Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants

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Summary

The likelihood that a plant's seeds will be dispersed by fruit-eating birds may depend upon the size and shape of its fruits. Assuming that elongate fruits can be swallowed more easily than spherical fruits of equal volume and that plant fitness is enhanced by seed dispersal by many individuals and species of birds, natural selection should favour increasing fruit elongation with increasing fruit size in bird-dispersed plants. According to this view, this allometric pattern would be adaptive. Alternatively, fruit shape in bird-dispersed plants may be constrained by development or phylogeny. To determine whether there was any evidence to support the adaptive allometry hypothesis, we examined allometric relationships between length and diameter in fruits and seeds in a group of neotropical bird-dispersed plant species. Using the major axis technique, we regressed ln(diameter) on ln(length) for fruits and seeds at various taxonomic levels: (1) within individual trees of *Ocotea tenera* (Lauraceae) (2) among 19 trees within a population of *O. tenera*, as well as among pooled fruits from multiple trees within 20 other species in the Lauraceae, (3) among 25 sympatric species within a plant family (Lauraceae) and (4) among 167 species representing 63 angiosperm families within a plant community in Monteverde, Costa Rica. At most taxonomic levels, a tendency for fruit length to increase more rapidly than fruit diameter among fruits (negative allometry) occurred more frequently than expected by chance. Estimated slopes of the regressions of fruit length on fruit diameter were < 1 within 15 of the 19 individual *O. tenera* trees, among tree means within *O. tenera*, among pooled fruits within 16 of the 20 other species in the Lauraceae, among species means within the Lauraceae and among means of all bird-dispersed species in the lower montane forests of Monteverde. Seed allometry showed similar patterns, although for both fruits and seeds the broad confidence intervals of the slopes estimated by major axis regression overlapped 1 in many cases. Among the 63 Monteverde family means, fruit length and diameter scaled isometrically. Based on measurements of ontogenetic changes in fruit shape in a single species, *O. viridifolia*, we found no evidence that negative allometry in fruit shape within the Lauraceae was an inevitable consequence of developmental constraints. Instead, increasing elongation of fruits and seeds in certain plant taxa is consistent with adaptation to gape-limited avian seed dispersers. Contrary results from vertebrate-dispersed species from Malawi and Spain may reflect differences between the New and Old World in plant taxa, seed dispersers or evolutionary history.

Keywords: allometry; comparative biology; Costa Rica; frugivory; seed dispersal; fruit form; fruit shape; Lauraceae; Monteverde; tropical ecology

Introduction

Fruits have evolved to promote seed dispersal by a variety of means. A fruit's form can often reveal whether its seeds are disseminated mainly by wind, water or animals (Ridley, 1930; van der Pijl, 1982). For example, fruits fed upon by birds commonly share a suite of traits or 'syndrome', despite their distinct anatomical origins (e.g. drupes vs berries) or taxonomic

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affiliation. Fruits of bird-dispersed plants tend to be characterized by small size, rounded shape, soft and nutritious pericarp, conspicuous colour, obvious and accessible presentation, persistence on the plant and the absence of appendages. This syndrome distinguishes them from fruits transported by water or wind and even from fruits eaten predominately by mammals and other vertebrates (van der Pijl, 1982; Janson, 1983; Debussche and Isenmann, 1989; Willson *et al.*, 1989). Not all fruits fall neatly into a particular syndrome, of course, and the evidence that avian seed dispersers act as selective agents on plants is often indirect or elusive (Wheelwright, 1988a,b). Nonetheless, field studies clearly demonstrate that birds have the potential to direct the evolution of fruit traits. Birds discriminate between fruits within and among species on the basis of a variety of features (e.g. size, colour, phenology, nutritional value, accessibility and ripeness) and as a result their behaviour as seed dispersers is thought to have important fitness consequences for plants (Denslow and Moermond, 1982; Howe and Smallwood, 1982; Moermond and Denslow, 1983; Gautier-Hión *et al.*, 1985; Estrada and Fleming, 1986; Debussche and Isenmann, 1989; Jordano, 1992).

An especially important trait from the perspective of foraging birds is fruit size, particularly when fruits must be swallowed whole (Terborgh and Diamond, 1970; Janson, 1983; Knight and Siegfried, 1983; Moermond and Denslow, 1983, 1985; Pratt and Stiles, 1985; Wheelwright, 1985; Jordano, 1987a,b, 1992; Debussche and Isenmann, 1989; Lambert, 1989; Hegde *et al.*, 1991; Jung, 1992). Fruit size, which varies widely within and between plant species, can influence the probability that a foraging bird will select a fruit and disperse its seeds (Wheelwright, 1993). Fruits that are too large relative to a bird's gape are likely to be avoided or discarded uneaten. Consequently, fruit size (specifically, maximum diameter) may restrict the number of individuals and species of birds that can feed on and successfully disperse a given plant species (Wheelwright, 1985, 1993).

If fruit-eating birds choose or handle fruits differently on the basis of fruit size and shape (Wheelwright, 1985; Levey, 1987), if fruit size and shape are heritable traits (Sinnott, 1936; Wheelwright, 1993) and if fruit removal and subsequent seed dispersal by birds influence plant reproductive success (Howe, 1990), natural selection could lead to predictable functional relationships between fruit size and shape within and among species. Assuming that elongate fruits are more easily swallowed and handled internally than spherical fruits of the same volume, fruit length should be selected to increase at a faster rate than fruit diameter with increasing size of mature fruits. The strength of selection for increased elongation (defined as the ratio of length: width) with increasing fruit size should be greatest in plant species that produce fruits whose size is similar to (rather than much smaller than) the gape width of their dispersers and in plant species whose fruits are swallowed whole rather than piecemeal (Levey, 1987). The same argument holds for the evolution of seed shape in the face of constraints imposed by intestine diameter (Karasov and Levey, 1990; Courtney and Sallabanks, 1992; Levey and Duke, 1992).

Under certain conditions selection may favour the evolution of large seeds despite the potential costs of reduced seed dispersal. For example, large seeds may be necessary for successful seedling establishment under conditions of low light or water (Baker, 1972; Howe and Richter, 1982; Foster and Janson, 1985; Mazer, 1989, 1990; Westoby *et al.*, 1992). In taxa in which fruits contain a single seed, a relatively large fruit will be the inevitable consequence of producing a large seed. What adjustments in fruit or seed shape are favoured in order to reduce the negative impact of increasing fruit size on seed dispersal?

In this paper we explore the idea that much of the variation in fruit form so frequently noted (Snow, 1971; Stiles, 1980; Herrera, 1981a,b, 1982, 1987; Wheelwright *et al.*, 1984; Johnson *et al.*, 1985; Thompson and Rabinowitz, 1989) might be explained as the evolutionary outcome of natural selection by size-sensitive avian seed dispersers. The results of a recent study of

interspecific variation in fruit shape, which found that fruit length and diameter of vertebrate-dispersed plants of the Iberian Peninsula scaled isometrically within and between species, rightly emphasizes the importance of considering alternative, 'null' hypotheses (Herrera, 1992). For example, Herrera (1992) demonstrated that phylogeny (taxonomic membership) was more highly correlated with fruit shape than dispersal mode and argued that evolutionary history and morphogenetic and physical mechanisms such as patterns of cell division, internal hydrostatic pressure and surface stresses could largely explain the prevalence of geometric similarity in fruit shape. Our study complements Herrera's (1992) study by examining allometric relationships at several taxonomic levels: among fruits and seeds within individual trees of *Ocotea tenera* (Lauraceae), among trees within a population of *O. tenera*, among pooled fruits representing multiple trees of other lauraceous species, among species of the Lauraceae and among other plant families in a diverse neotropical plant community in Monteverde, Costa Rica. We also describe the allometry of fruits at different stages of development in one of the species of Lauraceae, *Ocotea viridifolia*. As a preliminary comparison between Old and New World plant communities, we describe the relationship between fruit length and diameter among 94 vertebrate-dispersed species from Malawi using data presented by Dowsett-Lemaire (1988).

We address two main questions. First, within and among species, does fruit and seed shape change with size or are large fruits and seeds simply scaled-up versions of small ones, as suggested by Herrera's (1992) study? Second, if fruit shape does differ at the level of individuals, species or families, what is the nature of the allometric relationship at different taxonomic levels and what do allometric relationships at different taxonomic levels imply about the role of natural selection, speciation, taxonomic membership or developmental constraints in determining fruit form?

Methods

Fruits from bird-dispersed species in the family Lauraceae were collected as described below between 1979 and 1992 from natural and experimental populations in the lower montane forests of Monteverde, Costa Rica, from the 10 000-hectare Monteverde Cloud Forest Reserve and from surrounding woodlots (10° 18'N, 84° 48' W; Holdridge, 1967; see Wheelwright (1985) for a more complete description of the site).

Detection of allometric relationships

Using the major axis technique (Jolicoeur and Heusner, 1971; Sokal and Rohlf, 1981), we estimated the slope of the linear relationship between the following pairs of natural log-transformed (ln-transformed) variables: (a) fruit diameter vs fruit length and (b) seed diameter vs seed length. Major axis regression is appropriate for several reasons. First, the technique allows one to estimate the functional relationship between two variables without assuming that the value of one variable causally determines the value of the other. Second, major axis is preferable to least-squares regression when there is the possibility of measurement error in both X and Y variables and when the errors in X and Y are approximately equal, as is likely to be the case in the fruits and seeds measured in this study. Additionally, major axis regression tends to produce steeper (more positive) regression slopes than least-squares linear regression; in the case of this study, major axis regression provides a more conservative test of the hypothesis of negative allometry of fruit shape. In our analyses, major axis regression produced confidence intervals that averaged 51% wider than those produced by either reduced major axis or least-squares regression (two-tailed paired t-test, $p < 0.0001$). This result also made it more difficult to establish statistically significant negative allometry in our study than if we had used alternate regression methods. For a clear discussion of the different models for estimating allometric slopes

and the rationale for preferring major axis regression in studies of allometry, see Harvey and Pagel (1991).

In general, regression slopes of ln(fruit diameter) on ln(fruit length) <1 indicated negative allometry. We used the 95% confidence interval (CI) of the regression slope (s) to evaluate whether allometric coefficients were statistically significantly different from 0 or 1 (the lower limit of the 95% CI of the regression slope exceeded 0 or the upper limit was <1, respectively). In our study, statistically significant negative allometry was identified if the upper bound of the 95% CI did not exceed 1.0. When the estimated slope was <1 ($s < 1$) but the CI of the slope included both 0 and 1, a result that occurred when sample size was small or when variation about the regression line was high, the slope was not considered to be statistically significantly different from 1. In several cases, the CI was undefined due to small sample size and low r^2; in these instances the slope was also not considered significantly different from 1. A CI for which the lower limit was greater than 0 and the upper limit exceeded 1 was considered a case of isometry (geometric similarity of large and small fruits).

Except when noted otherwise, descriptive statistics represent mean ($\bar{x}$) ± 1 standard deviation; ranges and sample size (n) are also given.

Intraspecific studies

Intraspecific studies: Ocotea tenera. Mature fruits were collected from 19 trees of *O. tenera* during the early dry seasons of 1983–1992 ($n > 15$ fruits/tree' $\bar{x} = 27.7$ fruits/tree, there was little year-to-year variation in fruit shape within individual trees over an 11-year period; (Wheelwright (1993)). For trees with small fruit crops, all fruits were collected; for other trees, samples were gathered haphazardly. We measured length, diameter and mass for all fruits and seeds. Linear dimensions were measured to 0.1 mm with dial calipers. Fresh mass was measured to 0.1 g with a spring balance. For each tree we calculated mean values for fruit and seed lengths and diameters. We examined the allometry of fruit and seed shape at two levels in *O. tenera*: among mature fruits within each tree and among individual trees within the population, using tree means.

Intraspecific studies: 21 species in the Lauraceae. Mature fruits were collected from 20 additional species of the Lauraceae (Table 1, number of fruits/species = 5–106, number of trees/species = 1–9). As above, the number of fruits sampled per tree was sometimes limited by crop size and the number of trees sampled per species was limited by population size. Fruit length and diameter were measured as above for all fruits; fresh fruit mass, seed length, seed diameter and fresh seed mass were recorded for most fruits. The allometry of fruit and seed shape was determined within each species, pooling fruits from all sampled trees. Fruits were pooled to increase sample sizes and because variation in shape and size among tree means was generally lower than among individual fruits.

Interspecific studies

Interspecific studies: Lauraceae. For each of the 21 species in the Lauraceae described above (plus four more species for which sample sizes were too small to determine meaningful intraspecific allometric coefficients), we determined mean fruit and seed characters and estimated the allometric relationships among species within the family, using species means. We also compared the slopes of intraspecific and interspecific regressions to detect taxon-level effects on allometric relationships (Pagel and Harvey, 1988).

The advantage of focusing on the Lauraceae is that their general biology is well known; all are

Table 1. Mean (± 1 sd) fruit and seed dimensions for 21 bird-dispersed tree species in the Lauraceae

Species[a]	n	Fruit length (cm)	Fruit diameter (cm)	Fruit slope	Seed length (cm)	Seed diameter (cm)	Seed slope
Aiouea costaricensis	12	1.95 (0.14)	1.22 (0.07)	0.08	1.77 (0.17)	0.98 (0.07)	0.21
Beilschmeidia brenesii	20	3.63 (0.29)	2.31 (0.12)	0.51	3.42 (0.30)	1.95 (0.11)	0.57
Beilschmeidia ovalis	5	3.99 (0.32)	2.45 (0.10)	0.51	3.63 (0.32)	1.95 (0.10)	0.59
Beilschmeidia pendula	8	4.19 (0.38)	2.26 (0.13)	0.53	3.81 (0.39)	1.89 (0.12)	0.51
Nectandra membranacea	21	1.10 (0.08)	1.23 (0.09)	0.88	1.01 (0.08)	0.92 (0.06)	0.77
Nectandra sp. NG	12	2.31 (0.08)	1.72 (0.09)	2.53	2.12 (0.11)	1.38 (0.06)	0.88
Nectandra salicina	12	3.63 (0.38)	1.84 (0.16)	0.73	3.37 (0.39)	1.45 (0.15)	0.73
Nectandra sinuata	12	2.61 (0.26)	1.85 (0.17)	0.88	2.44 (0.27)	1.52 (0.17)	1.04
Ocotea endresiana	12	1.80 (0.30)	1.08 (0.05)	0.03	1.62 (0.27)	0.80 (0.08)	0.06
Ocotea floribunda	12	1.77 (0.10)	1.75 (0.07)	0.72	1.54 (0.12)	1.40 (0.06)	0.45
Ocotea insularis	106	1.70 (0.14)	1.14 (0.06)	0.21	1.50 (0.13)	0.83 (0.07)	1.54
Ocotea meziane	9	2.92 (0.23)	1.86 (0.18)	1.49	2.70 (0.22)	1.53 (0.20)	2.05
Ocotea 'near meziane'	12	3.01 (0.14)	2.04 (0.10)	1.08	2.73 (0.16)	1.60 (0.09)	1.01
Ocotea monteverdensis	20	2.93 (0.41)	1.85 (0.17)	0.21	2.59 (0.39)	1.42 (0.16)	0.60
Ocotea pittieri	11	1.84 (0.24)	1.19 (0.08)	0.22	1.72 (0.22)	1.00 (0.07)	0.11
Ocotea tenera	524	3.30 (0.30)	1.80 (0.14)	0.66	3.01 (0.29)	1.46 (0.12)	0.76
Ocotea valeriana	20	3.30 (0.55)	2.15 (0.19)	0.46	2.82 (0.60)	1.63 (0.22)	0.57
Ocotea viridifolia	10	2.13 (0.12)	1.75 (0.11)	1.15	1.93 (0.11)	1.37 (0.07)	1.00
Persea caerulea	24	0.71 (0.04)	0.82 (0.04)	0.72	0.59 (0.03)	0.64 (0.04)	1.16
Persea veraguensis	12	1.05 (0.05)	1.05 (0.05)	1.00	0.93 (0.06)	0.93 (0.06)	1.00
Phoebe cinnamomifolia	22	1.70 (0.30)	1.25 (0.13)	0.58	1.43 (0.27)	0.91 (0.08)	0.43

Slopes for fruit diameter regressed on fruit length and seed diameter regressed on seed length, were calculated using ln-transformed data and the major axis technique (see text for explanation). n = number of fruits or seeds measured.
[a] The taxonomy of the Lauraceae of Costa Rica has recently been clarified by Burger and van der Werff (1990). The names listed above correspond to the following species described in Wheelwright *et al.* (1984) and Wheelwright (1985): *Beilschmeidia mexicana, B. pendula; Beilschmeidia* sp. BL, *B. ovalis; Beilschmeidia costaricensis, B. brenesii; Nectandra davidsoniana, Ocotea viridiofolia; Nectandra gentlei, N. membranacea; Nectandra hypoglauca, Ocotea monteverdensis; Ocotea austinii, O. endresiana; Ocotea* sp. OD, *O. pittieri; Ocotea* sp. FL, *O. valeriana; Ocotea klotzschiana, O. meziane; Ocotea* sp. K2, *Ocotea* 'near meziane'; *Ocotea* sp. RP, *Aiouea costaricensis; Ocotea tonduzii, O. insularis; Ocotea wachenheimii, O. floribunda; Persea* sp. FL, *Nectandra sinuata; Persea* sp. RS, *P. caerulea; Phoebe mexicana, P. cinnamomifolia.*

dispersed primarily or exclusively by birds that swallow fruits whole and regurgitate seeds unharmed. Lauraceous trees provide most of the diet for a number of specialized fruit-eating birds (Wheelwright *et al.*, 1984). A disadvantage is that the phylogeny of the Lauraceae is poorly known. The most recent taxonomic treatment of the Lauraceae of Costa Rica (Burger and van der Werff, 1990) does not attempt a cladistic analysis. Even assignments of species to different genera within the family is sometimes arbitrary (R. Foster, personal communication; N. Wheelwright, personal observation). Despite the importance of considering phylogeny in comparative studies (Felsenstein, 1985; McDade, 1992) and of using independent comparisons in allometric analyses (Harvey and Pagel, 1991), unfortunately we are constrained by the uncertainty of evolutionary relationships within the Lauraceae. The reader should bear in mind that different species within the Lauraceae do not necessarily represent independent data points, although they are treated as such by regression analyses. It is important to note, however, that the taxonomic relatedness of these independently treated species does not preclude natural selection by avian dispersers on fruit shape from occurring independently in each species.

Interspecific studies: lower montane plant community. Fruits from 167 species in 122 genera and 63 plant families were collected in Monteverde; mean fruit and seed characters were recorded for a minimum of three fruits per species. Fruits of all of the species were believed to be eaten and their seeds dispersed primarily by birds (Wheelwright *et al.*, 1984). Examining allometric relationships among all bird-dispersed plant species at Monteverde by using species' means could result in a biased estimate of among-species allometric slopes because some families included more species than others and because confamilial species tended to be similar with respect to mean fruit size and shape, which makes them statistically non-independent due to phylogenetic relatedness. In fact, we found significant differences among families with respect to the mean fruit mass and fruit length : diameter ratio (one-way ANOVA, fruit mass, $r^2 = 0.62$, $p < 0.001$, fruit length : diameter ratio: $r^2 = 0.50$, $p < 0.01$, $n = 63$ families). In addition, families differed with respect to the residual of the regression (among the 167 species) of ln(fruit diameter) on ln(length) (one-way ANOVA for effect of family membership on the residual: $r^2 = 0.51$, $p < 0.006$). In the absence of adequate phylogenetic information on these poorly known tropical species, we tried to minimize taxonomic biases by using family means as well as species means in separate regression analyses conducted at the plant community level.

To obtain a preliminary sense of whether fruit shape is associated with the way in which it is handled by birds, we categorized each of the 167 plant species into those with fruits that were observed or suspected to be eaten piecemeal ('mashed', *sensu* Levey, 1987) or fruits that were observed or suspected to be swallowed whole by birds. Fruit shape was not considered when assigning handling category. The first category included 31 species with small-seeded berries or capsules with soft pulp in the following taxa: *Centropogon* (Campanulaceae), Ericaceae (two unidentified species), *Beslaria* (Gesneriaceae), *Miconia, Ossaea, Blakea, Conostegia* (Melastomataceae), *Ficus* (Moraceae), *Passiflora* (Passifloraceae), *Phytolacca* (Phytolaccaceae), *Fuchsia* (Onagraceae), *Hoffmannia, Xerococcus, Coccocypselum, Psychotria, Hamelia* (Rubiaceae) and *Lysianthes, Solanum, Witheringia* (Solanaceae). The second category included the remaining 136 species (see Wheelwright *et al.* (1984) for morphological descriptions of each species). A Mann–Whitney U-test was used to determine whether fruits presumed to be swallowed whole were significantly more elongate than 'mashed' fruits, as would be expected if they were under stronger selection for elongation.

Interspecific studies: bird-dispersed plants from Malawi. In an effort to evaluate the generality of our results, we examined data presented by Dowsett-Lemaire (1988; Table V), analysing separately the relationship between fruit size and shape in 84 fruit species listed as being eaten by birds alone and 10 species eaten by mammals alone. Dowsett-Lemaire's main study site, Nyika Plateau (10°30′ S), is similar in latitude to Monteverde, Costa Rica.

Developmental allometry

Within- and between-tree variation in Ocotea viridifolia. We examined allometric relationships among fruits of one species in the Lauraceae, *Ocotea viridifolia*, during development to assess whether the allometric relationships among mature fruits might be developmentally constrained. If so, then lauraceous species differing in fruit size and shape may simply represent distinct points along a deterministic ontogenetic trajectory.

On six dates between the time of fertilization and fruit maturity (12 April, 2 May, 22 May, 17 June, 10 July and 4 August, 1985), fruits were collected from each of two trees (trees A and C). A third tree (tree B) was sampled on the first three dates, but was then cut down for reasons unrelated to this study. We could not follow the ontogeny of individual fruits throughout their

development because examining developing fruits and seeds required destructive sampling. Instead we measured haphazard samples of 5–10 fruits from each tree on each sampling date. The sampling intervals insured that fruit size differences within and among trees corresponded to differences in fruit developmental age. Fruits sampled were divided into three age groups of approximately equal numbers of fruits. The age groups corresponded to the following size classes: (1) fruits less than 3.7 mm in length, (2) fruits 3.7–10.0 mm in length and (3) fruits longer than 10.0 mm. Fruits from each group were subject to major axis regressions between the following pairs of ln-transformed variables: fruit diameter vs fruit length and seed diameter vs seed length. Each group from each tree was analysed separately and then pooled for analysis across trees. For each fruit and seed, the length : diameter ratio was determined and two-way ANOVAs were conducted to detect the effects of tree identity and age group on fruit and seed elongation (PROC GLM; SAS Institute, 1987).

Results

Intraspecific studies: Ocotea tenera

In 15 of the 19 *Ocotea tenera* trees, the calculated slope of the major axis regression of ln(fruit diameter) on ln(fruit length) was <1, although in 12 cases it was not statistically significantly less than 1. In most cases, however, large fruits did appear to be more elongate than small fruits among fruits produced by a single tree (e.g. Fig. 1). Significantly more trees showed slopes <1 than would be expected by chance (binomial test with the assumption that slopes >1 and slopes <1 are equally likely, $p = 0.009$). The mean slope was 0.65 ($\pm$ 0.35, range 0.15–1.31, $n = 19$ trees), the median was 0.63. In 17 of the trees, the lower bound of the 95% CI was >0. In all cases the lower bound of the CI was <1, that is, there was no case of significant positive allometry. However, since the upper bound of the CI was >1 in 12 of the trees, slopes were
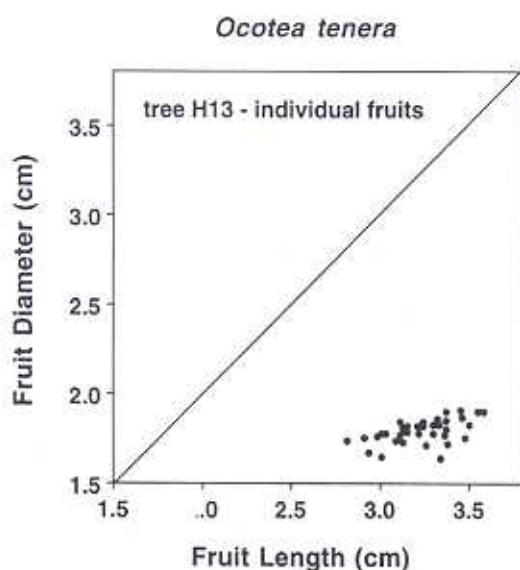

Figure 1. The relationship between fruit length and diameter within an individual tree of *Ocotea tenera* (Lauraceae) in Monteverde, Costa Rica. Each point represents a single fruit ($n = 37$ fruits). Spherically shaped fruits fall on the diagonal line; points to the right of the line designate elongate fruits. Major axis regression of ln(fruit diameter) on ln(fruit length) produced a slope of 0.45 (mean slope for 19 *O. tenera* trees is 0.65).

considered significantly negatively allometric in only seven of the 19 trees. Nevertheless, the predominance of individual trees with slopes <1 indicated that scaling of fruit shape within *O. tenera* trees tends to be negatively allometric rather than isometric or positively allometric.

Like fruits, seeds showed a tendency toward increasing elongation with size within individual trees, but we detected significant negative allometry in only three trees. The estimated slope of the major axis regressions of seed diameter on length was <1 in 14 of the 19 trees, a higher proportion of trees with negatively allometric seed shapes than would be expected by chance (binomial test, $p=0.032$). The mean slope (omitting two trees in which high variance in seed shape produced inflated slope estimates of 2.5 and 4.3) was 0.79 (±0.48; range, 0.04–1.84); the median slope including all trees was 0.72. In 15 trees the lower bound of the CI was >0. The upper bound of the CI was >1 in 16 trees. As above, none of the trees showed significant positive allometry (lower bound of the CI >1). Trees with seeds that were more elongate with increasing seed size also produced fruits with a similar allometric relationship between length and diameter. Thus, the values of the regression slopes for fruit allometry within trees were positively correlated with those for seed allometry (Spearman rank, $r_s=0.77$, $p<0.001$). However, regression slopes for seeds were significantly steeper (more positive) than those for fruits (two-tailed paired t-test, $p<0.01$), which reflected the fact that seeds showed less elongation with size than did fruits.

Among the 19 *O. tenera* trees in the population, individuals with relatively large fruits tended to produce more elongate fruits on average than small-fruited trees (Fig. 2). The slope of the major axis regression among trees, using tree means, was 0.52. However, due to a relatively low correlation coefficient, the CI was undefined but (based on reduced major axis regressions) the upper bound of the CI appeared to be >1, indicating that the negatively allometric slope for fruits was not statistically different from 1 at this level of analysis.

As in the case of fruit shape, major axis regression of ln(mean seed diameter) on ln(mean seed length) among trees resulted in a slope <1 ($s=0.38$), suggesting that trees producing large seeds tended to have disproportionately elongate seeds, but again the upper bound of the CI appeared to be >1, making the relationship statistically non-significant.
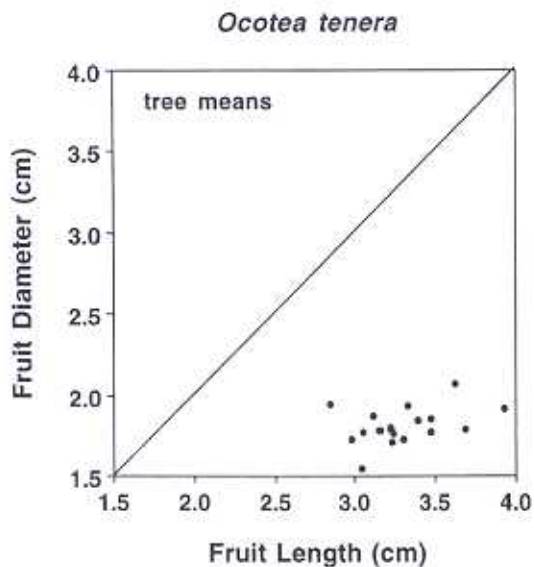

Figure 2. The relationship between fruit length and diameter among individual trees of *Ocotea tenera* (Lauraceae). Each point represents the mean of at least 15 fruits from a single tree ($n = 19$ trees). Major axis regression of ln(fruit diameter) on ln(fruit length) produced a slope of 0.52.

Intraspecific studies: 21 species in the Lauraceae

Within individual species in the Lauraceae, there was a tendency for large fruits to be more elongate than small fruits. In 16 of the 21 species major axis regression slopes of ln(fruit diameter) on ln(fruit length) were <1 (Table 1; binomial test, $p=0.013$). The upper bound of the CI fell below 1 within seven of the 21 species, exceeded 1 in eight species and was undefined in six species. In every case the lower bound of the CI was <1. The only species that produced spherical fruits was *Persea veraguensis*, a species whose fruits are smaller in diameter than all but one of the 21 species listed in Table 1. The mean slope of within-species regressions for species of Lauraceae was 0.72 (±0.56, $n=21$ species).

In 14 of the 21 species in the Lauraceae, regression slopes of ln(seed diameter) on ln(seed length) were <1 (Table 1; binomial test, $p=0.095$). The upper bound of the CI fell below 1 within six of the 21 species, exceeded 1 in eight species and was undefined in seven species. As with fruits, the lower bound of the CI was always <1. The mean slope of 21 species was 0.76 (±0.46). There was a positive correlation between the slope of the regression of fruit length on fruit diameter and the slope of the regression of seed length on seed diameter (Spearman rank, $r_s=0.67$, $n=21$ species, $p<0.003$).

In general, compared to fruits, seeds did not show less elongation with increasing size within the Lauraceae species. Among 21 species, the mean slope of the regression of fruit diameter on fruit length did not differ significantly from that of seed diameter on seed length (two-tailed paired t-test, $p=0.76$).

Interspecific studies: Lauraceae

Among 25 species in the Lauraceae, large-fruited species produced more elongate fruits than did small-fruited species (Fig. 3). The among-species slope of the regression of ln(fruit diameter) on ln(fruit length) was 0.63 ($r^2=0.83$), which was slightly less than the mean for 21 species in the Lauraceae. The CI was 0.47–0.82, clearly indicating statistically significant negative allometry at the plant family level.
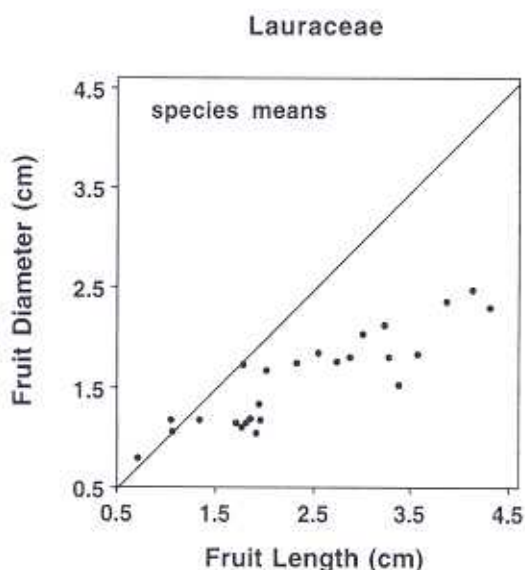

Figure 3. The relationship between fruit length and diameter among species in the Lauraceae. Each point represents the mean of at least 15 fruits from a single species ($n = 25$ species). Major axis regression of ln(fruit diameter) on ln(fruit length) produced a slope of 0.63.

Seed length also increased more rapidly than seed diameter among species, with a slope slightly less than the mean slope of individual species but similar to the among-species fruit shape slope ($s=0.63$, $r^2=0.80$). As with fruits, the slope for seeds was significantly negatively allometric.

Interspecific studies: lower montane plant community

The regression of ln(fruit diameter) on ln(fruit length) for all 167 available Monteverde species had a slope of 0.81, which was significantly <1 (Fig. 4; $r^2=0.73$, $p<0.0001$). However, when family means were used to reduce the potential bias due to unequal numbers of species per family, the relationship became indistinguishable from isometric (Fig. 5; $s=1.03$, lower bound of the CI=0.87, upper bound of the CI=1.22, $r^2=0.76$, $p<0.0001$). Among 63 bird-dispersed plant families at Monteverde, large-fruited taxa did not possess more elongate fruits on average than small-fruited families. Note, however, that the longest fruits had diameters considerably less than that predicted by isometry and that the variance in diameter increased with increasing fruit size (Fig. 5).

The plant species that were tentatively classified as producing fruits likely to be eaten piecemeal tended to be less elongate than the 136 species presumed to be swallowed whole. Fruit species eaten piecemeal had a mean fruit length : diameter ratio of 1.17 ± 0.70, which was significantly smaller than that of fruits swallowed whole (1.25 ± 0.30, Mann–Whitney U-test, $p<0.001$).

Interspecific studies: bird-dispersed plants from Malawi

Fruit shape did not appear to change with fruit size among 84 fruits of bird-dispersed plants in Malawi. A major axis regression slope of 0.98 for plants and 95% confidence intervals overlapping 1 indicated isometry (Fig. 6). The fruits of mammal-dispersed plants in Malawi also showed isometry ($s=0.91$).
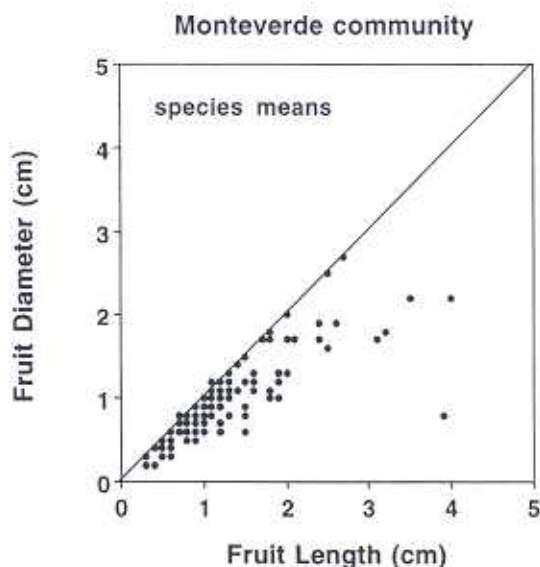

Figure 4. The relationship between fruit length and diameter among bird-dispersed species in the lower montane forests of Monteverde, Costa Rica. Each point represents the mean of at least three fruits from a single species (n = 167 species from 63 families). Major axis regression of ln(fruit diameter) on ln(fruit length) produced a slope of 0.81.

Developmental allometry: within- and between-tree variation in Ocotea viridifolia

The allometric relationship between fruit length and diameter varied with developmental stage in *O. viridifolia*. Likewise, the relative growth rate of seed length and diameter changed during ontogeny. During early development, when fruits were less than 3.7 mm in length, fruits tended to be spherical and growth was isometric; the slope of the regression of ln(fruit diameter) on ln(length) was not significantly different from 1 among fruits in any of the three trees (mean $s = 1.11$, $p < 0.0001$, $n = 41$ fruits). In mid-development, the slope of the regression was significantly
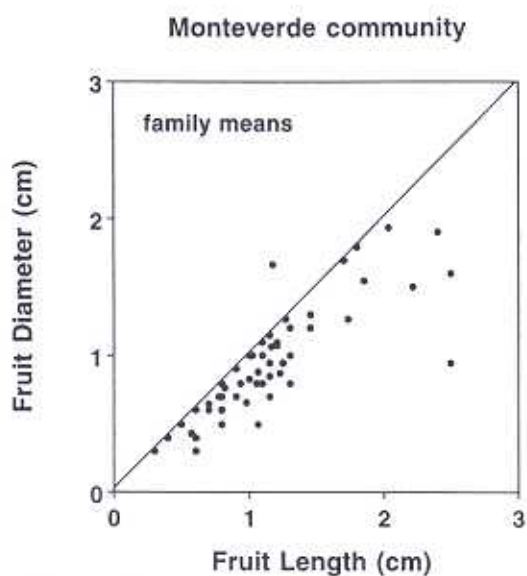
Monteverde community

Figure 5. The relationship between fruit length and diameter among families of bird-dispersed species in the lower montane forests of Monteverde, Costa Rica. Each point represents the mean of a plant family ($n = 63$ families). Major axis regression of ln(fruit diameter) on ln(fruit length) produced a slope of 1.03.
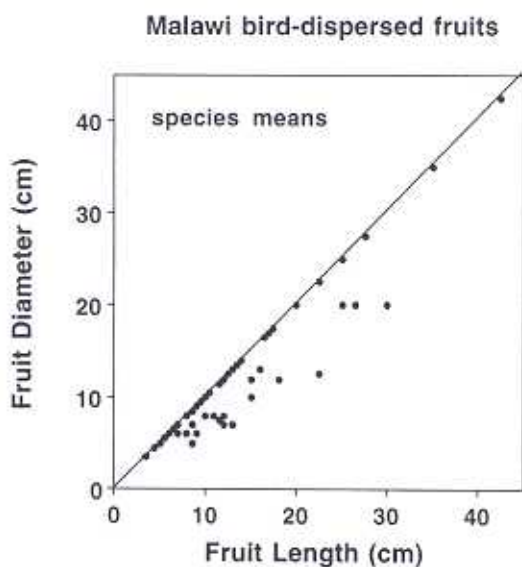
Malawi bird-dispersed fruits

Figure 6. The relationship between fruit length and diameter among bird-dispersed species in the upland forests of Malawi. Each point represents the mean of a single species ($n = 84$ species). Major axis regression of ln(fruit diameter) on ln(fruit length) produced a slope of 0.98.

<1 in all trees, indicating a period of elongation (mean $s = 0.71$, $p < 0.0001$, $n = 46$ fruits). Late in development, when fruit length was > 10 mm, the slope of the regression was slightly > 1, significantly so in two trees (mean $s = 1.16$, $p < 0.0001$, $n = 43$ fruits; Fig. 7). There was a significant association between fruit size and elongation but no tree effect on fruit elongation (two-way ANOVA, $p < 0.0001$).

Unlike fruits, seeds tended to be elongate rather than spherical early in development (mean seed length: diameter $= 1.55$). Nonetheless, the slope of the regression of ln(seed diameter) on ln(seed length) was not significantly < 1 during early- or mid-development. Within nearly-mature fruits, seed diameter increased more rapidly than seed length, indicating an ontogenetic shift in the scaling of seed length and diameter.

Discussion

This study addresses two main questions. First, do fruit and seed shape in bird-dispersed plants vary as a function of size? Second, do allometric relationships change with taxonomic level? To answer these questions, we examined allometric relationships between length and diameter in fruits and seeds in bird-dispersed plants at various taxonomic levels: among fruits within individual trees, among individual tree means, among fruits representing multiple trees, among species within a family and among species and families within a neotropical plant community.

The results of this study clearly show that, for the Lauraceae at least, large fruits are not simply scaled-up versions of small fruits. The mature fruits of *Ocotea tenera* (Lauraceae) showed a pattern of increasing elongation with size within individual trees, as fruit length increased more rapidly than fruit diameter. Although the wide confidence intervals produced by major axis regression made it difficult to rule out isometry in individual cases in all but seven trees, the fact that estimated slopes were < 1 in 15 of the 19 individual trees provides strong evidence for negative allometry at the level of fruits within trees of *O. tenera*.

Similarly, we found a strong association between mean fruit size and shape among trees within
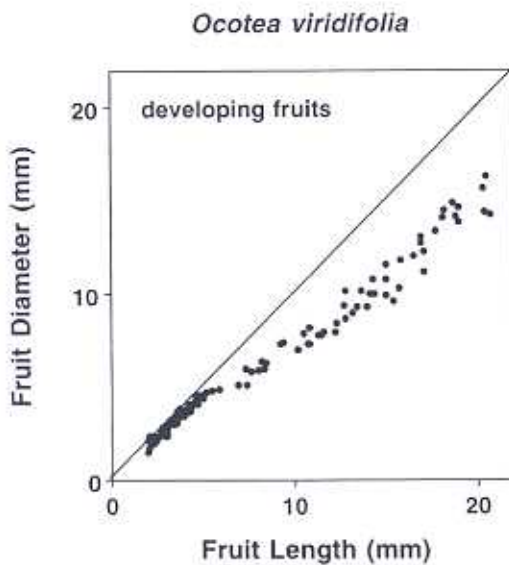

Figure 7. The relationship between fruit length and diameter during development in *Ocotea viridifolia* (Lauraceae) in Monteverde, Costa Rica. Each point represents a single fruit ($n = 130$ fruits). Major axis regression of ln(fruit diameter) on ln(fruit length) suggested isometric growth in early development, followed by a stage of negatively allometric growth, then positive allometric growth.

the *O. tenera* population: if a tree produced large fruits, its fruits also tended to be more elongate than the fruits of conspecific trees with small fruits. We also found considerable phenotypic variation among individuals with respect to fruit shape, which is a necessary condition for phenotypic selection by birds to result in evolutionary change in allometry. Preliminary results suggest that variation in fruit form is highly heritable (Wheelwright, 1993). Within 16 of the 20 other bird-dispersed species in the Lauraceae of Monteverde, Costa Rica, the relationship between fruit length and diameter also suggested negative allometry, although slopes were not statistically significantly different from isometry in most species.

Among 25 species within the Lauraceae, large-fruited species produced fruits that were significantly more elongate than those of small-fruited species. In a comparison of fruits of 167 bird-dispersed species representing a diversity of plant families in the same lower montane forest, fruit length also increased at a significantly faster rate than fruit diameter, which resulted in a tendency for large fruits to be disproportionately elongate. However, when 63 plant family means (rather than the 167 species means) were used, fruit length and diameter scaled isometrically. This result suggests that in this plant community, large-fruited families have not been subject to (or responded to) stronger selection favouring fruit elongation than small-fruited families.

Seed shape varied with seed size in a similar manner at most taxonomic levels of analysis, with large seeds tending to be more elongate than small seeds. The degree of negative allometry in fruit shape within species was positively correlated with the degree of negative allometry in seed shape. Allometric slopes tended to be more positive and more variable for seeds than for fruits. It may be that selection for negative allometry in seeds is weaker than in fruits because seeds are smaller than fruits and therefore less problematic for birds to handle or because gape limitations are more important than gut limitations. In any event, seed shape is more difficult to assess than fruit shape for birds choosing among fruits, weakening direct selection on their form. Alternatively, seed shape may be more constrained than fruit shape by ecology (e.g. germination requirements, predation, etc.), ontogeny or phylogeny.

In contrast to the species we studied in a neotropical lower montane site, the shape of bird-dispersed fruits of upland forest in Malawi (Dowsett-Lemaire, 1988) and from the Iberian Peninsula (Herrera, 1992) tended to scale isometrically with fruit size. The differences in our results may be due to various factors. This study focuses on the Lauraceae, a family of plants which produces fruits far larger than most found in Spain (although not necessarily larger than in Malawi), with bulky single seeds and a long evolutionary history of seed dispersal by gape-limited animals. The dominant plant families differ markedly between Costa Rica, Malawi and Spain. Undoubtedly, plants from Europe and Africa have interacted with very different suites of animal dispersers during their evolution. Whatever the reasons for our distinct findings, it is clear that in at least one plant community, mechanical considerations such as internal hydrostatic pressure and surface stresses during development have not imposed isometric fruit shape.

Ontogenetic changes in allometry

Variation in fruit shape during ontogeny may yield insights about the developmental flexibility of fruit form and revea the type of developmental changes necessary to create differences in fruit shape within species. If fruits of different but related species reach maturity at different stages of ontogeny (e.g. if something analogous to paedomorphosis results), the study of fruit ontogeny within a species may also explain differences in fruit shape among species (see Gould, 1975). Is mature fruit shape determined by an invariable ontogenetic trajectory initiated early in development or are developmental events flexible (Gould, 1975)? If fruit shape is developmentally constrained, the relationship of fruit length and diameter within or among species might be expected to mirror allometric relationships during ontogeny, with different fruits, trees or species

simply reaching maturity and stopping growth at different points along an ontogenetic curve. On the other hand, if disperser-mediated choice among fruits is the primary selective force influencing the shape of mature fruits, we might expect quite distinct allometric relationships among related species or changes in allometric scaling occurring relatively late in fruit development.

We found that the relative growth rates of fruit diameter and length in *Ocotea viridifolia* changed during development. Early in development, fruit diameter and length scaled isometrically. They then entered a stage of rapid elongation and completed development with a stage of positive allometry. If fruit ontogeny in *O. viridifolia* is representative of development in the family as a whole, these changes in the relationship between fruit diameter and length during development suggest that mature fruit shape is not simply the result of an inflexible developmental trajectory initiated early in development. Moreover, the relationship between fruit length and diameter and between seed length and diameter during development, in *O. viridifolia* at least, does not closely resemble relationships for mature fruits within or among trees or species (cf. Figs 1–3 vs Fig. 7). Studies of fruit development in other species of Lauraceae as well as species representing a diversity of families are needed to clarify the role of fruit development in determining mature fruit shape (e.g. Herrera, 1992). Ecologists habitually lump together fleshy fruits, regardless of their anatomical origin (e.g. Snow, 1971), but we may well be advised to consider the fact that berries, drupes or strobili face distinct developmental constraints on the evolution of fruit shape.

Allometric slopes at different taxonomic levels

In previous studies of allometry at different taxonomic levels, slopes have often been found to be steeper at increasingly higher taxonomic levels. Both biological and statistical explanations have been offered for such a 'taxon-level effect', which is frequently reported in animals, but has not previously been sought in plants (Gould, 1975; Lande, 1979; Smith, 1981; Martin and Harvey, 1985; Pagel and Harvey, 1988, 1989; Harvey and Pagel, 1991; see Herrera, 1992). We found negligible support for the taxon-level effect in fruit shape in this study. The allometric slope for pooled fruits representing 19 *O. tenera* trees was 0.66 ($n = 524$ fruits; the mean slope within individual *O. tenera* trees was 0.65). Among *O. tenera* trees, the slope was 0.52 while the mean slope within 21 species of Lauraceae was 0.72. Among species within the Lauraceae, the slope was 0.63. For seeds, allometric slopes decreased at higher taxonomic levels, from a mean slope of 0.79 among fruits within *O. tenera* trees, to a mean slope of 0.76 among pooled fruits within species of the Lauraceae, to a slope of 0.63 among species within the Lauraceae. The only indication of a steeper allometric slope at a higher taxonomic level occurred for fruit shape at the level of the plant family, where the slope was 1.03 (among Monteverde family means). Similarly, both Herrera's (1992) and Dowsett-Lemaire's (1988) data showed isometry among species' means representing a variety of plant families.

Smith (1981) and Pagel and Harvey (1988) have suggested that the taxon-level effect could largely be a statistical artifact, resulting chiefly when there are substantial differences between the total variance in the X variable observed at different taxonomic levels and when measurement error represents a significant proportion of the total variance in X at lower taxonomic levels. For the X variables in the current study (fruit and seed length), measurement error was small relative to the total variance. Thus, the differences in slopes among taxonomic levels may have a biological explanation.

A change from negative allometry to isometry as one progresses from lower to higher taxonomic levels would be expected if size-dependent selection on fruit shape by gape-limited seed dispersers was most intense within species or among closely related species and diminished

in strength or changed direction as one considered progressively less ecologically similar taxa, such as distinct families. The degree of negative allometry between fruit diameter and length is also likely to depend on the degree to which individual plants or species share seed dispersers. For example, if large-fruited species within a plant family are dispersed chiefly by large-gaped birds and small-fruited species are dispersed chiefly by small-gaped birds, allometric scaling may be negative within each species but isometric among species (Fig. 8). Because conspecifics and confamilial species are more likely to share dispersers than are plants from distinct taxonomic families, negative allometry should be more pronounced within species and families than among families. Speciation events unrelated to fruit shape may also influence interspecific allometry. For example, speciation could result in the formation of new species with larger or smaller mean fruit sizes, while retaining the ancestral species' intraspecific negative allometry (e.g. species E vs C and F in Fig. 8). Similar patterns of fruit size and shape could thus be the result of either parallel or convergent evolution.

If disperser preferences have acted as a strong selective force on the relationship between size and shape in fruits and seeds, we can make the following predictions about the allometry of fruit form based on the way fruits are handled and seeds dispersed. First, we would expect increased elongation with fruit size in fruits that are swallowed whole, but not necessarily for fruits that are eaten piecemeal (e.g. figs). Second, the fruits of bird-dispersed plants should show greater negative allometry than mammal-dispersed plants (many of which are gnawed rather than swallowed), which in turn should show greater negative allometry than plants dispersed by wind or water. A corollary is that among-species allometry should be more negative in plant communities dominated by or with a lengthy evolutionary history of interactions with avian or other gape-limited seed dispersers. Third, negative allometry should be more pronounced within large-fruited species compared to small-fruited species, assuming that seed dispersal in large-fruited species is more likely to be limited by disperser availability. Fourth, selection for increased elongation with size should be weaker on seeds than on fruits because seeds, which are inevitably smaller in diameter than the fruits that contain them, impose less of a constraint on
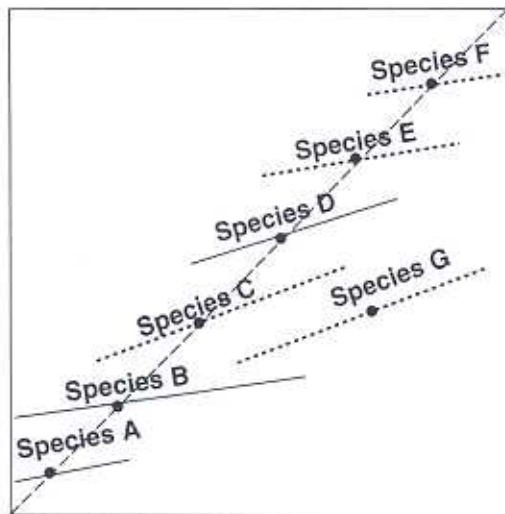

Figure 8. A model illustrating how the relationship between fruit length and diameter may differ at distinct taxonomic levels. Axes as in previous figures. Short lines designate negatively allometric slopes within species of two clades (solid lines, species A, B and D; heavy dashed lines, species C, E, F and G). The long diagonal dashed line represents the isometric slope among species, whose mean ln(fruit length) and mean ln(fruit diameter) are shown by large dots.

gape-limited seed dispersers. Moreover, birds can immediately evaluate fruit diameter but not seed diameter (except in the rare case of translucent fruits), so their discrimination of fruit shape should have a more important effect on seed dispersal than their discrimination of seed shape. Finally, there should be greater seed elongation with increasing seed size in single- or large-seeded fruits compared to multi- or small-seeded fruits because seed shape should be more important to fruit-eating animals as relative seed size increases.

We also expect a negative allometric relationship between fruit or seed diameter and length at all taxonomic levels (among fruits within a tree, individual plants within a population or species within a community). Although the mechanisms responsible for variation in fruit shape clearly differ at different taxonomic levels, the selective forces operating at all levels – gape-width constraints and fruit preferences of seed disperses – should be similar in direction and set upper limits on fruit or seed diameter as a function of fruit or seed length. Allometric slopes may be different at distinct taxonomic levels not only because of statistical artifacts but also because factors such as developmental constraints, maternal effects, variation in pollen donors, selection among genotypes, speciation, species selection and shifting disperser assemblages contribute differentially to variance in fruit size and shape at different taxonomic levels.

Several questions remain about the role of avian seed dispensers as selective agents in the evolution of fruit shape. First, it must be demonstrated that fruit size, shape and allometric relationships are heritable characters within species in nature as they have been shown to be in several agricultural varieties (e.g. Sinnott, 1936, 1958; Paterson *et al.*, 1991). Parent–offspring regressions of *Ocotea tenera* trees grown in common gardens suggests that a variety of morphological traits have a genetic basis (Wheelwright, 1993). In the related avocado (Lauraceae, *Persea americana*), fruit and seed size are highly heritable (Bergh, 1976). Genetic correlations between characters must also be understood to interpret the response to selection on any particular trait (Primack, 1987). Second, the phylogenetic relationships of different species must be elucidated to avoid the potential biases of statistically non-independent species. Moreover, the evolutionary history of plant taxa and their reproductive structures needs to be understood to reconstruct long-term changes in fruit form under possible selection by different seed dispersers (Janzen and Martin, 1982; Herrera, 1985). From the limited fossil record, it is quite clear that at least some lauraceous fruits (e.g. *Laurus macrocarpus*) were elongate rather than spherical as long ago as 97 million years (Dilcher, 1979), but no one has described the allometry of fruit form over evolutionary (vs ontogenetic) time. The differences between the fruit shape patterns that we found in a neotropical forest and those in Malawi (Dowsett-Lemaire, 1988) and Spain (Herrera, 1992) may be due to geographic differences in phylogeny and in the interactions between plants and their seed dispersers during their evolutionary history. Third, field and laboratory experiments need to be performed to measure birds' handling and preference of fruits that vary in size and shape and the effects of their fruit choices on patterns of seed dispersal and seedling survival. The model of adaptive allometry assumes that birds benefit by a negatively allometric relationship between fruit length and diameter and by upper limits to fruit diameter and that birds can and do discriminate among fruits, individual trees and species on the basis of such allometric patterns and it assumes that plants benefit by avian seed dispersal. Finally, a key test of the model of disperser-mediated selection on fruit shape would be to compare allometric relationships of fruit diameter and length in families in which there is a range of dispersal mechanisms, such as the palm family (Arecacae), which includes bird-dispersed, mammal-dispersed and water-dispersed species or the rose family (Rosaceae), which includes bird-dispersed, mammal-dispersed and wind-dispersed species.

Howe (1986) was pessimistic about using fruit traits to distinguish dispersal syndromes, calling them 'at best, marginally predictive'. One of the aims of this paper has been to draw attention to

an under studied aspect of fruits, their shape and to suggest that fruit shape may in fact bear a predictable relationship to fruit size in bird-dispersed plants. Although we do not wish to overemphasize adaptive explanations for negative allometry in fruit shape at the exclusion of alternative interpretations, we propose several specific hypotheses to test the proposition that fruit shape reflects adaptation to different dispersers. We also wish to encourage the application of allometry in comparative studies in plant biology, where it has long been neglected. Traditionally reserved for describing morphological relationships among plant parts and crop yields (Bidabe, 1978; Hamid and Grafius, 1978; Alaback, 1986), allometry in plant biology has recently been applied to biomechanics (Niklas, 1991) and patterns of tissue allocation in the context of competition (Weiner and Thomas, 1992). Allometry may also allow us to make sense of the diversity of form in fruits, seeds and other plant structures at different taxonomic levels.

Acknowledgements

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