gradient analyses.—The results of the ordination analyses based on presence/absence of all species (Fig. 2A), on presence/absence of oaks only, and on relative basal area of oaks (Fig. 2B) indicate that the community structure we observed is well described by the first and second axis of ordination. For brevity, the analysis of presence/absence of oaks only is not shown, but the results closely resemble the first analysis. The eigenvalues for the first axis ranged from 0.66 to 0.88 and from 0.42 to 0.53 for the second axis (Table 2). Both ordinations show clustering of species within each of the three community types. In the analysis using relative basal area of oaks, however, there is greater resolution in the spatial distribution of hammock species and less resolution in the distribution of scrub species relative to the presence/absence ordination.

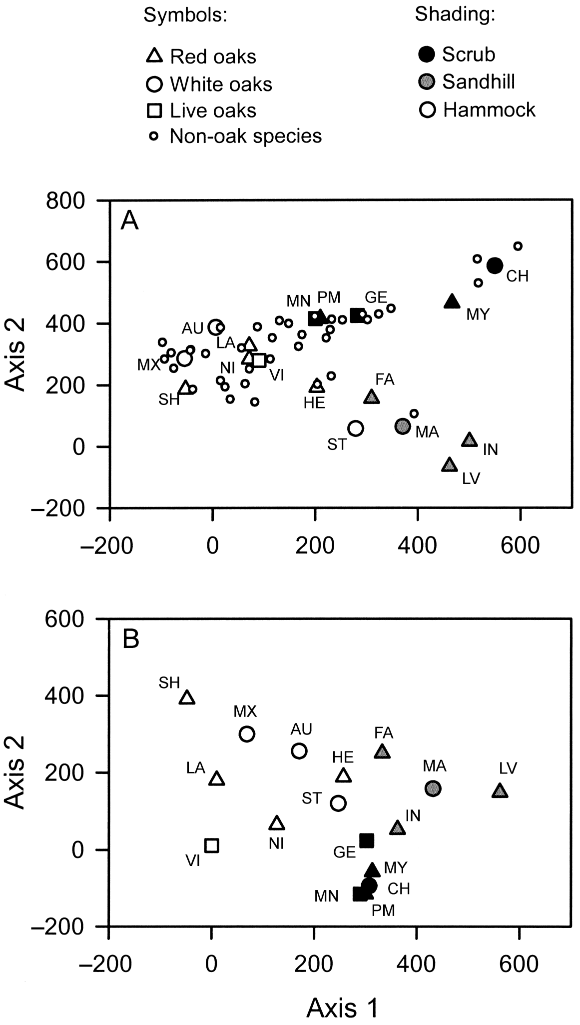

FIG. 2. Scatter diagrams showing species scores in relation to the first and second axes after DCA using presence/absence for (A) all woody species within plots and (B) relative basal area of oak species. Phylogenetic lineages of each species are shown with symbols. Three distinct community types can be identified and are indicated with different shading (shown for oaks only): scrub, black; sandhill, gray; hammock, open symbols.

Average plot values of soil moisture and all soil fertility factors, except soil pH, were significantly negatively correlated with the first axis of ordination in all three analyses (Table 2). Soil moisture and soil fertility parameters across plots covaried to a large extent (Table 3) and cannot be statistically separated. The highest covariance was found among the cations, Ca, Mg, and K. Fire frequency classification of tree species by Jackson et al. (1999) (Table 1) was also highly correlated with this axis (see also Table 6) indicating that fire frequency covaries inversely with soil moisture and resource availability. Soil moisture was the only environmental parameter significantly correlated with the second axis in the presence/absence analyses (Fig. 2A). In the analysis using relative basal area (Fig. 2B), the species are distributed somewhat differently across the two axes and the second axis is weakly correlated with

TABLE 2. Pearson and Kendall correlation coefficients (r) of soil parameters measured in 74 plots in relation to the first and second ordination axes based on presence or absence of all species or relative basal area of oaks within the 74 plots.

	Presence/absence: all species		Relative basal area: oaks	
Parameters	Axis 1 (r)	Axis 2 (r)	Axis 1 (r)	Axis 2 (r)
Soil moisture	**−0.55**	**0.31**	**−0.58**	0.19
NH_4-N	**−0.58**	0.21	**−0.47**	**0.35**
NO_3-N	**−0.33**	0.09	**−0.41**	0.04
Organic matter	**−0.47**	0.27	**−0.43**	0.10
P (soil samples)	**−0.38**	0.05	−0.15	0.26
P (resin bags)	**−0.38**	0.16	−0.27	**0.39**
Ca	**−0.59**	0.20	**−0.56**	**0.32**
Mg	**−0.57**	0.18	**−0.36**	**0.36**
K	**−0.58**	0.26	**−0.50**	**0.48**
pH	−0.19	−0.28	−0.12	**0.38**
Eigenvalues	0.66	0.42	0.88	0.53

Notes: Eigenvalues are shown below the columns for each axis. Correlation coefficients >0.3 or <-0.3 are shown in boldface (df = 73).

pH, K, Mg, Ca, NH_4 and P, due to the low fertility in scrub plots (low axis scores) and higher fertility in hammock plots, particularly those in which *Q. michauxii* and *Q. shumardii* occur (high axis scores).

The presence/absence ordination analysis shows a separation of species along the second axis at the dry end of the gradient (right hand side in Fig. 2A). In particular, scrub species such as *Q. chapmanii*, *Q. myrtifolia,* and *Q. geminata* clearly form a distinct group relative to sandhill species, such as *Q. laevis*, and *Q. margaretta*, and *Q. falcata*. For simplicity, the non-oak species are not labeled, however, sandhill oak species were found in association with *Pinus palustris* and the scrub oak species, particularly *Q. chapmanii* and *Q. myrtifolia,* were found in association with *Lyonia ferruginea* and *L. lucida*. Hammock oak species were found in association with a high diversity of woody species, including *Liquidambar styraciflua*, *Pinus glabra*, *Carya* spp., and *Magnolia* spp.

Species distributions across resource axes and niche overlap.—Proportion of total basal area per soil moisture level are shown in Fig. 3 for seven resource bins. The upper row shows sandhill species that are restricted to dry sites, particularly *Q. laevis* and *Q. margaretta*, which only occur in the driest resource level. *Q. incana* and *Q. falcata* occur in the first two driest resource levels, and *Q. falcata* also has a small presence in wetter sites. The second row shows scrub species, which also largely occur in dry sites, but are less restricted than sandhill species. *Q. minima* and *Q. pumila* (similar distribution as *Q. minima*, but not shown) actually occur in intermediate soil moisture regimes. *Q. geminata* shows its highest abundance at low soil moisture but still maintains a low presence even in the wettest soil moisture level. Hammock species, shown in the third and fourth rows, all occur in the wettest soils but many of them also occur in dry soils. Hammock species, in general, tend to have broader distributions across the soil moisture gradient than sandhill or scrub species.

Mean niche overlap of all species, based on Pianka's niche overlap test, was significantly less than expected across gradients of soil moisture and pH (Table 4). Species pairwise overlap values for soil moisture are given in Appendix E. The same result was obtained if

TABLE 3. Pearson correlation coefficients for relationships among soil parameters within plots (N = 74).

Parameter	Soil moisture	OM	NO_3-N	NH_4-N	P	K	Mg	Ca
OM	**0.50**							
NO_3-N	0.29	**0.64**						
NH_4-N	**0.51**	**0.72**	**0.51**					
P	**0.36**	**0.41**	0.19	**0.42**				
K	**0.51**	**0.53**	0.29	**0.74**	**0.63**			
Mg	**0.54**	**0.58**	**0.45**	**0.59**	**0.82**	**0.77**		
Ca	**0.50**	**0.67**	**0.77**	**0.67**	**0.48**	**0.67**	**0.78**	
pH	0.00	0.14	**0.53**	**0.31**	0.20	0.29	**0.41**	**0.66**

Notes: Coefficients >0.30 are shown in boldface. The table indicates a high degree of covariance among soil fertility parameters and soil moisture. Organic matter is abbreviated as OM.

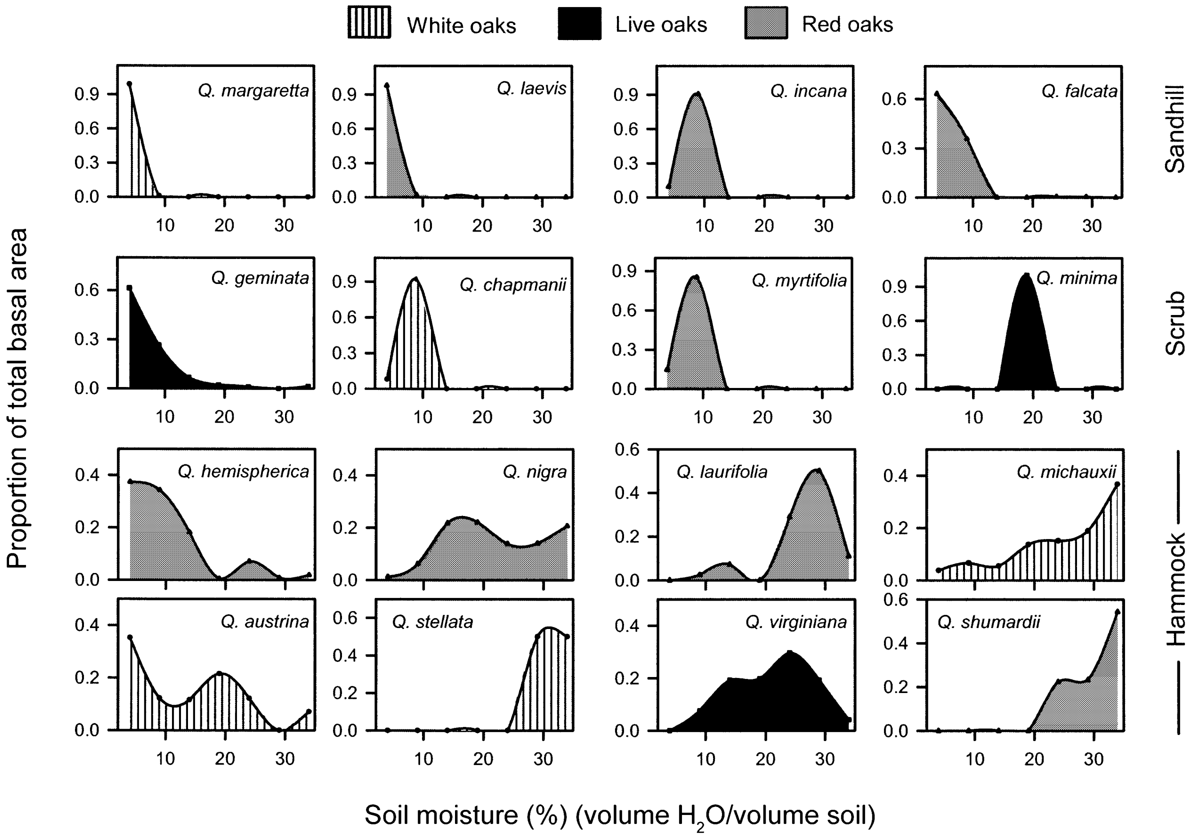

FIG. 3. Plots show the proportional basal area of species across seven levels of soil moisture for 16 species. The proportion is calculated as the ratio of basal area in each level over the total basal area along the gradient; soil moisture levels shown are the midpoints of seven ranges of values. *Q. pumila* is not shown but has a distribution very similar to *Q. minima*.

soil moisture data were converted to soil water potential based on soil moisture release curves for Arredondo Fine Sand (Carlisle et al. 1988) and divided into seven bins ($P < 0.001$; 1000 simulations > observed). A sensitivity analysis for soil moisture showed that the analyses were robust to changes in bin width and that a two-fold increase in the number of bins still gave rise to lower niche overlap than expected. Forty-eight out of 136 total species pairs showed less overlap than expected across the soil moisture gradient. Only 10 pairs showed more overlap than expected. Mean niche overlap of all species across all soil factors tested was significantly less than expected ($P < 0.001$, Table 4). Soil moisture is less important for niche partitioning among hammock species, examined by themselves ($P = 0.192$, Table 4), although hammock species are partitioning the pH gradient ($P < 0.002$). At the same time, calcium is more important for niche partitioning among hammock species ($P < 0.056$), than among all species ($P < 0.49$).

MANOVA results show that spatial distributions of species are highly significantly explained by preassigned community affiliations, but not by phylogenetic lineage. This result is the same whether DCA axes scores from the presence/absence analysis (Table 5) or from the relative basal area analysis are used (not shown). Species habitat preferences with respect to soil properties are also significantly explained by community affiliation but not by phylogenetic lineage (Table 5). Species habitat preferences for soil moisture, soil nitrate and ammonium, soil calcium, organic matter content, and pH differed among the communities, but not among lineages. Scheffe's post hoc tests show the significant difference in species soil preferences among communities arises from differences between preferences of hammock and scrub species and between hammock and sandhill species, but not between sandhill and scrub species. The same result emerges if soil properties of scrub, hammock and sandhill plots are compared, rather than species habitat preferences.

Functional traits of species in relation to community structure, habitat preferences, and phylogenetic lineage

Species traits in relation to ordination axes.—Native embolism, radial growth rate, whole-shoot transpiration normalized by sapwood area, asymptotic height, seed mass, A_{mass}, and maximum K_s of mature trees were all significantly correlated with species scores for the first axis of ordination (Table 6). Seedling traits related

TABLE 4. Pianka's pairwise niche overlap values averaged for all oak species pairs and for hammock oak species only across each of six soil factors (seven resource levels).

Soil factor	Mean overlap	Expected overlap	P
All oak species			
Soil moisture	**0.312**	**0.429**	$<$**0.001**
pH	**0.324**	**0.429**	$<$**0.001**
Ca	0.394	0.395	0.49
P, exchangeable	0.426	0.444	0.33
Organic matter	0.357	0.413	0.15
NO_3-N + NH_4-N	0.453	0.453	0.56
All soil factors	**0.378**	**0.431**	$<$**0.001**
Hammock oak species			
Soil moisture	0.496	0.533	0.192
pH	**0.397**	**0.527**	**0.002**
Ca	*0.369*	*0.454*	*0.056*
P, exchangeable	0.486	0.531	0.175
Organic matter	0.493	0.476	0.619
NO_3-N + NH_4-N	0.610	0.541	0.909
All soil factors	*0.478*	*0.514*	*0.081*

Notes: Lower observed mean overlap values than expected are shown in boldface. Marginally significant values are shown in italics.

to gas exchange and growth, including absolute growth rate, whole plant transpiration, A_{mass}, and RGR, were significantly correlated with the first axis of ordination. Fire-frequency classification of individual species (Table 1) was highly correlated with the first axis of ordination for all ordination analyses (correlation excludes scrub species shown in black). Both rhizome sprouting potential and sapling outer bark thickness were also correlated with the first axis of ordination, with hammock species having little rhizome resprouting potential relative to scrub species and sandhill species having greater bark protection than hammock and scrub species (Table 6, Fig. 4).

Period of canopy foliation for mature trees was correlated with the second axis of Fig. 2A: scrub species tend to be evergreen or brevideciduous while sandhill species are largely deciduous. Other leaf-level traits of mature trees, including laminar leaf area, chlorophyll content, A_{max}, SLA, period of canopy foliation, and mean or maximum leaf life span were not correlated with either of the DCA axes. A_{max} is defined as the maximum CO_2 assimilation rate on a leaf-area basis, measured in the morning under saturating light at ambient temperature and 350 μL/L CO_2. Seedling leaf life span was also correlated with the second axis of ordination: the two scrub species in the seedling experiment (*Q. myrtifolia* and *Q. geminata*) had longer-lived leaves (both evergreen) than the sandhill hill species (*Q. margaretta*, *Q. laevis*, and *Q. falcata*), all deciduous. The brevideciduous scrub species, *Q. pumila* and *Q. chapmanii*, which have intermediate leaf life spans, and the sandhill species (*Q. incana*), which has a short leaf life span (5.4 mo) were not included in the seedling study, which accounts for the significant correlation for seedling leaf life span but not leaf life span of mature trees.

Species traits in relation to environment.—Outer bark thickness of species was highly correlated with fire frequency ranking ($r = 0.92$, $P < 0.0001$) for a subset of the species excluding scrub species (cf., the fire-frequency ranking by Jackson et al. [1999] does not include scrub species, Table 1). Sandhill species had significantly thicker bark than either scrub or hammock species, corresponding to high frequency/low severity ground fires in sandhill communities (Fig. 4A and inset to 4B). The capacity of species to resprout from roots and rhizomes and to spread clonally was maximal in scrub communities, where severe canopy fires destroy the aboveground biomass, and least evident in hammock communities (Fig. 4B), where canopy fires are rare. At the same time, asymptotic height was greatest in hammock communities, where competition for light is most intense, and fire frequency is very low and unpredictable (Fig. 4C).

Species mean values for seed size and growth-related traits increased with soil resource availability, shown as species habitat preferences for soil nitrate N plus ammonium N and soil moisture (Fig. 5). Soil NO_3-N + NH_4-N was chosen as the representative measure of soil fertility, as various soil measures are correlated with each other (Table 3). Seed mass, seedling absolute growth rate, mature tree growth rate (Fig. 4), were significantly correlated with both mean soil NO_3-N +

TABLE 5. MANOVA results testing whether communities or phylogenetic lineages, treated as main fixed effects, significantly explain the variance among groups of dependent variables: spatial distribution and habitat preferences.

	Spatial distribution (DCA axis scores)†			Habitat preferences (soil factors)‡		
Main effect	Wilks' lambda	P	df	Wilks' lambda	P	df
Phylogenetic lineage§	0.888	0.807	4, 26	0.477	0.757	12, 18
Community‖	0.078	0.0001	6, 24	0.081	0.006	12, 18

† First and second axis scores for oak species from detrended correspondence analysis of occurrences of all woody species within random plots.

‡ Species weighted mean values for soil moisture, organic matter content, exchangeable phosphorus, exchangeable nitrate and ammonium, pH, and calcium content.

§ Red, white, and live oaks.

‖ Sandhill, scrub, and hammock.

TABLE 6. Correlation coefficients for species means of trait values for mature trees and seedlings grown in a common garden vs. axis scores for the two DCA ordinations.

	Presence/absence: all species		Basal area: oaks		
Trait	Axis 1 (*r*)	Axis 2 (*r*)	Axis 1 (*r*)	Axis 2 (*r*)	*N*
Mature trees: field					
Fire-frequency ranking	**−0.88**	**0.83**	**−0.90**	0.12	13
Sapling bark thickness	0.41	**−0.78**	**0.62**	0.30	17
Rhizome sprouting potential	**0.76**	0.25	**0.74**	**−0.71**	17
PLC	**−0.66**	−0.17	**−0.61**	0.40	17
Radial growth	**−0.60**	−0.14	**−0.68**	**0.51**	17
Whole-shoot transpiration	**−0.56**	−0.08	−0.46	0.45	17
Asymptotic height	**−0.53**	−0.43	−0.41	**0.80**	17
Seed mass	**−0.53**	−0.23	−0.44	**0.73**	17
A_{mass}	**−0.51**	**−0.48**	−0.39	**0.48**	17
Maximum K_s	**−0.49**	−0.07	**−0.51**	0.24	17
Leaf size	−0.32	−0.39	−0.18	**0.68**	17
Chlorophyll content	−0.26	0.22	−0.03	−0.28	17
A_{max}	−0.23	−0.19	−0.08	−0.10	17
SLA	−0.18	−0.19	−0.25	**0.48**	17
Period of canopy foliation	0.05	**0.49**	−0.11	**−0.58**	17
Leaf life span	0.09	0.44	−0.06	−0.35	17
Wood density	0.12	0.47	0.02	**−0.61**	17
Huber value	0.18	0.16	0.21	−0.40	17
Seedlings: common garden					
AGR	**−0.87**	0.14	**−0.68**	**0.51**	9
Whole-plant transpiration	**−0.77**	0.02	**−0.57**	**0.61**	9
A_{mass}	**−0.67**	0.43	**−0.79**	−0.04	9
RGR	**−0.65**	0.39	**−0.72**	−0.06	9
SLA	−0.31	−0.28	−0.11	**0.69**	9
LAR	**0.58**	**−0.60**	**0.71**	0.11	9
A_{max}	−0.39	0.50	**−0.57**	−0.39	9
Leaf life span	0.05	**0.73**	−0.28	**−0.76**	9
Laminar leaf area	−0.54	−0.03	−0.28	**0.70**	9

Notes: Correlation coefficients ≥ 0.48 are shown in boldface. *N* is the number of species for which data were available. For mature trees, units are as follows: maximum K_s (maximum hydraulic conductance; kg $H_2O \cdot s^{-1} \cdot m^{-1} \cdot MPa^{-1}$); transpiration per sapwood area (mmol $H_2O \cdot m^{-2} \cdot s^{-1}$); chlorophyll content (relative units); radial growth increment (cm/yr); fire frequency ranking (excluding scrub species; taken from Jackson et al. [1999]); asymptotic height (m); rhizome resprouting potential (index); sapling bark thickness (mm); period of canopy foliation (d); wood density (g/m^3); leaf life span (d); maximum assimilation rate (A_{max}; μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$), maximum assimilation rate-mass basis (A_{mass}; μmol $CO_2 \cdot g^{-1} \cdot s^{-1}$); chlorophyll content (mg/m^2); seed size (seed mass without the seed coat; g); leaf size (laminar leaf area; cm^2); Huber value (ratio of sapwood area to leaf area); native percentage loss of conductivity (PLC). For seedlings, units are: absolute growth rate (AGR; g/yr); relative growth rate (RGR; $g \cdot g^{-1} \cdot d^{-1}$); whole-plant transpiration (mmol $H_2O \cdot m^{-2} \cdot s^{-1}$); laminar leaf area (cm^2); SLA (cm^2/g); leaf life span (d); A_{max} (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$); A_{mass} (μmol $CO_2 \cdot g^{-1} \cdot s^{-1}$); leaf area ratio (LAR; m^2/g).

NH_4-N and mean soil moisture of species habitats. Both mature tree radial growth and seedling RGR showed a trend of asymptotically higher values with higher resource availability (Fig. 5E–H).

Traits known to be important in influencing water transport and loss in other systems, including wood density, hydraulic conductance, native embolism (PLC), and whole-shoot transpiration, were examined in relation to species soil moisture preferences using standard correlations and independent contrast correlations. Interestingly, using a standard correlation, wood density was not directly correlated with the soil moisture gradient (Fig. 6A) because the trait is conserved within lineages, and live oaks have much denser wood than other species. Independent contrasts, however, which allow trait conservatism within lineages to be factored out, showed a significant decrease in wood density with increasing soil moisture (Fig. 6B), consistent with findings in other systems (Meinzer 2003). Hydraulic conductance, native embolism (PLC), and whole-shoot transpiration were all significantly correlated with soil moisture preferences and showed significant patterns of correlated evolution with habitat preferences using independent contrasts (Fig. 6C–H).

These patterns give rise to very clear evolutionary trade-offs, for example, between maximum height and the ability of plants to resprout from rhizomes after fire (Fig. 7A) or the native embolism of the xylem and the hydraulic capacity of stems (Fig. 7C), providing support for a safety–efficiency trade-off (Sperry 1995, Hacke and Sperry 2001). At the same time, growth and height show a strong correspondence, as documented in other systems (Thomas 1996, Baker et al. 2003).

At the leaf level, A_{mass} and SLA were significantly correlated with foliar N concentration when examined

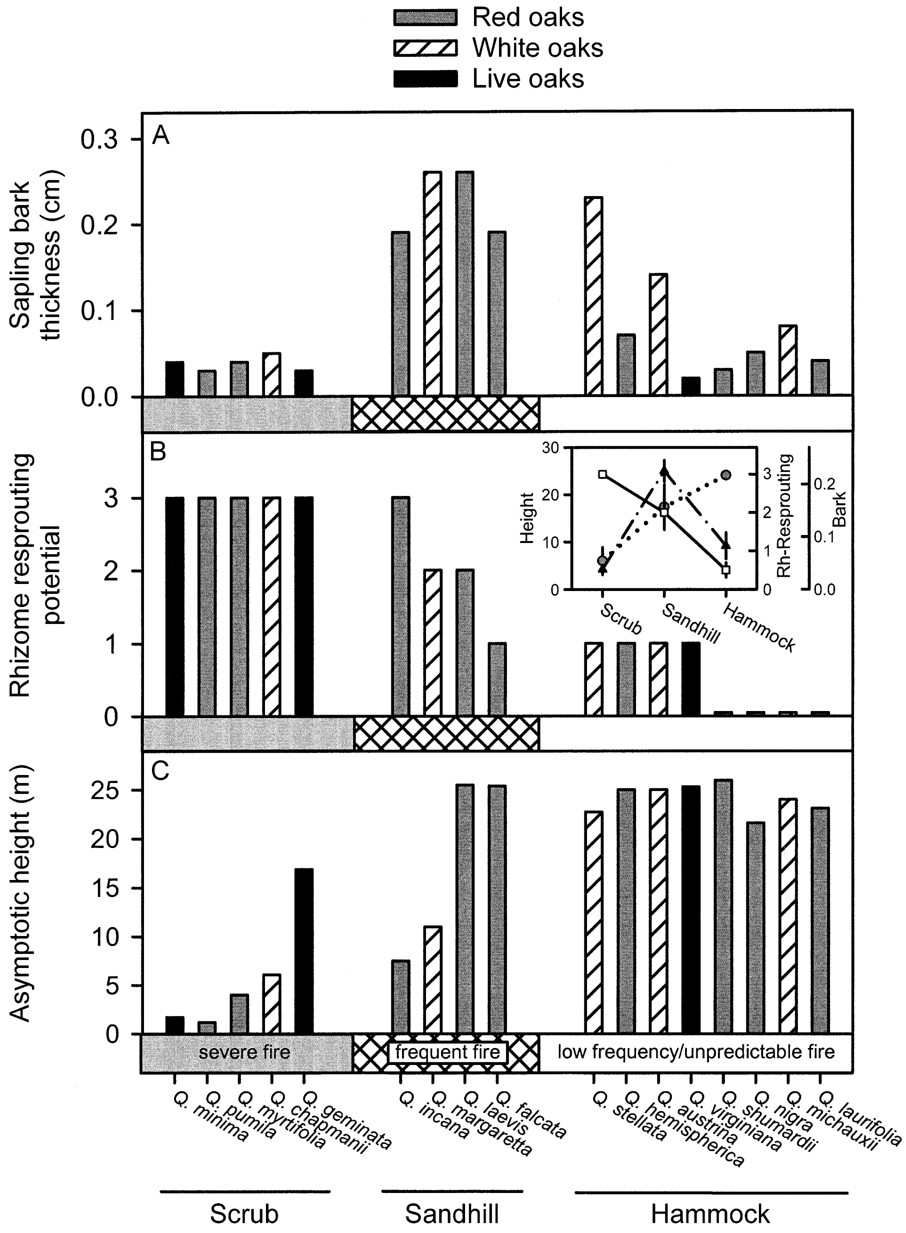

FIG. 4. Species trait values for bark thickness (for saplings at 5 cm dbh), rhizome sprouting potential, and asymptotic height in relation to fire regime, which varies by community. Phylogenetic lineages of species are indicated by shading. The inset in (B) shows means for each trait within communities: height, gray circles and dotted line; rhizome resprouting, open squares and solid line; bark, solid triangles and dashed line.

on an individual leaf basis (Appendix F). These relationships varied across phylogenetic lineages, however, and were strongest within the live oak group. SLA was not significantly correlated with %N within the red oaks or white oaks. An overall correlation arises because live oaks have relatively low SLA and low %N while white oaks tend to have higher %N and higher SLA (Appendix F). There is high variation in the relationships among leaf traits within the red oaks. In particular, *Q. incana* behaves as an outlier species with relatively high A_{mass}, high SLA, and short leaf life spans but low %N. Indeed, A_{mass} and %N are correlated within the red oaks only when *Q. incana* is removed from the analysis (Appendix F). At the species level, leaf traits including A_{mass} and leaf life span were only weakly correlated with foliar N concentration (Table 7). Other traits, however, including period of canopy foliation and SLA were more strongly correlated with leaf N. Yet, contrary to expectation, leaf-level traits were not correlated with soil fertility or soil moisture (Table 7). These results are the same regardless of which soil factors are examined and if independent contrast cor-

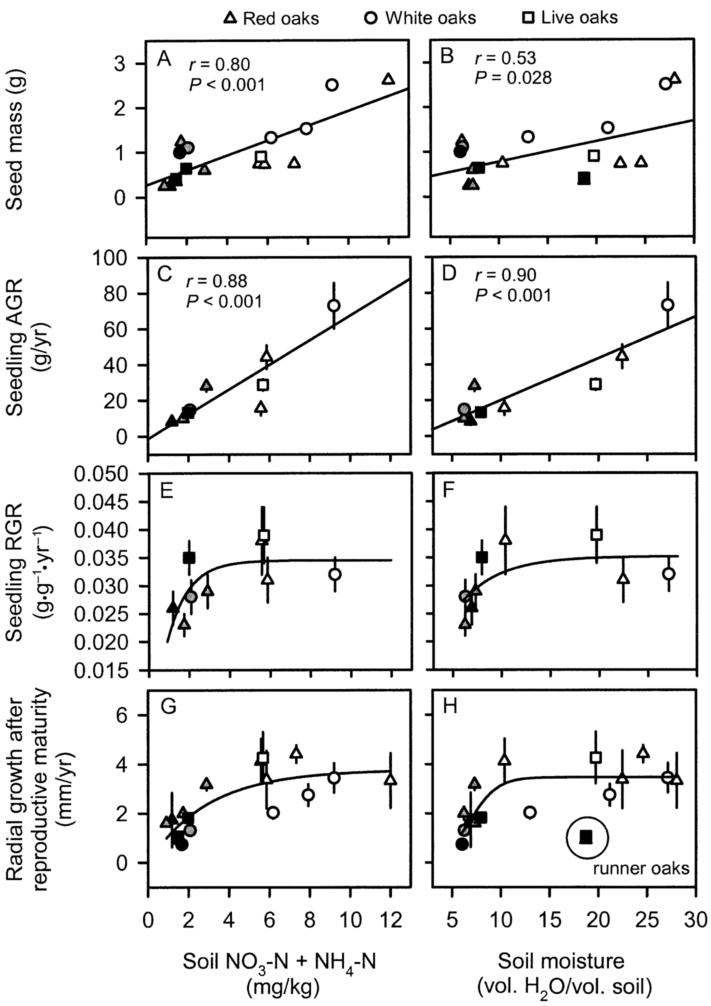

FIG. 5. Correlations between species means of four whole-plant traits in relation to soil fertility, as measured by nitrate plus ammonium concentration, or soil moisture of species' habitats: (A, B) seed mass with seed coat removed; (C, D) absolute growth rates of seedlings in the common garden experiment; (E, F) relative growth rates of seedlings; and (G, H) radial growth rates of mature trees. In panels (E)–(H), two-parameter sigmoidal curves are fit to the data. In panel (H), the runner oaks, *Quercus pumila* and *Q. minima*, are not included in the curve. Symbol shapes indicate the phylogenetic groups. Community affiliations are distinguished by shading: scrub, black; sandhill, gray; hammock, open.

relations are used instead of standard correlations (data not shown). If sandhill species are removed, leaf life span and period of canopy foliation tend to decline with increasing soil fertility as expected, although the statistical power is limited with only 13 species, and these trends are not significant. In contrast, leaf-level traits, with the exception of SLA, correspond well to the northern range limit of the species geographic distributions (Table 7). Southern species have longer leaf life spans and shorter periods of canopy foliation than northern species. In addition, southern species have smaller leaves, lower A_{mass}, and lower N concentration than northern species.

Adult traits measured in situ vs. seedling traits in a glasshouse

The degree to which traits measured in the field reflect intrinsic properties of species rather than responses to the environment is not known. However, a substantial component of these traits appears to be intrinsic, given strong correlations between seedling traits measured in a common environment and mature traits measured in the field (Appendix G). Several of the traits measured on seedlings could be directly compared to the same traits or to similar kinds of traits as those measured on mature trees in the field (Appendix G). Radial growth rates of adult trees were correlated with relative growth rates of seedlings (RGR) measured under standardized favorable conditions in a glasshouse ($r = 0.66$; Appendix G). Seedling absolute growth rates were highly correlated with max. hydraulic conductance ($r = 0.823$) and with transpiration rates on a sapwood area basis of mature trees ($r = 0.86$). Physiological correlates of plant growth rates, e.g., transpiration rates, SLA, and A_{max}, were also correlated between adult trees and seedlings. Shoot-level transpiration rates (per unit sapwood area) of adult trees were also positively correlated with whole plant transpiration of seedlings ($r = 0.90$; Appendix G). SLA of seedlings and mature trees showed a strong correlation ($r = 0.81$; Appendix G), although seedlings had much higher SLA than mature trees. Laminar leaf area was also significantly correlated ($r = 0.76$) but seedlings had smaller leaves than mature trees. Light saturated

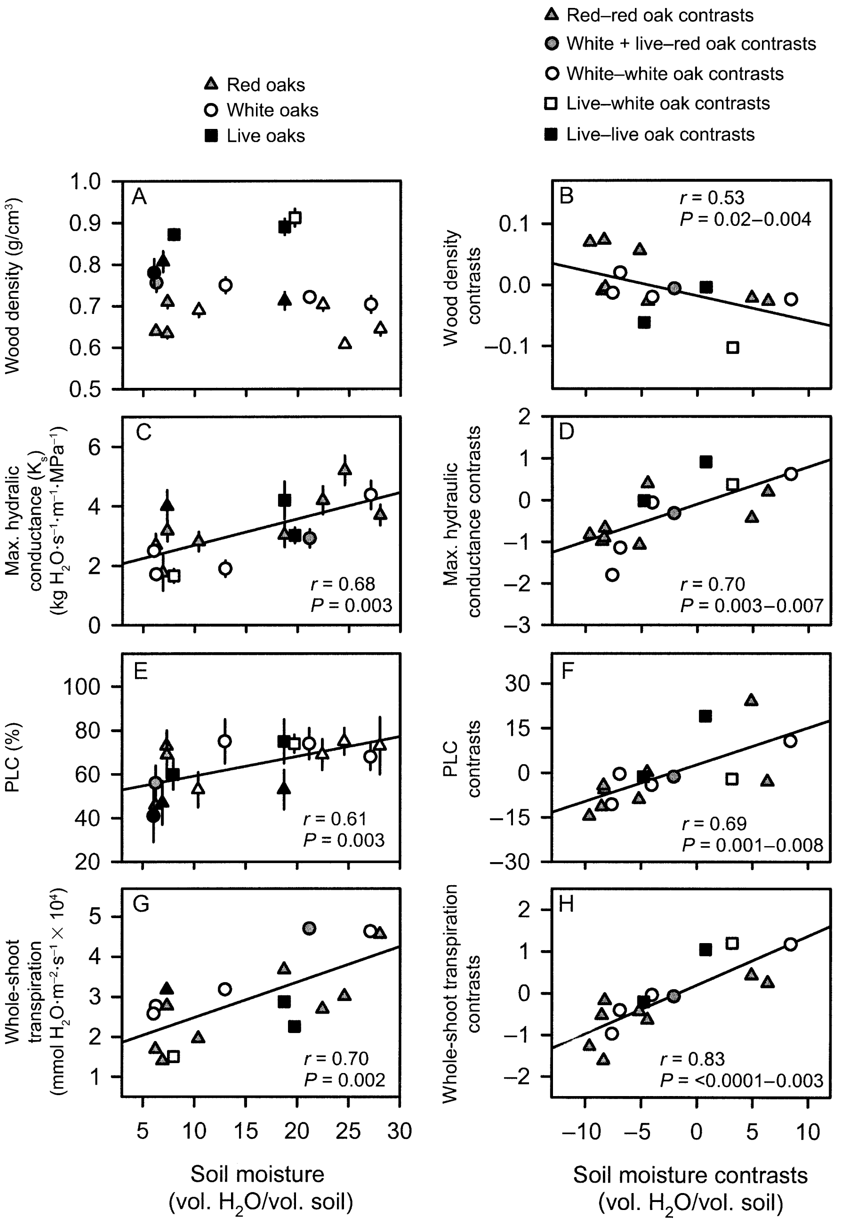

FIG. 6. Correlations between species trait means and soil moisture (left-hand panels), as well as independent contrast correlations for contrasts of the same traits in relation to contrasts in soil moisture preferences (right-hand panels): (A, B) wood density; (C, D) maximum hydraulic conductance normalized by sapwood area (maximum K_s); (E, F) native percentage loss of hydraulic conductivity; and (G, H) whole-shoot transpiration normalized by supporting sapwood area. Symbols for the left-hand panels indicate phylogenetic lineages. Due to the fact that species often share traits by common descent rather than through independent evolution, standard correlations, which assume independence of species, may not be appropriate in making inferences about adaptation (Felsenstein 1985). Independent contrast correlations (right-hand panels) take advantage of information about the evolutionary relationships among species and determine whether evolutionary change (magnitude and direction) is correlated between two traits (in this case, between traits and species habitat preferences). Symbols and shading represent contrasts within or between lineages. R values for the plotted contrasts are given along with a range of P values for contrasts using four equally likely phylogenies.

photosynthetic rates measured on a leaf area basis (A_{max}) in the common garden and in the field were strongly correlated ($r = 0.81$) although mature trees had higher photosynthetic rates than seedlings. A_{mass} was not correlated between seedlings and mature trees ($r = 0.41$). Thus, the significant correlation of A_{max} between adult and seedlings was largely due to SLA. Seedling leaf life span was very highly correlated with leaf life span of mature trees ($r = 0.92$). The relationship was very close to the 1:1 line, but seedling leaf

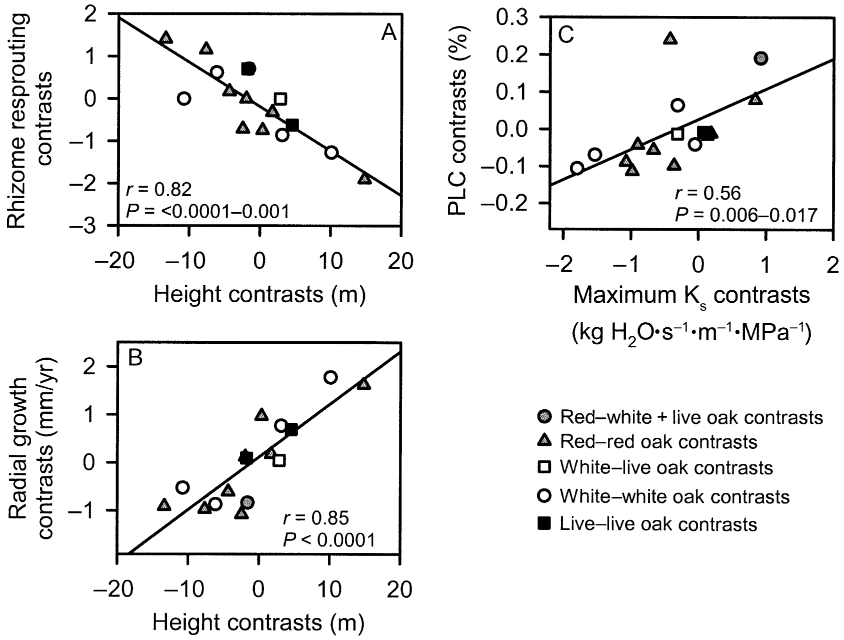

FIG. 7. Independent contrast correlations of species traits showing evolutionary trade-offs and correlations: (A) contrasts in rhizome resprouting potential in relation to contrasts in asymptotic height; (B) contrasts in radial growth in relation to height; (C) contrasts in percentage loss of hydraulic conductivity in relation to maximum hydraulic conductivity. R values for the plotted contrasts are given along with a range of P values for contrasts using four equally likely phylogenies. Symbols and shading represent contrasts within or between lineages, as in Fig. 5.

life spans were shorter than adults especially in species with greater leaf longevity (Appendix G), an ontogenetic difference that follows theoretical predictions (Kikuzawa and Ackerly 1999).

Principal components analysis of species traits

Eigenvalues for axis 1 and axis 2 of the principal components analysis of traits of mature trees (Fig. 8A) explained 42% and 18%, respectively, of the total variation. For simplicity, only the first two axes are presented. Species clustered well according to their community affiliation (Fig. 8A), although *Q. falcata*, a tall tree from the sandhill community, was more closely associated with hammock species than sandhill species in the PCA. Scrub and hammock species were separated by differences in rhizome resprouting potential, asymptotic height, radial growth rate, native embolism (PLC), maximum hydraulic conductance, and A_{mass}

TABLE 7. Correlation coefficients (R) for leaf traits in relation to habitat factors, including species soil preferences and northern range limits (N latitude) and other leaf traits.

Habitat factors and leaf traits	Leaf life span	Period of canopy foliation	Leaf size	SLA	A_{max}	A_{mass}	Foliar N (%)	Chlorophyll content
Habitat factors								
Soil NO_3-N + NH_4-N	−0.17	−0.28	**0.57**	0.39	−0.02	0.45	**0.70**	−0.05
Soil pH	−0.19	−0.46	**0.57**	0.41	0.03	**0.54**	**0.58**	−0.34
Soil calcium	−0.20	−0.32	**0.59**	0.38	0.05	**0.53**	**0.69**	0.00
Soil P	−0.25	−0.37	**0.60**	0.06	0.10	0.20	0.49	0.14
Soil moisture	−0.20	−0.05	0.35	0.27	0.12	0.44	0.35	0.20
N range limit	−**0.563**	−**0.723**	**0.706**	0.405	0.048	**0.568**	**0.646**	−0.159
Leaf traits								
Chlorophyll content	0.168	0.22	0.1	−**0.512**	**0.596**	0.064	0.019	
Foliar N	−0.456	−**0.738**	**0.733**	**0.549**	−0.095	0.441		
A_{mass}	−**0.568**	−0.475	0.288	0.33	0.495			
A_{max}	0.073	0.174	0.005	−**0.61**				
SLA	−**0.66**	−**0.651**	0.345					
Leaf size	−0.38	−**0.63**						
Period of canopy foliation	**0.829**							

Note: R values >0.5 or <−0.5 are shown in boldface.

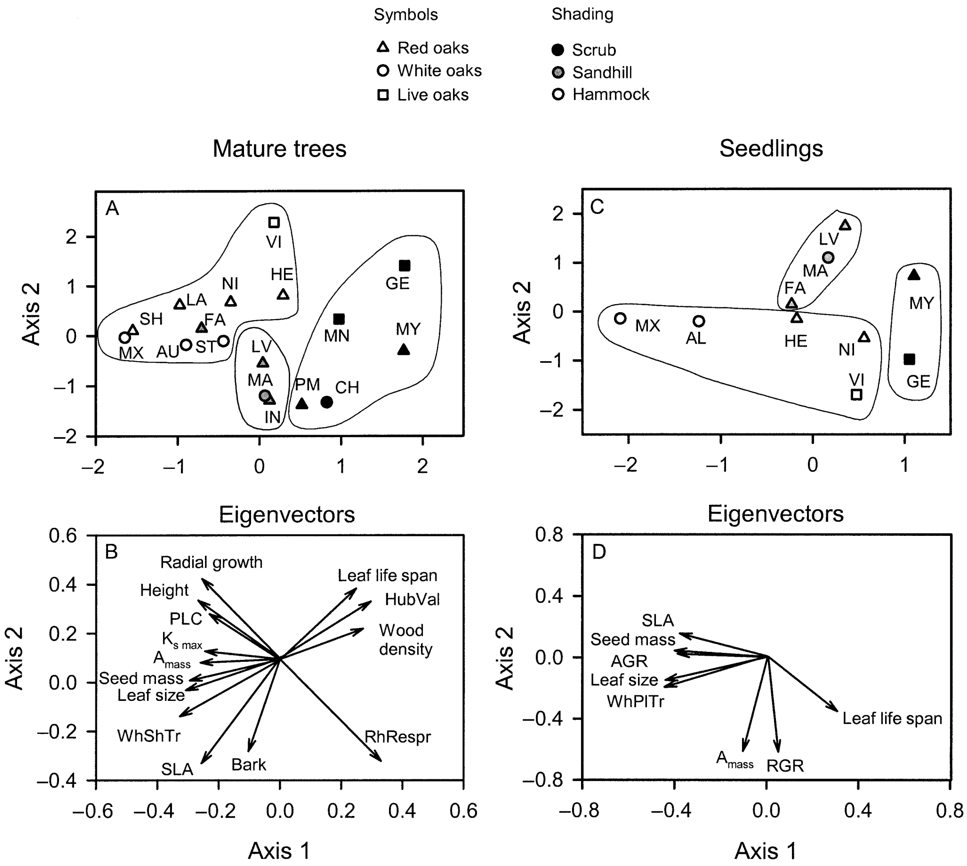

FIG. 8. (A) Principal components analysis of species traits for mature trees measured in the field. The following traits were used: leaf life span, laminar leaf area (leaf size), carbon assimilation rate on a mass basis (A_{mass}), specific leaf area (SLA), maximum hydraulic conductance ($K_{\mathrm{s\ max}}$), Huber value (Hub Val), whole-shoot transpiration divided by sapwood area (WhShTr), native percentage loss of conductivity (PLC), asymptotic tree height (height), rhizome resprouting potential (RhRespr), outer bark thickness of saplings (bark), wood density, radial growth increment, and seed mass. (B) Eigenvectors indicating direction and magnitude of the weighting of individual traits in the PCA are shown for the same axes as in panel (A). (C) Principal components analysis of species traits for seedlings measured in a common garden. *Quercus alba* (AL), a hammock species, was included in the common-garden experiment, although it does not occur in the field study sites. The following seedling traits were used: leaf life span (LL), laminar leaf area (leaf size), carbon assimilation rate on a mass basis (A_{mass}), specific leaf area (SLA), whole-plant transpiration (WhPlTr), seed mass, absolute growth rate (AGR), and relative growth rate (RGR). Eigenvectors of the traits are shown in panel (D). For (A) and (C), community affiliations, phylogenetic lineages, and habitat types are distinguished by the same symbols and shading as in Figs. 1 and 3. Species codes (from Table 1) are shown next to symbols.

(Fig. 8B). Sandhill species were intermediate between hammock and scrub with respect to these traits. Species that group together in the scrub community, including *Q. minima*, *Q. pumila*, *Q. myrtifolia*, and *Q. geminata* have higher rhizome resprouting potential, greater wood density, shorter stature, lower SLA, higher Huber values, and thinner bark than species that group together in the sandhill community, including *Q. laevis*, *Q. margaretta*, and *Q. falcata*.

The PCA for traits measured on seedlings in the common garden experiment also distinguished between the three community types (Fig. 8C). Again, *Q. falcata* aligned closely to hammock species as well as sandhill species. Scrub and hammock species differed with respect to absolute growth rates, seed size and whole plant transpiration, with hammock species having higher values for these traits (Fig. 8D). Sandhill and hammock species were separated by differences in A_{mass} and relative growth rates, with sandhill species having lower values for these traits than hammock species. Scrub species had longer leaf life spans, lower SLA, smaller seeds, and smaller leaves than sandhill species (Fig. 8D).

Taking into consideration both the mature tree and seedling analyses, hammock species are characterized by their tall stature, fast growth rates, high hydraulic conductance, high A_{mass}, thin bark, and low rhizome resprouting potential. Scrub species are characterized by high rhizome resprouting potential, low growth rates, short stature, relatively long periods of canopy foliation (although not necessarily long leaf longevities), and thin bark. Finally, sandhill species have thick

TABLE 8. Univariate ANOVAs for leaf and whole-plant traits with community (three levels) or clade (three levels) treated as the main fixed effects (df = 2, 14).

Trait	Community (scrub, sandhill, hammock)			Clade (red, white, live oak)		
	MS	F	P	MS	F	P
A_{max}	4.560	0.240	0.790	71.93	7.687	0.006
Chlorophyll content	396.0	0.781	0.477	1158	2.906	0.088
Vessel diameters	17.49	0.971	0.403	56.93	4.598	0.029
Ks_{max}	1.326	1.248	0.317	0.864	0.766	0.484
Huber value	1.309	1.383	0.283	5.638	17.19	<0.0001
SLA	286.9	1.526	0.251	896.4	8.886	0.003
Whole-shoot transpiration	1.673	1.740	0.211	1.874	2.008	0.171
Leaf life span	6825	2.663	0.105	8410	3.600	0.055
Leaf size	1291	2.761	0.098	1388	3.058	0.079
Wood density	0.021	3.189	0.072	0.049	20.95	<0.0001
PLC†	0.058	3.268	0.068	0.011	0.453	0.645
Seed mass	1.297	3.410	0.062	0.977	2.293	0.138
Period of canopy foliation	5762	3.940	0.044	9484	10.19	0.002
A_{mass}	0.003	5.276	0.020	0.0002	0.236	0.793
N (%)	0.412	6.357	0.011	0.475	8.501	0.004
Bark thickness	0.042	14.73	<0.0001	0.014	2.050	0.166
Asymptotic height	504.5	15.74	<0.0001	11.79	0.115	0.892
Rhizome resprouting	10.06	35.21	<0.0001	1.014	0.643	0.541
Radial growth	9.360	17.59	<0.0001	0.528	0.295	0.749

† PLC is percentage loss of conductivity.

bark, short leaf life spans, and are intermediate in many of the traits that distinguish hammock and scrub species.

Analysis of variance for correspondence of traits to community or lineage affiliations

A number of whole plant traits were significantly different among the three communities (Table 8), corroborating the clusters shown by the principal components analyses. According to Scheffe's post hoc tests, sandhill species had significantly thicker outer bark and greater asymptotic height than scrub species, while scrub species had greater rhizome resprouting potential than the other two groups, and hammock species had greater radial growth rates than the other two groups. Despite low statistical power, two measures of growth rates of seedlings grown under standardized conditions showed differences among species in the different communities (highest for hammock species) when examined using MANOVA ($F_{4,12} = 2.87$, $P = 0.07$), but there were no differences among phylogenetic lineages ($F_{4,12} = 1.99$, $P = 1.6$). Variation in leaf-level traits were explained somewhat better by lineage than by community affiliation, with the exception of A_{mass} (Table 8). Significant or marginally significant differences among lineages were found for A_{max} ($P = 0.006$), period of canopy foliation ($P = 0.002$), foliar N concentration ($P = 0.004$), SLA ($P = 0.003$), leaf life span ($P = 0.055$), and chlorophyll content ($P = 0.088$). Differences for period of canopy foliation and leaf N were also found among communities, but were less significant. A_{mass} showed significant differences only among communities. For mature trees, A_{mass} was significantly lower for scrub species than hammock species, while period of canopy foliation was significantly longer among scrub species relative to sandhill species and longer in live oaks than in white oaks. In general, traits that were similar within communities were not similar within lineages, and vice versa, with the exception of foliar nitrogen concentration, which was different among communities and among lineages (white oaks had higher leaf N than live oaks) and period of canopy foliation (longer for live oaks than white oaks). Vessel diameters, Huber value (ratio of sapwood area to supported leaf area), and wood density differed among lineages, showing significant evolutionary conservatism, but not among communities (Table 8).

Species diversity in relation to soil resources

The number of woody species per plot increased with soil fertility initially (from less than six to more than ten) and then remained constant with subsequent increases in soil fertility. In contrast, the average number of oak species per plot remained constant (between 3 and 4) across all soil fertility levels, even at very low fertility sites.

DISCUSSION

Our results show that oak species are not randomly distributed across the Florida landscape but show clear patterns of ecological sorting and specialization along the major environmental gradients in this region, including soil moisture, soil fertility, and fire regime. Oak species in different habitats possess functional traits that are known a priori to provide advantages for survival in those habitats, and there appear to be fundamental trade-offs in life history and physiological traits that prevent species from performing well across all environments. Thus, at the landscape scale, i.e., the scale at which major shifts in soil moisture, fertility and fire regime occur (1–100 ha), maintenance of high oak diversity can be explained by niche partitioning of the important environmental gradients. At smaller spatial scales, however, other mechanisms of species coexistence must be invoked (Cavender-Bares et al. 2004).

Species distributions, community structure, and niche partitioning

Soil moisture, soil fertility, and fire regime play an important role in explaining the distributions of oak species in north-central Florida. All soil moisture and soil fertility factors, with the exception of pH, were negatively correlated with the first axis of ordination in the detrended correspondence analyses (Table 2) indicating that species are differentially distributed along a gradient of soil moisture and availability of various nutrients, which covaried to a large extent (Table 3). These results corroborate previous studies in the region indicating that soil resource availability, driven by differences in soil hydrology, is important in the structuring of forest communities (Monk 1965, 1968, Hook 1984, Hodges 1995). Studies of oak species in other regions have also shown that they are distributed differentially across gradients of soil moisture or rainfall (Monk et al. 1989, Knops and Koenig 1994, Villar-Salvador et al. 1997).

Species cluster spatially within three major community types (hammock, scrub, and sandhill) that differ in fire regime (Fig. 2A and B). Fire plays a major role in maintaining oak diversity because both sandhill and scrub communities, which collectively contain eight oak species, are fire dependent. Differences in the severity and frequency of fire maintain these two very distinct fire-dependent communities. In contrast, most hammock species are not fire tolerant and they occur largely where fire is excluded for long periods of time. The strong correlation of the first axis of ordination (Fig. 2A) with fire frequency index indicates that the soil resource gradient and fire frequency covary as a function of soil moisture regimes. Fire frequency and water availability are generally inversely correlated, such that fire frequency increases as water availability or flooding period diminishes (Bonnicksen and Christensen 1981, Swetnam and Betancourt 1990). It is likely that fire patterns reinforce distributions of vegetation corresponding to water availability. However, because the fire frequency index does not include scrub species, the first axis of ordination (Fig. 2A) should be interpreted only as an approximation of fire frequency, with hammock species (low axis scores) having very low frequency fires (on the order of every 100 yr) and scrub and sandhill species (high axis scores) having higher frequency fires (every ~50 yr for scrub; every 1–15 yr for sandhill).

The second axis may be interpreted in terms of fire severity, with scrub species (high axis scores) having high severity canopy fires and sandhill species (low axis scores) having more frequent, low severity ground fires. While soil moisture is weakly correlated with the second axis, soil fertility is not correlated as there are no detectable differences in soil fertility between scrub and sandhill communities. In a series of studies comparing successional patterns after a range of fire exclusion intervals, Myers (1985, 1990) concluded that scrub and sandhill communities are separated by their fire regime, facilitated by the vegetation itself. This interpretation is supported in the present study by the actual fire histories in these communities, to the extent that they are known, and by current fire management practices. Oak species in these two communities differ in various functional traits that are best interpreted to reflect adaptation to contrasting fire regimes as discussed in the section of functional traits below. Hammock species (intermediate axis scores) incur unpredictable fire severity, depending on topography and fluctuations in drought and temperature (Ewel 1990). In the absence of fire, low-fertility sites can become hammock communities that support several of the opportunistic hammock oak species that do not survive fire, including *Q. hemispherica* and *Q. nigra*. In addition, oak species that may be fire tolerant in terms of bark thickness but are also competitive in hammock communities (due to tall stature and relatively high growth and photosynthetic rates), including *Q. falcata* and *Q. stellata* (intermediate first-axis scores, Fig. 2A), may also be found in low-fertility hammock communities where fire has been excluded. In contrast, some hammock oak species appear to be found only in nutrient/cation rich hammocks (*Q. michauxii*, *Q. shumardii*, *Q. austrina*) or hydric hammocks (e.g., *Q. laurifolia*). These species tend to be large seeded, to have high hydraulic conductance and gas exchange rates and to be poor resprouters.

Partitioning the abiotic environments

Our results show strong evidence for niche partitioning across major soil resource gradients. Average overlap of species within plots, calculated according to Pianka's niche overlap (Pianka 1973), was significantly less than expected by chance across all soil factors (Table 4). The lowest overlap values, considering all species pairs, were along soil moisture and pH gradients. In the north-central Florida landscape, niche differentiation among the soil moisture gradient corresponds to the differentiation among fire regimes, as these variables are coupled. Within hammock communities, however, differentiation across the soil moisture gradient is less pronounced than it is for the entire landscape (Fig. 3, Table 4). Hammock species are still significantly differentiated across the pH gradient but also appear to be differentiated with respect to soil calcium (Table 4). The partitioning of the pH and calcium gradients among hammock species corresponds to the separation among hammock species on the second axis of the third DCA ordination (Fig. 2B), showing that *Q. shumardii* and *Q. michauxii*, in particular, prefer higher pH sites and sites with higher cation availability than other species.

Specialization for specific habitats

Partitioning of the abiotic environment is consistent with the hypothesis that species have suites of functional traits that allow them to specialize for particular ranges along resource gradients where they can be most competitive. A high degree of variation in the abiotic environment can thus maintain high numbers of specialists for these environments. Here we discuss evidence for the correspondence of critical functional traits of species to their habitat preferences for traits known a priori to be adaptive to particular environments based on theoretical understanding of their function and on previous empirical evidence.

Traits related to fire tolerance.—Traits related to fire tolerance and post-fire recovery, such as bark thickness, rhizome resprouting potential and asymptotic height are well distinguished among species of the three community types (Table 8) and consequently to the three major fire regimes they experience. Species that group together in scrub communities, including *Q. minima*, *Q. pumila*, *Q. myrtifolia*, *Q. chapmanii*, and *Q. geminata*, have higher rhizome resprouting and clonal spreading than species that occur in sandhill communities, including *Q. laevis*, *Q. margaretta*, *Q. incana*, and *Q. falcata*. The former group can sprout from roots and forms clonal domes or very large and long-lived rhizomatous runners (Kurz and Godfrey 1962, Guerin 1993). *Q. margaretta*, *Q. laevis*, *Q. incana*, and *Q. virginiana* can also resprout from rhizomes to some extent (Kurz and Godfrey 1962), but do not form clonal domes or long lived runners and are more likely to resprout from aboveground stem tissue (Burns and Honkala 1990). Hammock species, in general, have low rhizome resprouting potential, although most oaks can resprout from aboveground stems. Only *Q. shumardii* and *Q. michauxii* show very limited resprouting capacity (Burns and Honkala 1990), which may explain, in part, why they are restricted to the wettest sites.

Sandhill species have thicker outer bark as saplings than hammock or scrub species, made clear by the strong correlation between sapling bark thickness and the second DCA axis (Table 6, Fig. 2A and B) that separates sandhill species from scrub and hammock species. Outer bark thickness insulates against high temperatures (Martin 1963, Bond and Wilgen 1996) and has been shown to affect survival during surface fire (e.g., Uhl and Kaufmann 1990). Thick bark provides an adaptive advantage to sandhill species, which experience frequent ground fires, particularly during the vulnerable juvenile life stage. Scrub species, which experience severe fires, do not invest in protective bark, as all of the above ground biomass is likely to burn. They also have short stature, which minimizes loss of tissue after fire. Instead, they show a high ability to recover from severe fire by clonal spreading and resprouting from roots or rhizomes. Other authors have shown that species in those contrasting fire regimes actually facilitate the perpetuation of those regimes through fuel loading, differences in the flammability of leaves and biomass, or the formation of clonal dome structures that prevent the spread of surface fires until there is sufficient fuel loading to promote severe crown fires (Webber 1935, Myers 1985, Guerin 1993).

Growth-related traits.—Traits related to growth rate, including radial growth rate, maximum hydraulic conductance, whole-shoot transpiration on a sapwood area basis, seed mass, and AGR, are negatively correlated with the first axis in all three ordination analyses, such that species with faster growth and higher resource uptake rates tend to be found in hammock communities where soil moisture and nutrients are more available (Table 6). Previous theoretical and empirical work shows that in relatively fertile soils, sites that might be considered ‘‘choice habitats’’ (Bazzaz 1991), competition for light is very high, and traits that promote rapid achievement of larger size, such as large seed size and high absolute growth rates, are likely to be favored by selection (Tilman 1984, 1988). Such growth-related traits are well correlated with species habitat preferences for soil resources (Fig. 5). Traits related to rapid resource acquisition, including hydraulic conductivity and whole shoot gas exchange on a sapwood area basis, were also directly correlated with resource availability (Fig. 6). Relative growth rates, measured on seedlings, and radial growth rate measured on mature trees (Fig. 5E–H), showed differentiation among hammock communities on the one hand and scrub and sandhill communities on the other. Clear evolutionary trade-offs between traits are also apparent. For example, species have specialized for either tall stature and rapid mature growth rates (competitive advantages in resource rich environments where light is limiting beneath the canopy) or for rapid resprouting from belowground roots and rhizomes (critical for recovering from severe fire; Fig. 7A and B). Species with high capacity for hydraulic conductance also tended to have high native embolism during a drought summer (Fig. 7C), indicating that oak species specialize for either safety or efficiency in their water transport. Similar trade-offs in hydraulic architecture have been found for a range of species in other systems (Hacke and Sperry 2001). Taken together, these trait-environment relationships and trait-trait correlations build a strong case for ecological sorting and habitat specialization among the oaks.

Leaf-level traits

Contrary to expectation and to previously documented relationships in other systems (e.g., Karlsson

1992, Reich et al. 1992, Wright et al. 2001), leaf-level traits, including leaf life span, period of canopy foliation, specific leaf area, and $A_{\max}$, were not correlated with any of the soil factors measured, including soil nitrate and ammonium or soil moisture (Table 7), although A_{mass} was correlated with species habitat preferences for soil pH and soil calcium. The lack of correlation results from the phenomenon that species with contrasting leaf phenologies often occur together, particularly in hammock communities, but also to some extent in scrub communities. In a separate study, leaf life spans of oaks co-occurring within 0.10-ha plots were found to be more contrasting than expected by chance (Cavender-Bares et al. 2004).

Given that the ranges of leaf life spans and other leaf traits are relatively narrow relative to other studies linking leaf traits to nutrient availability (Schlesinger and Chabot 1977, Chabot and Hicks 1982, Reich et al. 1992, 1997, Karlsson 1994, Eckstein et al. 1999, Wright et al. 2001), their lack of correlation with soil fertility is not necessarily surprising. However, leaf-level traits do show correlations with leaf N concentration at the level of individual leaves (Appendix F) and/or at the species level (Table 7). While leaf N cannot be considered a measure of soil fertility, given complexities of interactions between soil moisture and nutrient supply (Wright et al. 2001) and the conservative nature of leaf N within species and within lineages (Table 8), these results leave open the possibility that at small spatial scales (tens of meters) species may be partitioning microenvironments by foraging at different depths. No differences in predawn water potential have been found among species occurring together in this system (Cavender-Bares and Holbrook 2001), although fine root placement could nevertheless be occurring at different depths leading to differential access to nutrient supplies (Goulden 1996, Hooper and Vitousek 1997). Such a mechanism is testable and could contribute to species coexistence at small spatial scales.

Leaf longevity may also be linked to successional status of the species within a given community (Mulkey and Kitajima 1995), as well as to fire regime. Interestingly, the lack of correlation between leaf traits and soil nutrients results partially from the short leaf longevities and deciduous leaf habits of the sandhill species that grow in habitats with low soil resource availability, but with relatively high light availability. This gives rise to significant or marginally significant difference among community types with respect to several leaf traits, including period of canopy foliation (Table 8). Cost–benefit theory of leaf longevity at the leaf and whole-plant level (Kikuzawa and Ackerly 1999, Givnish 2002) suggests that leaf-longevity is a function of time to recover initial investment, which should be shorter under high light and nutrient availability. Frequent fires in sandhill communities maintain relatively open canopies and provide frequent pulses of nutrients (although post-fire nutrient pulses may be rather small; Webber 1935, Abrahamson 1984, Myers 1985). High litter accumulation during the period of deciduousness may encourage fire when the trees are dormant and more tolerant of fire (Glitzenstein et al. 1995), leading to a positive feedback between short leaf longevity and fire frequency. In contrast to sandhill oaks, scrub oaks have more densely arranged foliage, apparently a greater degree of self-shading, and lower daily photosynthetic income per unit leaf mass (J. Cavender-Bares, *unpublished data*). These traits are apparently coupled with greater leaf longevity and evergreen habit as predicted by cost. Evergreen habits of many scrub and some hammock oaks would be disadvantageous where fire occurs very frequently as in sandhill communities.

In contrast to soil fertility, the northern range limits of species were significantly correlated with leaf longevity, period of canopy foliation, and A_{mass} (Table 7). Hence, leaf longevities may be more adapted to broader climatic factors, such as the length of the growing season, than to local edaphic factors. As a result, oak species may not be optimally distributed across local soil fertility gradients with respect to nutrient use efficiency. Rather, in the assembly of the current communities, species may have preferentially tracked environmental factors for which they had narrower tolerances (Ackerly 2003), such as fire regime and soil moisture. This hypothesis is supported by the fact that species showed narrower niche distributions across the soil moisture gradient than expected, but not across the nitrate and ammonium or phosphorus gradient (Table 4). Leaf-level traits also tend to be conserved within the major lineages (Table 8), and may not be as evolutionarily labile as other traits, limiting the extent to which leaf traits could have adapted through natural selection to local soil fertility gradients.

Association of multiple traits in relation to habitat preference

The DCA ordinations show good correspondence with the grouping of oak species into three main communities—hammock, sandhill, and scrub—distinguished on the first axis by fire frequency and resource availability, and on the second axis by fire intensity. When the first and second axis scores of the species are analyzed as the dependent variables in MANOVA, the distinctiveness of the three communities are significant (Table 5). The community affiliations are also significantly distinguished in terms of species preference for edaphic properties, including soil moisture and nutrient availability (Table 5). Scheffe's post hoc analyses reveal that these distinctions arise from differences between hammock and scrub species, as well as between hammock and sandhill species, rather than from differences in soil preferences between scrub and sandhill species. This is consistent with other studies that have failed to find consistent chemical differences in soils between the two communities, making fire regime the distinguishing abiotic factor (Myers 1985).

ANOVAs of individual traits show clear differences in species from different communities for a number of traits, particularly life history traits related to fire tolerance and growth (Table 8, Fig. 4). In terms of adult traits measured in situ, scrub and hammock oaks were separated by differences in rhizome resprouting potential, height, radial growth rate, native embolism (PLC), maximum hydraulic conductance, and A_{mass}. Sandhill species were intermediate between hammock and scrub species with respect to these traits. Rhizome resprouting and clonal spreading are a defining characteristic of the scrub oaks, in addition to short stature, slow growth, low hydraulic conductance, low rates of gas exchange, and low native embolism. In contrast, the hammock oaks are characterized by tall stature, fast growth, high gas exchange rates, high native embolism, and high hydraulic conductance. Sandhill species tend to have relatively tall stature, and intermediate growth and gas exchange rates. Thick bark is a critical functional trait that distinguishes sandhill species from scrub and hammock species (Fig. 4).

The PCA for traits measured on seedlings in the common garden experiment also distinguished between the three types of community affiliations. *Q. falcata* aligned closely to hammock species as in DCA analysis. Scrub and hammock species differed with respect to absolute growth rates, and whole plant transpiration, with hammock species having higher values for these traits. Sandhill and hammock species were separated by differences in A_{mass} and relative growth rates, with sandhill species having lower values for these traits than hammock species. Although this analysis includes a smaller number of species, it corresponds well to PCA for traits of mature trees and indicates that the three types of community affiliations are differentiated by growth-related traits.

Interpreting trait–environment correlations

One difficulty in interpreting trait–environment correlations in field studies is that the differences in traits between species may be the result of both genetic differences and plasticity if species are measured in different environments. Common garden experiments can help determine the extent to which trait differences observed among species in the field are genetic vs. environmentally induced (Givnish et al. 2004). Practically, however, it is very difficult to adequately reproduce all of the representative field conditions in a common garden. Moreover, many traits cannot be measured on seedlings, making the study of long-lived species particularly challenging. In our study, the high degree of correlation between traits measured in the field and in the common garden indicates that trait differences among species measured on mature trees in the field have a strong genetic component and are not merely the result of plasticity in traits of species that have contrasting distributions. There were important differences in magnitude between seedlings and adults for some of the traits, but the relative ranking of the species was similar (Appendix G). This result is important given that ontogenetic shifts in traits can be significant in oaks (Cavender-Bares and Bazzaz 2000), and it gives us confidence in the interpretation of niche differentiation as an explanation for co-occurrence because trait differences among species appear to have a genetic basis.

The relative importance of maternal effects in the common garden experiment is unknown. However, the intraspecific variation in seed size, which is one measure of maternal effects (Sultan 1996), was small relative to the variation across species (Fig. 5). Given that seeds were collected from a range of sites and that mean seed sizes compare well with previously published ranges, it is likely that seed size, itself, reflects an intrinsic property of the species. Nevertheless, the role of maternal effects in influencing species distributions is an important issue warranting further study.

Explaining oak diversity at smaller spatial scales

At large spatial scales (1–100 ha), environmental heterogeneity supports a high number of oak species specialized for different habitats. At smaller spatial scales, where soil moisture, fertility and fire regime are not changing significantly (i.e., within 0.1-ha plots), other mechanisms must be invoked to explain the co-occurrence of multiple oak species. In many systems, increasing soil fertility permits increasing biological diversity until a saturation point is reached (e.g., Huston 1994, Cornwell and Grubb 2003). In this system, it also appears that increasing nutrient supply permits increases in diversity of woody plants, particularly at the low end of the soil fertility gradient (Fig. 9). However, the same pattern is not shared by the oaks, which maintain a constant number of oak species per 0.1-ha plot across the entire soil fertility gradient (Fig. 9) as well as across communities (not shown). This suggests that there is a limit to the maximum diversity of oak species at small spatial scales that cannot be explained by resource availability, other abiotic factors, or community composition.

We suggest that within the oak genus, phylogenetic diversity may control the maximum number of oaks that can occur together at small spatial scales. In a related study, Cavender-Bares et al. (2004) provide strong evidence that these communities show a distinct pattern of phylogenetic overdispersion, whereby oak species from different lineages (more distantly related) are more likely to occur together than species from the same lineage (more closely related). This can be viewed to some extent in Fig. 2A and B, which shows that in all communities, species from different phylogenetic lineages are represented. Among the regional species pool of oaks, it appears that there is sufficient phylogenetic diversity to allow the co-presence of three or four oak species per plot, regardless of the abiotic environment or local species composition. Within plots,

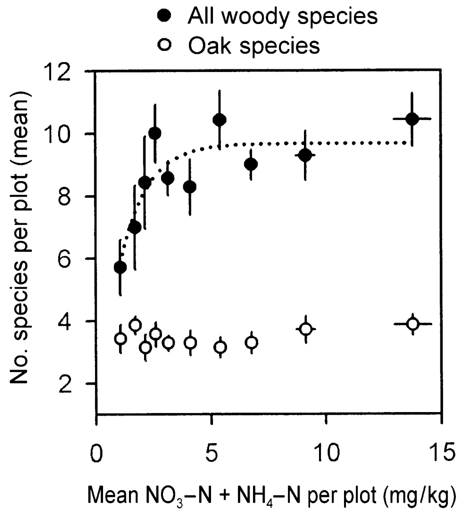

FIG. 9. Mean number of woody species (black circles) or oak species (open circles) in relation to mean soil fertility (nitrate N + ammonium N). All 0.1-ha plots were rank-ordered by their soil fertility and divided into seven consecutive groups of 10 plots each. The number of woody species, the number of oak species, and the soil fertility were averaged for each of the groups of plots to determine whether woody species diversity or oak species diversity per 0.10-ha plot increased with soil fertility.

more distantly related species may co-occur due to differences in seed maturation time (two years in red oaks, one year in white and live oaks) that may give rise to asynchrony in masting and temporal staggering of regeneration among red and white or live oak lineages. Climate variability can differentially affect seed survival which may stagger regeneration among lineages. If suitable patches for seedling regeneration are limiting, this would reduce competition and increase the likelihood of co-occurrence among red and white plus live oaks (Chesson and Warner 1981, Chesson 1985). Differences in leaf longevity among live oaks and white oaks, or among red oaks of different lineages, may be another mechanism that promotes co-occurrence by reducing competition for nutrient resources either through temporal differences in resource uptake (Sakai 1992) or to differences in nutrient use efficiency coupled with differences in rooting depth, as discussed above. Patterns of host specificity of pathogens or herbivores that lead to higher density dependent mortality (Janzen 1970, Connell 1971) if too many species of the same phylogenetic lineage occur in close proximity could also promote the coexistence of more distantly related species. Understanding the mechanisms of coexistence at this scale requires further investigation and is the subject of ongoing research (J. Cavender-Bares, *unpublished data*).

Conclusions

This study provides strong evidence that at the landscape scale niche partitioning and habitat specialization contribute to the coexistence and maintenance of high diversity within the oak genus in north-central Florida. We have shown that species exhibit less overlap in their distributions across environmental gradients than expected and that species show significant differentiation in functional traits that allow them to specialize for contrasting physical environments, particularly with respect to fire frequency and severity, soil moisture, and soil fertility. Three previously described community types—hammock, sandhill, and scrub—are clearly distinguished by species composition, the abiotic environment, and the functional traits of the oak species in them. Species within the three major phylogenetic lineages of oaks represented in Florida are distributed across these communities and environmental gradients, exhibiting evolutionary convergence in habitat preferences. This pattern of phylogenetic overdispersion and evolutionary convergence is explored in detail in a related study (Cavender-Bares et al. 2004) and may explain coexistence of multiple oak species at small spatial scales. While the results presented here do not preclude other mechanisms of coexistence, they provide a strong case for habitat differentiation at the landscape level (1–100-ha scale) and an explanation for both species diversity and functional diversity.

ACKNOWLEDGMENTS

Jimi Sadle, Jason Teisinger, and Rachel Seman are gratefully acknowledged for their assistance in all aspects of the field work. Eric Weis, in particular, but also Nicole Lancaster and Tiffany Fecht, were instrumental in the completion of the common garden experiment. We thank David Ackerly for critical advice on the design of the study, statistical analysis of the data, and for comments on earlier versions of the manuscript. We also thank Martin Lechowicz, Janneke Hill-RisLambers, and two anonymous reviewers for valuable comments which improved the manuscript. Christine Muth, Sebastian Catovsky, and Catherine Lovelock provided valuable commentary on earlier versions of the manuscript. Angus Gholson and Terry Henkel are gratefully acknowledged for assistance with the local flora and locating field sites. Terry Henkel also helped collect acorns for the common garden experiment. We thank Francis Putz, Tom Sinclair, Nicholas Sturgeon, Mike Binford, Walter Judd, the Florida District II Park Service, Randy Brown, and Sam Cole for valuable discussions, equipment, and/or assistance in the field. Funding was provided by a Mellon Foundation Grant and by an NSF Dissertation Improvement Grant (DEB-9801455).

LITERATURE CITED

Abrahamson, W. G., and D. C. Hartnett. 1990. Pine flatwoods and dry prairies. Pages 103–149 *in* R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Gainesville, Florida, USA.

Ackerly, D. D. 1996. Canopy structure and dynamics: integration of growth processes in tropical pioneer trees. Pages 619–658 *in* A. Smith, editor. Tropical forest plant ecophysiology. Chapman and Hall, New York, New York, USA.

Ackerly, D. D. 2003. Community assembly, niche conservatism and adaptive evolution in changing environments. International Journal of Plant Sciences **164**:S165–S184.

Ackerly, D. D., C. A. Knight, S. B. Weiss, K. Barton, and K. P. Starmer. 2002. Leaf size, specific leaf area and microhabitat distributions of chaparral woody plants: contrasting patterns in species level and community level analyses. Oecologia **130**:449–457.

Adams, D. C., and J. F. Jackson. 1995. Estimating the allometry of tree bark. American Midland Naturalist **134**: 99–106.

Baker, T., M. Swaine, and D. Burslem. 2003. Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. Perspectives in Plant Ecology Evolution and Systematics **6**:21–36.

Bazzaz, F. A. 1987. Experimental studies on the evolution of niche in successional plant populations: a synthesis. Pages 245–272 *in* P. J. Edwards, editor. Colonization, succession and stability. Blackwell Scientific Publications, Oxford, UK.

Bazzaz, F. A. 1991. Habitat selection in plants. American Naturalist **137**:S116–S130.

Bazzaz, F. A. 1997. Allocation of resources in plants: state of the science and critical questions. Pages 1–30 *in* J. Grace, editor. Plant resource allocation. Academic Press, San Diego, California, USA.

Binkley, D., and P. Matson. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. Soil Science Society of America Journal **47**:1050–1052.

Bond, W. J., and B. W. v. Wilgen. 1996. Fire and plants. Chapman and Hall, London, UK.

Bonnicksen, T. M., and N. L. Christensen. 1981. Integrating summary. Pages 177–180 *in* W. A. Reiners, editor. Fire regimes and ecosystem properties. USDA Forest Service General Technical Report **WO-26**.

Brokaw, N., and R. T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. Trends in Ecology and Evolution **15**:183–188.

Burns, R. M., and H. H. Honkala. 1990. Silvics of North America: hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.

Carlisle, V., F. Sodek, M. Collins, L. Hammond, and W. Harris. 1988. Characterization data for selected Florida soils. University of Florida, IFAS Soil Department, Soil Characterization Laboratory, Gainesville, Florida, USA.

Carrington, M. E. 1999. Post-fire seedling establishment in Florida sand pine scrub. Journal of Vegetaion Science **10**: 403–412.

Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. American Naturalist **163**:823–843.

Cavender-Bares, J., S. Apostol, I. Moya, J. M. Briantais, and F. A. Bazzaz. 1999. Chilling-induced photoinhibition in two oak species: are evergreen leaves inherently better protected than deciduous leaves? Photosynthetica **36**:587–596.

Cavender-Bares, J., and F. A. Bazzaz. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. Oecologia **124**:8–18.

Cavender-Bares, J., and N. M. Holbrook. 2001. Hydraulic properties and freezing-induced xylem cavitation in evergreen and deciduous oaks with contrasting habitats. Plant, Cell and Environment **24**:1243–1256.

Cavender-Bares, J., M. Potts, E. Zacharias, and F. A. Bazzaz. 2000. Consequences of CO_2 and light interactions for leaf phenology, growth, and senescence in *Quercus rubra*. Global Change Biology **6**:877–887.

Chabot, B. F., and D. Hicks. 1982. The ecology of leaf life spans. Annual Review of Ecology and Systematics **13**:329–359.

Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theoretical Population Biology **28**:263–287.

Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. American Naturalist **117**:923–943.

Clark, D. A., and D. B. Clark. 1999. Assessing the growth of tropical rain forest trees: issues for forest modeling and management. Ecological Applications **9**:981–997.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–310 *in* P. J. d. Boer and G. R. Gradwell, editors. Dynamics of populations. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Cornwell, W. K., and P. J. Grubb. 2003. Regional and local patterns in plant species richness with respect to resource availability. Oikos **100**:417–428.

Daghlian, C. P., and W. L. Crepet. 1983. Oak catkins, leaves and fruits from the Oligocene Catahoula formation and their evolutionary significance. American Journal of Botany **70**: 639–649.

Damesin, C., S. Rambal, and R. Joffre. 1998. Co-occurrence of trees with different leaf habit: a functional approach on Mediterranean oaks. Acta Oecologica **19**:195–204.

Diamond, J., and T. J. Case. 1986. Community ecology. Harper and Row, New York, New York, USA.

Eckstein, R. L., P. S. Karlsson, and M. Weih. 1999. Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. New Phytologist **143**:177–189.

Ewel, K. C. 1990. Swamps. Pages 281–323 *in* R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist **125**:1–15.

Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology **41**:18–32.

Givnish, T. J. 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. Silva Fennica **36**:703–743.

Givnish, T. J., R. A. Montgomery, and G. Goldstein. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. American Journal of Botany **91**:228–246.

Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs **65**:441–476.

Goldberg, D. E. 1997. Competitive ability: definitions, contingency and correlated traits. Pages 286–306 *in* J. L. Harper, editor. Plant life histories. Cambridge University Press, Cambridge, UK.

Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C., USA.

Goulden, M. L. 1996. Carbon assimilation and water-use efficiency by neighboring Mediterraean-climate oaks that differ in water access. Tree Physiology **16**:417–424.

Greenberg, C., and R. Simons. 1999. Age, composition, and stand structure of old-growth oak sites in the Florida high pine landscape: implications for ecosystem management and restoration. Natural Areas Journal **19**:30–40.

Guerin, D. N. 1993. Oak dome clonal structure and fire ecology in a Florida longleaf pine dominated community. Bulletin of the Torrey Botanical Club **120**:107–114.

Hacke, U. G., and J. S. Sperry. 2001. Functional and ecological xylem anatomy. Perspectives in Plant Ecology Evolution and Systematics **4**:97–115.

Hill, M. O. 1979. DECORANA—A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, New York, USA.

HilleRisLambers, J., J. S. Clark, and B. Beckage. 2002. Density-dependent mortality and the latitudinal gradient in species diversity. Nature **417**:732–735.

Hodges, J. D. 1995. The southern bottomland hardwood region and brown loam bluffs subregion. Pages 227–269 *in* J. W. Barrett, editor. Regional silviculture of the United States. John Wiley and Sons, New York, New York, USA.

Hollinger, D. Y. 1992. Leaf and simulated whole-canopy photosynthesis in two co-occurring tree species. Ecology **73**: 1–14.

Hook, D. D. 1984. Waterlogging tolerance of lowland tree species of the south. Southern Journal of Applied Forestry **8**:136–149.

Hooper, D., and P. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. Science **277**:1302–1305.

Hubbell, S. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hunt, R. 1982. Plant growth curves: the functional approach to plant growth analysis. Edward Arnold Publishers, London, UK.

Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, UK.

Hutchinson, G. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology **22**:415–427.

Jackson, J. F., D. C. Adams, and U. B. Jackson. 1999. Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. American Naturalist **153**:614–632.

Janzen, D. 1970. Herbivores and the numbers of tree species in tropical forests. American Naturalist **104**:501–528.

Karlsson, P. S. 1992. Leaf longevity in evergreen shrubs: variation within and among European species. Oecologia **91**:346–349.

Karlsson, P. S. 1994. Photosynthetic capacity and photosynthetic nutrient-use efficiency of *Rhododendron lapponicum* leaves as related to leaf nutrient status, leaf age and branch reproductive status. Functional Ecology **8**:694–700.

Kikuzawa, K. 1995. The basis for variation in leaf longevity of plants. Vegetatio **121**:89–100.

Kikuzawa, K., and D. D. Ackerly. 1999. Significance of leaf longevity in plants. Plant Species Biology **14**:39–45.

Knops, J. H., and W. D. Koenig. 1994. Water use strategies of five sympatric species of *Quercus* in central coastal California. Madroño **41**:290–301.

Kurz, H., and R. K. Godfrey. 1962. Trees of northern Florida. University of Florida, Gainesville, Florida, USA.

Lawlor, L. R. 1980. Structure and stability in natural and randomly constructed competitive communities. American Naturalist **116**:394–408.

Long, T. J., and R. H. Jones. 1996. Seedling growth strategies and seed size effects in fourteen oak species native to different soil moisture habitats. Trees **11**:1–8.

Martin, R. E. 1963. Thermal properties of bark. Forest Products Journal **13**:419–426.

McCune, B., and M. J. Mefford. 1997. PC-ORD, multivariate analysis of ecological data. MjM Software, Gleneden Beach, Oregon, USA.

McKane, R. B., L. C. Johnson, G. R. Shaver, K. J. Nadelhoffer, E. B. Rastetter, B. Fry, A. E. Giblin, K. Klelland, B. L. Kwiatkowski, J. A. Laundre, and G. Murray. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature **415**:68–71.

Meinzer, F. C. 2003. Functional convergence in plant responses to the environment. Oecologia **134**:1–11.

Menges, E., and C. V. Hawkes. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. Ecological Applications **8**:935–946.

Menges, E. S., and N. Kohfeldt. 1995. Life history strategies of Florida scrub plants in relation to fire. Bulletin of the Torrey Botanical Club **122**:282–297.

Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio **69**:89–107.

Mishler, B. D., and M. J. Donoghue. 1982. Species concepts: a case for pluralism. Systematic Zoology **31**:491–503.

Monk, C. D. 1965. Southern mixed hardwood forests of north central Florida. Ecological Monographs **35**:335–354.

Monk, C. D. 1966. An ecological significance of evergreenness. Ecology **47**:504–505.

Monk, C. D. 1968. Successional and environmental relationships of the forest vegetation of north central Florida. American Midland Naturalist **79**:441–457.

Monk, C. D., D. W. Imm, R. L. Potter, and G. Parker. 1989. A classification of the deciduous forest of eastern North America. Vegetatio **80**:167–181.

Mulkey, S., and K. Kitajima. 1995. Photosynthetic capacity and leaf longevity in the canopy of a dry tropical forest. Selbyana **16**:169–173.

Myers, R. L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. Bulletin of the Torrey Botanical Club **112**:241–252.

Myers, R. L. 1990. Scrub and high pine. Pages 150–193 *in* R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Myers, R. L., and J. J. Ewel. 1990. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Nixon, K. C. 1985. A biosystematic study of *Quercus* series *Virentes* (the live oaks) with phylogenetic analyses of Fagales, Fagaceae and *Quercus*. University of Texas, Austin, Texas, USA.

Nixon, K. C. 1997. Fagaceae. Pages 436–506 *in* Flora of North America Editorial Committee, editor. Flora of North America north of Mexico. Oxford University Press, New York, New York, USA.

Peet, R. K., T. R. Wentworth, and P. S. White. 1996. The North Carolina vegetation survey protocol: a flexible, multipurpose method for recording vegetation composition and structure. Castanea **63**:262–274.

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics **4**:53–74.

Platt, W. J., and M. W. Schwartz. 1990. Temperate hardwood forests. Pages 194–229 *in* R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology **80**:1955–1969.

Reich, P. B., C. Uhl, M. B. Walters, and D. S. Ellsworth. 1991. Leaf life span as a determinant of leaf structure and function among 23 Amazonian tree species. Oecologia **86**: 16–24.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs **62**: 365–392.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. Proceedings of the National Academy of Sciences **94**: 13730–13734.

Reich, P., I. Wright, J. Cavender-Bares, J. Craine, J. Oleksyn, M. Westoby, and M. Walters. 2003. The evolution of plant functional variation: traits, spectra and strategies. International Journal of Plant Sciences **164**:S143–S164.

Sakai, S. 1992. Asynchronous leaf expansion and shedding in a seasonal environment: result of a competitive game. Journal of Theoretical Biology **154**:77–90.

Schlesinger, W. H., and B. F. Chabot. 1977. The use of water and minerals by evergreen and deciduous shrubs in Okefenokee Swamp. Botanical Gazette **138**:490–497.

Schwilk, D. W., and D. D. Ackerly. 2001. Flammability and serotiny as strategies: correlated evolution in pines. Oikos **94**:326–336.

Sperry, J. S. 1995. Limitations on stem water transport and their consequences. Pages 105–124 *in* Plant stems. Academic Press, London, UK.

Sultan, S. E. 1996. Phenotypic plasticity for offspring traits in *Polygonum persicaria*. Ecology **77**:1791–1807.

Swetnam, T. W., and J. L. Betancourt. 1990. Fire–Southern Oscillation relations in the southwestern United States. Science **249**:1017–1020.

ter Braak, C., and C. Looman. 1995. Regression. Pages 29–77 *in* O. vanTongeren, editor. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.

Thomas, S. C. 1996. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. American Journal of Botany **83**:556–566.

Thomas, S. C., and F. A. Bazzaz. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology **80**:1607–1622.

Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. Ecology **65**:1445–1453.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Uhl, C., and J. B. Kaufmann. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. Ecology **71**:437–449.

VanValen, L. 1976. Ecological species, multispecies, and oaks. Taxon **25**:233–239.

Villar-Salvador, P., P. Castro-Díez, C. Pérez-Rontomé, and G. Montserrat-Martí. 1997. Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain. Trees **12**:90–96.

Vines, R. G. 1968. Heat transfer through bark, and the resistance of trees to fire. Australian Journal of Botany **16**: 499–514.

Webber, H. J. 1935. The Florida scrub, a fire-fighting association. American Journal of Botany **22**:344–361.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology and Systematics **33**:125–159.

Westoby, M., E. Jurado, and M. Leishman. 1992. Comparative evolutionary ecology of seed size. Trends in Ecology and Evolution **7**:368–372.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs **26**:1–80.

Whittaker, R. H. 1975. Communities and ecosystems. Second edition. MacMillan, New York, New York, USA.

Whittemore, A. T., and B. A. Schaal. 1991. Interspecific gene flow in sympatric oaks. Proceedings of the National Academy of Sciences (USA) **88**:2540–2544.

Williams, K., C. B. Field, and H. A. Mooney. 1989. Relationships among leaf construction cost, leaf longevity, and light environment in rain-forest plants of the genus *Piper*. American Naturalist **133**:198–211.

Wills, C., R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. Proceedings of the National Academy of Sciences (USA) **94**:1252–1257.

Wright, I. J., P. B. Reich, and M. Westoby. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Functional Ecology **15**:423–434.

Wright, S. J. 2002. Plant diversity in tropical rain forests: a review of mechanisms of species coexistence. Oecologia **130**:1–14.

APPENDIX A

A list of non-oak woody species used in the gradient analyses is available in ESA's Electronic Data Archive: *Ecological Archives* M074-014-A1.

APPENDIX B

A table showing leaf-level traits for 17 oak species is available in ESA's Electronic Data Archive: *Ecological Archives* M074-014-A2.

APPENDIX C

A table showing whole-plant traits for 17 oak species is available in ESA's Electronic Data Archive: *Ecological Archives* M074-014-A3.

APPENDIX D

A table of seedling biomass equations as a function of other measured variables for calculation of relative growth rate (RGR) is available in ESA's Electronic Data Archive: *Ecological Archives* M074-014-A4.

APPENDIX E

Species pairwise niche overlap values across a soil moisture gradient are presented in ESA's Electronic Data Archive: *Ecological Archives* M074-014-A5.

APPENDIX F

Graphs showing leaf trait relationships for individual leaves for A_{mass}, SLA, and %N are presented in ESA's Electronic Data Archive: *Ecological Archives* M074-014-A6.

APPENDIX G

Graphs showing the relationship between traits measured on seedlings grown in a common garden and traits measured on mature trees measured in the field are presented in ESA's Electronic Data Archive: *Ecological Archives* M074-014-A7.