

## Correspondence

### Do big acorns matter? — a reply to R.J. Jensen

We are delighted that our original paper (Aizen & Patterson 1990, hereafter A&P) stimulated further work by Jensen (this issue, pp. 000–000) on the relationship between acorn size and the range area of oaks. We are pleased to have the opportunity to respond to his comment on our work. We feel that a reexamination of our original analysis as well as careful scrutiny of Jensen's work further strengthen our original conclusion.

In this reply we comment on Jensen's perceived sources of bias in A&P (i.e. use of a subset of species of eastern North American oaks, erroneous and ambiguous acorn size estimations, and lumping of the two subgenera in a single analysis). We also examine the current status of the 'range area vs. acorn size' relationship under the light of new empirical and experimental evidence.

Although Jensen's as yet unpublished monograph may eventually resolve the taxonomy of the genus, there has not, in the past, been uniform agreement on the number of species in the genus *Quercus* (see Moore, 1984). Aware of this, we chose to select a subset of oak species for which published range area data are available (Cornell & Washburn, 1979). We knew that Cornell & Washburn (1979) selected only species censused for Cynipinae galls, but we felt that their subset represents an unbiased, random, sample for our purposes. Aside from providing range area data, the selection of Cornell & Washburn's subset was not influenced by the objective of our study (i.e. to examine the relationship between range area and acorn size).

We fail to see how Jensen could conclude that our selection process introduced bias into our analysis. If subsetting was a source of bias in our analysis then we would expect the significance of the correlation between range area and acorn size for the subgenus *Erythrobalanus* (for which subsetting has the greatest effect in terms of sample size reduction) to change. Indeed, the significance of the relationship (based on Jensen's data) is not substantially altered ( $P = 0.16$  for  $n=25$ , and  $P = 0.13$  for  $n=15$ ).

With respect to acorn size estimates, we always used Sargent (1961) as the first source. The photographs in Schopmeyer (1974) were only used as a second, alternative source when dimensions were unavailable or ambiguous in Sargent. We did not state in our paper that the values we used are 'normal' (as attributed to us by Jensen), but we did assume that dimensions in Sargent (1961) and photographs in Schopmeyer (1974) are typical for the species we examined. As noted by Jensen and as is evident in our subsequent herbarium measurements (Aizen & Woodcock,

1992), this is not the case for many of Schopmeyer's photographs. A few of the discrepancies between our estimates of acorn size and those of Jensen are due to differences in interpretation of the sometimes imprecise descriptions of length and width in Sargent's manual (Sargent, 1961). Jensen correctly derived our technique for estimating acorn size from these descriptions, and many of the differences shown in his Table 1 result from rounding errors, which are inflated when linear measures are combined to estimate volumes.

Jensen specifically questions our estimates for some species. He worries about the vague description in Sargent for *Q. laurifolia*, but uses a volume estimate based on his measurements of herbarium specimens that is identical to the one we derived! Acorn size in *Q. phellos* and *Q. rubra* were actually estimated from Schopmeyer (1974). The symbol indicating so in A&P was inadvertently deleted from the final version of the Appendix. In the case of *Q. phellos*, we consulted Schopmeyer (1974) because, as pointed out by Jensen, there was no reference to acorn size in Sargent. As for *Q. rubra* L., the extent of the geographical range described in Sargent did not correspond to that reported in either Cornell & Washburn (1979) or Little (1971). Actually, the extent of distribution described for Sargent's *Quercus borealis* var. *maxima* Ashe (= *Quercus rubra* Du Roi; not L.) better approximates the one reported in Cornell & Washburn (1979) or Little (1971). [We could not find, in Sargent (1961), the dimensions for *Q. rubra* L. cited by Jensen: length =  $3/4 - 1 1/4$ , width =  $1/2 - 1$ ]. Given this confusion, we also turned to Schopmeyer's photograph of *Q. rubra*. We accept that the dimensions given by Jensen as well as those in Aizen & Woodcock (1992) are more typical of *Q. phellos* and *Q. rubra* than those taken from Schopmeyer's photographs. However, the exclusion of these two estimates or replacement by Jensen's estimates does not radically change either the strength or significance of our original relationship (compared with our original values of  $r = 0.635$ ,  $P < 0.005$ ;  $r = 0.605$ ,  $P < 0.005$  with exclusion; and  $r = 0.562$ ,  $P < 0.005$  with replacement). Differences in the estimation of acorn size are indeed a major source of the discrepancies between Jensen's analysis and ours, but as we show below the significance of the relationship between range area and acorn size does not depend on the use of a particular data set.

Like Jensen, we think that consideration of phylogeny (as well as other ecological criteria) would be desirable in the analysis of any comparative data set. One way to increase

analysis of any comparative data set. One way to increase statistical power in testing the relation between geographical range and acorn size among species within subgenera while simultaneously considering phylogeny as a separate factor within the same analysis, is to include acorn size as a covariate in an analysis of covariance (Bell, 1989). An ANCOVA performed on Jensen's log-transformed data shows that the covariate 'acorn size' accounts for a significant portion (13%) of the variance in geographical range ( $F_{1,36} = 5.31$ ,  $P < 0.05$ ). We feel, however, that despite the subgeneric life history differences cited by Jensen, the only way that lumping of species of the two subgenera could introduce bias (in terms of the purpose of our analysis) is if species belonging to one of the subgenera have, on the average, both larger range areas and acorn sizes than species in the other subgenus. Although mean acorn size across species of the white oak group is significantly larger than across species in the black oak group ( $t_{37} = 2.28$ ,  $P < 0.05$ ), there is no difference between the subgenera in mean geographical range area ( $t_{37} = 0.05$ ,  $P < 0.95$ ) using Jensen's log-transformed data. Because the criteria for bias stated above are not met, we feel justified in lumping species of both subgenera. We found that when Jensen's estimations for all his thirty-nine species are considered in a single statistical analysis, the association between acorn size and geographical range area is still significant ( $r = 0.338$ ,  $P < 0.05$ ).

Aizen & Woodcock (1992) recently compiled information on acorn size from 1407 herbaria specimens representing most of the geographical range of thirty-two oak species (including thirty-one of those listed in Jensen's Table 1). Using Jensen's corrected range areas and our new herbaria measures, we again found a significant relationship between geographical range and mean acorn size ( $r = 0.365$ ,  $n = 31$ ,  $P < 0.05$ ).

Jensen comments on the potential danger of including outliers and species with excessive leverage values. We can lessen these problems, including poor fits to linear correlation and regression models, by using non-parametric statistics. Spearman's rank correlations applied on Jensen's data showed significant correlation coefficients for all species combined ( $r = 0.430$ ,  $P < 0.01$ ) as well as for species of the subgenus *Erythrobalanus* ( $r = 0.432$ ,  $P < 0.05$ ).

Jensen emphasizes the relationship between leaf size and range area, and notes positive correlations between leaf and acorn size. Whether this association represents the product of independent adaptation, co-adaptation, or a pleiotropic manifestation without fitness consequences is not known. Aizen & Woodcock (in prep.), however, have found that 1-month-old seedlings germinating from large acorns of *Q. rubra* exhibit higher survival and resprouting capacity after exposure to frost. Thus, large acorns could represent an adaptive character for establishment at high latitudes. We also found (M.A. Aizen, unpublished data) that acorn sizes

of species inhabiting semi-arid and arid regions are unexpectedly large for their small leaf sizes, suggesting again an adaptive advantage of large acorns in marginal environments (cf. Baker, 1972).

We do not argue that acorn size is the *only* or *most important* character that determines the extent of geographical range in *Quercus*. We do, however, feel that the significant relationship between acorn size and range area that we have demonstrated deserves further consideration in studies of species distribution and adaptation to harsh environments. This is specially true in light of the obvious sensitivity of germinating seedlings to environmental stress. In general, we feel that there is too much emphasis on explaining distributional limits and range areas in terms of characteristics important primarily to mature plants. A wealth of evidence is available from arboreta and botanical gardens on the successful establishment of plant species (including many species of oaks) well beyond their present geographical limits when care is provided in nurturing seedlings and saplings.

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