Acorn size and geographical range in the North American oaks (*Quercus* L.)

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Abstract. Seed size can be an important factor influencing the extent of the range of a plant species that has recently expanded or shifted the area it occupies as a consequence of climatic changes. A positive correlation exists between acorn size and geographical range of the North American oaks (*Quercus* L.) of eastern North America. An independent analysis of oaks native to the California region suggests that this is a continental pattern. Two hypotheses – size-dependent dispersal and niche availability as a function of seed food reserves – are examined as factors that could account for the relationship between range area and seed size. Available information suggests that the niche-related hypothesis provides the best explanation for patterns we observed.

Key words. Seed dispersal, acorns, *Quercus* L., trees, seed size, range area, North America.

INTRODUCTION

The geographical range of a plant species is determined by several factors: (a) physiological, anatomical and ecological traits expressed at each stage of the life cycle; (b) the amount of phenotypic and genotypic variability in those characteristics; and (c) the evolutionary and biogeographical history of the taxon. However, traits related with seed dispersal and successful seed establishment (Salisbury, 1942; Harper, Lovell & Moore, 1970; Grubb, 1977; Cook, 1980) may be particularly important in understanding biogeographical patterns of species that are constrained to the same geographical region and have expanded or shifted their ranges in relation to major environmental changes (Davis, 1981, 1986). [The term *seed* is used in the general sense defined by Harper *et al.* (1970: 328).]

Following the retreat of the Wisconsin ice sheet 10,000 – 15,000 years ago (Denton & Hughes, 1981), many North American tree species expanded or shifted their ranges northward (Davis, 1976). Differential migration rates and patterns among several eastern North American tree species are well documented (Davis, 1976, 1981, 1983). Many species with heavy seeds migrated as quickly as species with wind-dispersed light seeds. This has been attributed to active dispersion of species with large seeds by mammals and, especially, birds (Johnson & Adkisson, 1985, 1986; S. L. Webb, 1986). Once seeds were dispersed, seed size could have been important in determining successful establishment (Salisbury, 1942; Harper *et al.*, 1970; Baker, 1972), particularly among species with little or no seed dormancy where no temporary escape from unfavourable seedbed conditions is possible.

In this work we show that among North American oak species, acorn size and geographical range are correlated. Two geographically isolated sets of oak species are evaluated. The ecological significance of a positive relationship between acorn size and geographical range is explored.

METHODS

Worldwide, the genus *Quercus* L. has more than 300 species with complex taxonomic relationships (Moore, 1984). About fifty species are reported in the United States, with oaks of the Atlantic and California regions (Trelease, 1924) accounting for 80% of these. Oaks of these two regions [cited in previous works on insect diversity/oak-host area (Opler, 1974; Cornell & Washburn, 1979; Taper & Case, 1987)] were taken as the basis of this study.

Specific nut lengths and widths (Sargent, 1961; Schopmeyer, 1974) were used to estimate acorn volume as the volume of an ellipsoid. Although this is a rough approximation of acorn size, we chose volume rather than length or width, because acorn volume is better correlated with variables of biological meaning (e.g. amount of food reserves). Specific geographical range areas were obtained from Cornell & Washburn (1979) and Taper & Case (1987). We have followed the example of others in measuring geographical extent of species distributions (e.g. Rapoport, 1975; Stevens, 1986) and breadth of tolerances (e.g. Brown & Maurer, 1987). Our results were checked by planimetric measurements of species range maps published by Little (1971, 1976, 1977). Where differences occurred, we accepted our measurements from Little's maps. The species were also classified by subgenera: Leucobalanus, Erythrobalanus and Protobalanus. Examples of acorns

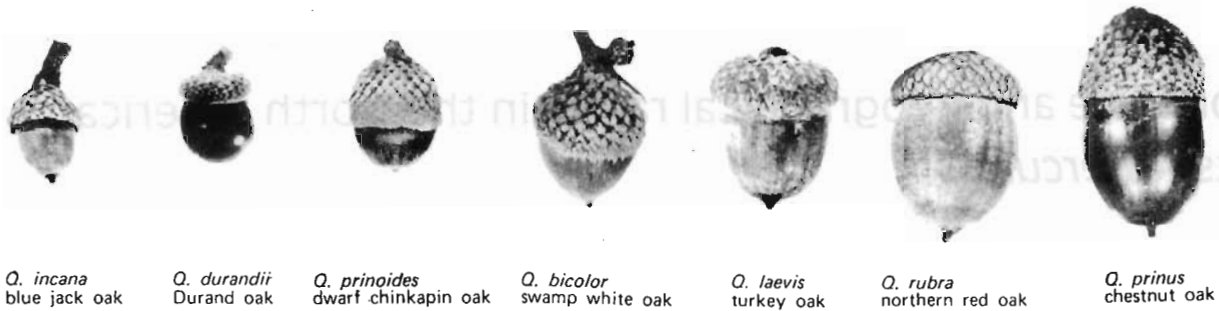| *Q. incana* | *Q. durandii* | *Q. prinoides* | *Q. bicolor* | *Q. laevis* | *Q. rubra* | *Q. prinus* |
| blue jack oak | Durand oak | dwarf chinkapin oak | swamp white oak | turkey oak | northern red oak | chestnut oak |

FIG. 1. Examples of North American acorns (~1×) representing a range of sizes (after Shopmeyer, 1974).

representing a range of sizes are found in Fig. 1. Data are summarized in the Appendix.

RESULTS

Logarithmically transformed geographical areas and acorn volumes were correlated for oaks of each of the Atlantic and California regions (Fig. 2). A highly significant positive correlation was found for twenty-eight Atlantic species ($r=0.635$, $P<0.0005$). For the eleven California oaks the correlation was not significant ($r=0.02$, $P>0.95$), but the exclusion of *Quercus tomentella* Engelm, the only non-continental species, resulted in a highly positive correlation ($r=0.667$, $n=10$, $P<0.05$). The small range of *Quercus tomentella* is a function of the species being confined to the Channel Islands of southern California and the oceanic island of Guadalupe off the dry coast of Baja California (Little, 1976). The large acorns in this species could, in fact, be related to its condition as an island species (Carlquist, 1974).

Oak species with larger trees could bear bigger and more seeds and larger and more exposed amounts of wind-dispersed pollen grains than species with smaller trees. Morphological evidence (Kaul & Abbe, 1984) and self-pollination experiments (Wright, 1953) indicate that the oak group is composed principally of outcrossing species.

Therefore tree size might be positively correlated with geographical range, for taller trees could reproduce more successfully than smaller ones if distances between trees are large. Tree size could thus be a possible source of spurious correlation between acorn size and geographical range. Data on average height by species were extracted from Sargent (1961), Gleason & Cronquist (1963) and Schopmeyer (1974). Tree height is significantly correlated with the log of acorn size ($r=0.377$, $n=28$, $P<0.05$) and with the log of oak area ($r=0.412$, $n=28$, $P<0.05$) in the Atlantic region. However, when the variable height is included in a stepwise regression with log of acorn volume, this last variable is entered first. The addition of height as an independent variable changed the r^2 from 0.403 ($P<0.0005$) to 0.438 ($P<0.001$), which is not a significant improvement ($P>0.20$). For the contintental California oaks a positive but nonsignificant relationship was found between log of acorn volume and tree height ($r=0.559$, $n=10$, $P>0.05$) and a significant relationship between log of range area and tree height ($r=0.754$, $n=10$, $P<0.05$). The significance of this last relationship relies on the inclusion of the shrub *Quercus vaccinifolia* Engelm. A multiple regression with log of acorn volume and tree height as independent variables explains 65% of the variation in log of the range of the California oaks. When *Quercus tomentella* is included in the analysis, no significant correlations are found ($r=0.545$,

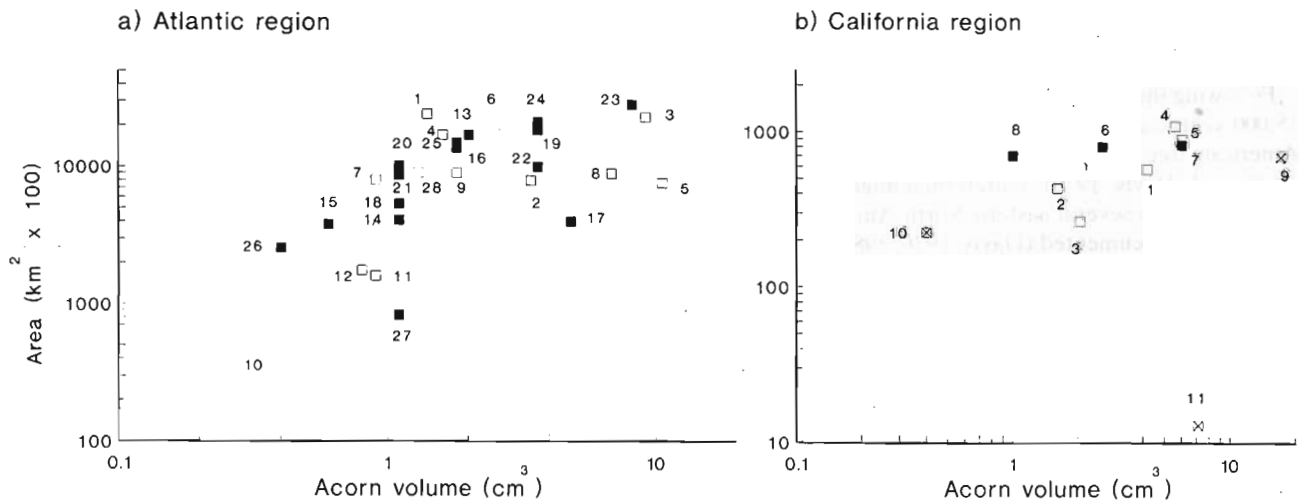### a) Atlantic region

b) California region

FIG. 2. Geographical range plotted against estimated acorn volume for oaks of (a) the Atlantic region, and (b) the California region. Numbers represent sequence number for oaks listed in the Appendix. Open squares are white oaks (Leucobalanus), filled squares are black oaks (Erythrobalanus), and crossed squares are intermediate oaks (Protobalanus).

$n=11$, $P>0.05$ for log of acorn volume versus tree height, and $r=0.291$, $n=11$, $P>0.35$ for log of range versus tree height). Although tree height is correlated with both oak range and acorn size, the latter variable explains an independent part of the variability in oak ranges.

Taxonomic clustering could also indicate possible spurious correlation between acorn volume and oak range (see Taper & Case, 1987: 256). Fig. 2 reveals no apparent taxonomic clustering among species belonging to the same subgenus.

DISCUSSION

Today, many oak species occupy areas that were glaciated during the last ice age. Thus oak distributions must have changed as climate changed during the postglacial period. In the Atlantic region most oak species with smaller geographical ranges are restricted to the southeastern United States (Little, 1971, 1977), whereas species with larger ranges are ubiquitous throughout the east. This implies that oaks as a group realized a net increase rather than a shift in their geographical ranges after the ice retreated (Fig. 3). Specific patterns of migration can not be established from palynological records, however, because different species of oaks possess pollen of similar size and morphology.
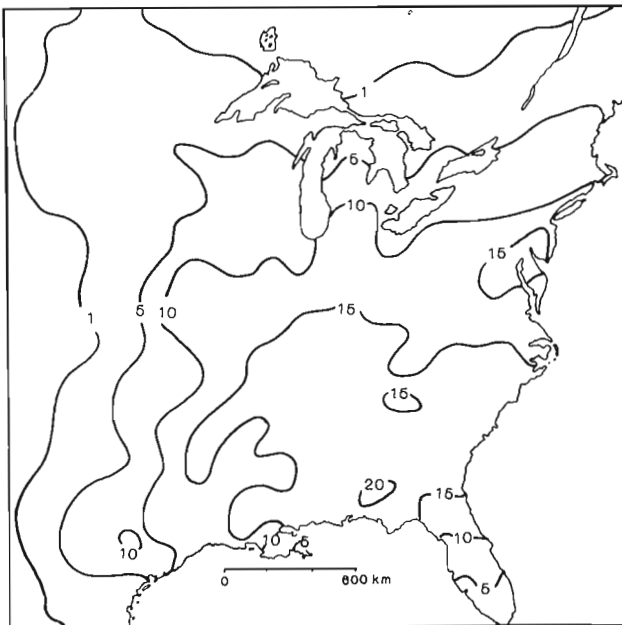

FIG. 3. Regional diversity ($\propto$ diversity) map of oak species of the Atlantic region. Numbers indicate number of oak species. Isopleths were drawn from a grid in which the number of oak species present in cells 125×125 km was recorded.

Increases in range areas could have occurred under two quite different sets of ecological conditions. Range area expansions may have tracked closely with climate changes, with the result being species distributions that were in *equilibrium* with climate conditions (i.e. rapid 'vegetation response times' *sensu* T. Webb, 1986). Alternatively, climate changes may have been so rapid that the rates at which ranges expanded did not keep up with changes in the environment (i.e. *nonequilibrium* conditions). In the second case, acorn dispersal mechanisms could have been at least partially responsible for limiting the rate of range expansion. Given the rather low rate of climatic change during the last several millennia, current ranges have probably been relatively stable since the time either that climate first stabilized (the equilibrium theory) or dispersal-delayed migration caught up with stable environmental conditions (the nonequilibrium theory). In fact, climate is not and has not been stable for periods of more than a few decades at best, but in terms of the effect of climate change on species ranges, conditions are relatively more stables now than they were in the late-glacial and early post-glacial periods.

Two hypotheses are proposed to explain the positive relationship between acorn size and range area for North American oak species. We call the first the dispersal-related hypothesis. It requires that acorn dispersal mechanisms limited range expansions during the early part of the Holocene (i.e. that biogeographical ranges were not in equilibrium with climate at least for the first few millennia after the retreat of Wisconsin ice sheets). The second hypothesis is based on the fact that seedling success is positively correlated with seed size for many genera, and that seedlings from large seeds can thus take advantage of a broader range of seedling niche conditions (the niche-related hypothesis). This hypothesis could hold under either equilibrium or nonequilibrium conditions as described above.

The dispersal-related hypothesis

This hypothesis states that during postglacial migrations, oak species with large acorns were preferentially dispersed by animals, particularly birds, and thus had a better chance of colonizing newly available birds, and thus had a better chance of colonizing newly available sites. Initially these sites may have been free of *locally stable* tree competition because of the continuing advance of boreal species to the north. The initial colonizers of a site, including large-seeded oak species, could impose a more restrictive competitive environment (i.e. through either canopy or root competition) on smaller seeded species with similar autecological characteristics. This would limit the rate of expansion of the smaller-seeded oaks. Under this hypothesis the present biogeographical range stasis can be explained if one assumes that the species that first colonized a site fully occupied it and changed the seedling environment to the extent that the establishment of late-arriving species was impeded.

The niche-related hypothesis

This hypothesis holds that oak species with large acorns can exploit regeneration sites (niches) representing a broader range of environmental conditions than those favourable to smaller-seeded oaks. Species with large acorns thus enjoy greater success in seedling establishment than those with small acorns, especially when conditions for seedling establishment are highly variable within a region.

For an area the size of northeastern North America, the breadth of conditions represented by niches available for seedling establishment are almost certainly a function of the size of the geographical area within which niches are defined. Thus we would expect a positive relationship between acorn size and oak geographical range if this hypothesis holds true.

The niche-related hypothesis is valid under either equilibrium or non-equilibrium conditions as described above. If species migration rates were in equilibrium with rates of climate change, the present range–area relationships among oak species are probably similar to those that prevailed during the glacial period when oaks were restricted to areas in the southern United States (Fig. 4). If species migration rates were not in equilibrium with rates of climate change and were limited by dispersal mechanisms, the niche-related hypothesis implies a scenario in which larger acorns enjoy a greater success in seedling establishment once seeds are dispersed. Oaks with large acorns would have initially established more seedings under the harsher conditions to the north and west of their glacial refugia. Once new areas were colonized, the larger-seeded species would have restricted the access to new establishment sites of the smaller-seeded oaks, because the trees already on the site would have imposed a more severe competitive regime on newly arriving propagules. Although less is known about late-glacial and Holocene changes in the range area of the genus *Quercus* in the California region,

the greater topographic relief in the west insures a wide range of site conditions despite the fact that the total area occupied by the western oaks is smaller than that occupied by eastern species.

Indirect evidence seems to favour the niche-related hypothesis. Oaks do not possess an ability to temporarily avoid adverse conditions for early growth through delayed germination. Acorns of the white oak group (Leucobalanus) show little or no dormancy, and acorns of the black oak group (Erythrobalanus) germinate the first spring after fall sowing (Schopmeyer, 1974). Thus, dispersion in oaks is followed almost immediately by germination, the success of which seems to be independent of acorn size. Once germinated, larger acorns produce stronger seedlings, however (Bonner, 1988). First-year seedling growth, for instance, is positively correlated with acorn weight in *Quercus Prinus* L. (McComb, 1934) and in *Quercus Kelloggii* Newb. (Hunter & Van Doren, 1982).

Differential establishment success for seeds of different sizes is common, both within and among plant species (Harper *et al.*, 1970). Larger seeds are most likely to establish seedlings, especially under conditions of shading (Grime & Jeffrey, 1965; Gross & Werner, 1982; Gross, 1984; Winn, 1985), drought (Baker, 1972; Wulff, 1986), and in high latitudes characterized by short growing seasons (McWilliams, Landers & Mahlstede, 1968). Advantages are in part the result of higher growth rates for seedlings from large seeds. Cook (1980) argues that transient seed dormancy and large seed size are characteristics that are usually associated with specialization to shaded habitats in closed communities that are biologically unpredictable. A similar hypothesis is proposed by Carlquist (1974) to explain the rule that island species usually have larger seeds than their continental relatives (e.g. *Quercus tomentella* on the coastal islands off southern California).

Several studies have examined the role of mammals and birds as seed dispersers, but there is little support for the idea that dispersers favour large seeds over small ones. Johnson & Adkisson (1986) argue against mammals such as squirrels, which are undoubtedly capable of transporting the largest seeds, as effective long-distance dispersers. They note that mammals rarely transport seeds much beyond the crown area of individual trees, and they favour the blue jay (*Cyanocitta cristata* L.) as 'the most likely candidate for the role of long-distance acorn disperser, both past and present'. Studies indicate that jays and other nut-dispersers favour sound over unsound seeds, but that among the various species of oaks, jays are more likely to transport smaller rather than larger acorns (e.g. Darley-Hill & Johnson, 1981). Observations by Fry & Vaughn (1977) support this. They found that a large migratory population of band-tailed pigeons (*Columba fasciata* Say) selectively predated the smallest acorns among a heavy crop of blue oak (*Quercus Douglasii* Hook. & Arn.). S. L. Webb (1986) suggests that the recently extinct passenger pigeon (*Ectopistes migratorius* L.) was an important contributor to the rapid rate of post-glacial migration of nut-bearing tree species, but there is no reason to believe that the acorn size preference of passenger pigeons differed from that of other dispersers. Thus, although dispersers
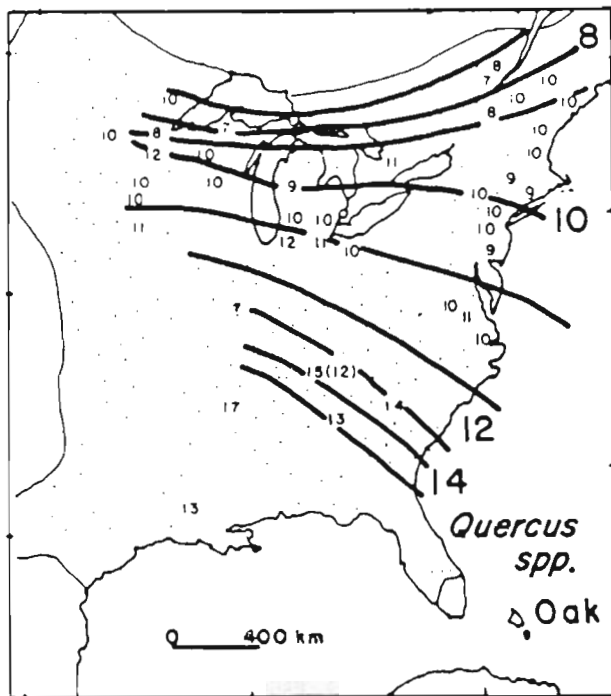

FIG. 4. Map showing the times of the first arrival of oaks moving northward during the late Wisconsin and early Holocene. Small numbers indicate arrival times in thousands of years at individual sites; isopleths connect points of similar age and represent the frontier for the genera at 1000-year-intervals. Stippled areas are modern ranges for the eastern oaks as a group (from Davis, 1983).

transported acorns to new sites, there is no reason to believe that large-seeded species were favoured and hence dispersed more widely. It seems more likely that greater food reserves provided a competitive advantage to large seeded species as they established in new areas under either equilibrium or nonequilibrium conditions. This could have contributed to the pattern that we observed of large-seeded oak species having larger range areas than smaller-seeded ones.

ACKNOWLEDGMENTS

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APPENDIX

Geographic range, acorn size, and tree height for oak species of the Atlantic and California regions.

Species	Range area (km²×100)	Acorn size† (cm³)	Tree height† (m)
Atlantic region			
Leucobalanus			
1. *Quercus alba* L.	24196	1.4	27
2. *Quercus bicolor* Willd.	7900	3.4	21
3. *Quercus macrocarpa* Michx.	23038	9.1	25
4. *Quercus prinoides* Willd.	17042	1.6‡	3
5. *Quercus Prinus* L.	7646	10.5	24
6. *Quercus stellata* Wang.	19938	2.5	17
7. *Quercus virginiana* Mill.	7985	0.9	15
8. *Quercus Michauxii* Nutt.	8897	6.8	30
9. *Quercus lyrata* Walt.	8982	1.8	24
10. *Quercus Laceyi* Small.	233	0.3	11
11. *Quercus Chapmanii* Sarg.	1598	0.9	15
12. *Quercus Durandii* Buckl.	1745	0.8	23
13. *Quercus Muehlenbergii* Engelm.	17042	2.0	24
Erythrobalanus			
14. *Quercus ilicifolia* Wang.	4082	1.1	3
15. *Quercus incana* Bartr.	3775*	0.6‡	13
16. *Quercus falcata* Michx.	13688	1.8‡	30‡
17. *Quercus laevis* Walt.	3978	4.8	9
18. *Quercus laurifolia* Michx.	5328	1.1	27
19. *Quercus marilandica* Muenchh.	18480	3.6	9
20. *Quercus nigra* L.	10161	1.1	24
21. *Quercus palustris* Muenchh.	8643	1.1	23
22. *Quercus Phellos* L.	9920	3.6	27
23. *Quercus rubra* L.	28389	8.1	24
24. *Quercus velutina* Lam.	21067	3.6	23
25. *Quercus imbricaria* Michx.	14870	1.8	18
26. *Quercus myrtifolia* Willd.	2540	0.4	9
27. *Quercus texana* Buckl.	829	1.1	9
28. *Quercus coccinea* Muenchh.	8992	1.2	4
California region			
Leucobalanus			
1. *Quercus Douglasii* Hook. & Arn.	559	4.1	18
2. *Quercus dumosa* Nutt.	433	1.6	6
3. *Quercus Engelmannii* Greene	259	2.0	17
4. *Quercus Garryana* Hook.	1061	5.5	20
5. *Quercus lobata* Nee.	870	5.9‡	30
Erythrobalanus			
6. *Quercus agrifolia* Nee.	803	2.6	23
7. *Quercus Kelloggii* Newb.	826	6.0	26
8. *Quercus Wislizenii* A. DC.	699	1.0	21
Protobalanus			
9. *Quercus chrysolepis* Liebm.	690	17.1	15
10. *Quercus vaccinifolia* Engelm.	223	0.4	1§
11. *Quercus tomentella* Engelm.	13	7.1	18

* Our measurement differs from the estimation of Taper & Case (1987).

† Estimated from Sargent (1961) except as indicated.

‡ Estimated from Schopmeyer (1974).

§ Estimated from Gleason & Cronquist (1963).