Ecological correlates of single-seededness in a woody tropical flora

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Summary. A reduction in seed number per fruit is recognized as a common evolutionary trend among flowering plants. In order to evaluate the ecological role of single-seededness and its possible adaptive significance, we used van Roosmalen's (1985) descriptions of fruits for woody species in the Guianan flora to identify fruit and seed characters and dispersal syndromes associated with the single-seeded trait. We coded the following characters: seed number (one seed or more than one seed), fleshiness (dry or fleshy), dehiscence (dehiscent or indehiscent), dispersal syndrome, seed size (length), and fruit size (length). We ordered the data in a multi-dimensional contingency table and used maximum likelihood logistic regression to identify traits significantly correlated with single-seededness. Seed size and fruit size were treated as quantitative variables. Indehiscence and endozoochory are positively associated with single-seededness, with indehiscence contributing most to the best-fit model. Fruit size and seed size are also important with the probability of single-seededness generally increasing with seed size and decreasing with fruit size, although a (fruit size) × (seed size) interaction term is significant. Dry fruits are positively associated with single-seededness and dispersal by synzoochory or myrmecochory negatively associated when the full data set is examined, but neither parameter is significant in two models constructed to remove effects of phylogeny. A nested ANOVA revealed that most variation occurs below the family level for almost all of the traits considered, with the exception of the dry vs. fleshy trait for which there is no variation within genera. We argue that the strong association between indehiscence and single-seededness suggests selective advantages for single-seeded dispersal units but acknowledge that energetic trade-offs between seed number and seed size probably also occur. We suggest that the post-dispersal fates of seeds – especially those deposited in clumps by endozoochory – should be examined with the idea of identifying selective pressures on seed number per fruit.

A reduction in seed number per fruit is recognized as a repeated evolutionary trend among flowering plants (Stebbins 1967; Cronquist 1968). Reduced seed numbers are achieved either by the production of fewer ovules or by a regular pattern of ovule abortion; strikingly, the latter almost always results in a single seed (Casper and Wiens 1981; Uma Shaanker et al. 1988).

Several possible adaptive explanations exist for reduced seed number in general and the evolution of single-seededness in particular. Fewer seeds per fruit may permit a compensatory increase in seed size or number of fruits (Adams 1967; Marshall et al. 1985). In species with wind-dispersed fruits, reduced seed numbers may increase dispersal distance. An apparent association between indehiscent fruits or other indehiscent dispersal units (e.g. carpels) and single-seededness may reflect past selective pressure from sibling competition generated by more than one seed germinating in the same place (Cronquist 1968; Casper and Wiens 1981; Casper 1990). Although few empirical studies have addressed the significance of single-seededness, experiments have demonstrated sibling competition in two-seeded dispersal units of *Cryptantha flava* (Casper 1990) and enhanced dispersal by wind of single-seeded, compared with multi-seeded, fruits of *Lonchocarpus pentaphyllus* (Augspurger and Hogan 1983) and *Platypodium elegans* (Augspurger 1986). Less severe seed predation in single-seeded fruits has also been reported for some species (Herrera 1984).

We were interested in determining what fruit and seed characters and dispersal modes are associated with single-seededness, regardless of how it is achieved, and in evaluating the relative importance of the associations. By identifying these associations we hoped to gain insight into the ecological role of single-seededness and the most likely adaptive explanations for its evolution. For instance, single-seededness might be more common in spe-

cies with a particular dispersal syndrome. If post-dispersal sibling competition has been an important selective force, then there should be a strong association between single-seededness and indehiscence. Our approach also evaluates how much fruit size and seed size contribute to the probability that a fruit is single-seeded.

We constructed a multi-dimensional contingency table of fruit and seed characters and dispersal syndromes described by van Roosmalen for species in the woody flora of the Guianas (van Roosmalen 1985) and applied logistic regression to examine the relationships between seed number per fruit and all other characters simultaneously. The procedure allows us to compare the relative strengths of associations and controls for associations among explanatory variables (see discussion in Muenchow 1987). Consideration of a tropical, woody flora assured taxonomic diversity and eliminated certain large herbaceous groups (e.g. grasses) that are uniformly single-seeded.

Methods

Data collection – For each species described by van Roosmalen (1985), we scored dispersal syndrome, the lengths (in cm) of seeds and fruits, and the following dichotomous fruit characters: seed number (one vs. more than one seed), dry vs. fleshy, and dehiscent vs. indehiscent. van Roosmalen recognized seven dispersal syndromes: hydrochory, anemochory, autochory (mechanical dispersal), endozoochory, epizoochory, synzoochory (scatter-hoarding or animals dropping seeds after carrying them for some distance), and myrmecochory. We combined hydrochory ($n = 20$) with anemochory ($n = 83$) and synzoochory ($n = 18$) with myrmecochory ($n = 23$) in our classification to reduce the number of parameters and increase sample size per cell. These lumpings did not qualitatively change the eventual model. The lengths of fruits and seeds were divided into 10 classes (0–0.3, 0.3–0.69, 0.7–0.99, 1.0–1.9, 2–2.9, 3–4.9, 5–6.9, 7–8.9, 9.0–11.0, and >11.0 cm).

In most cases van Roosmalen's literal descriptions were used in scoring characters, but for our purposes some interpretation of dehiscence was necessary. Any fruit that fails to open easily and release seeds was classified as indehiscent. This included fleshy fruits with simple, stony endocarps (pyrenes). For the few species in which the stony endocarp splits into more than one pyrene, the fruit was considered dehiscent if each pyrene contains only one seed but indehiscent if each pyrene contains more than one seed. Because strictly fleshy pericarps are generally digested by frugivores and otherwise split or rot easily, berries were classified as dehiscent. In some cases, interpretation of fruit type did not correspond to the usual botanical definition of a fruit. For example, the fleshy receptacle of figs, which encloses many one-seeded drupes, was classified as a multi-seeded dehiscent fruit because it functions as a berry. Multiovulate fruits described by van Roosmalen as usually producing one seed were considered single-seeded.

Only 577 of the 1705 species coded provided complete records and were used in the analysis. These represent 273 genera, 63 families, and 29 orders. In the data set used, 143 species (24.8%) are single-seeded. None of the 577 is epizoochorous. Descriptions of the omitted species usually lacked seed size, which proved to be an important variable in our final model.

Statistical methods. Data were ordered in a multi-dimensional contingency table and analyzed by logistic regression techniques (SAS version 5.18 CATMOD procedure; SAS Institute, Inc. 1985) to examine relationships between seed number and all other variables simultaneously and to control for associations among the explanatory variables. The technique permits use of qualitative data alone or in combination with continuous or discrete quantitative variables. The model thus developed predicts logit-transformed probabilities. In this case the predicted variable is

$$F = \log_e(P(\text{single-seeded}))/(P(\text{multi-seeded}))$$

A typical model for qualitative data resulting from this procedure is of the form

$$F_{ijk} = \tau + \chi^{A}_{i} + \chi^{B}_{j} + \chi^{C}_{k} + \chi^{AB}_{ij} + \chi^{AC}_{k} + \chi^{BC}_{jk} + \chi^{ABC}_{jk}$$

Here τ is analogous to an intercept and αA_i is a term (parameter estimate) for the effect of category i of variable A. Terms with multiple sub- and super-scripts represent interactions. A predicted logit is the sum of the intercept and the appropriate parameter estimates from the set of possible parameter estimates for each explanatory variable. Variables whose classes can be meaningfully ordered, such as seed size, are modelled as linear (or higher order) functions of the variable values. The fruit size and seed size values used were the midpoints of the size classes. The "midpoint" of the class of fruits larger than 11.0 cm was arbitrarily set at 15.0 cm. Parameters were estimated by maximum likelihood methods, which are robust to empty cells in the contingency table data (Bishop et al. 1975).

Model-building involves fitting a series of models to the data, each one containing a term (an explanatory variable or interaction) not included in the last. Each model has a goodness-of-fit statistic (with associated degrees of freedom), and the difference between these for two successive models is used to test the significance of adding the variable (Everitt 1977). A model is considered sufficient when no other possible terms significantly improve its fit. The signs and magnitudes of the fitted parameter estimates indicate the relative contributions of different explanatory variables and interactions to the predicted logit. The set of parameter estimates for each qualitative variable sums to zero, but parameters for numerical variables do not.

Phylogenetic effects. To check whether phylogenetic effects seriously biased our results, the model was run omitting the species in the six most speciose families: Annonaceae, Apocynaceae, Bignoniaceae, Caesalpiniaceae, Euphorbiaceae and Papilionaceae. The remaining 280 species represent 57 families. In addition, the model was repeated using a single species per genus. For genera with more than one species, a species was selected at random. This procedure eliminated 304 species. A Model II nested ANOVA (PROC NESTED; SAS Institute, Inc. 1985) was used to examine the percentage of variation occurring at the species, genus, and family level for each trait.

Results

All variables made highly significant contributions ($p < 0.001$) to the model constructed from all 577 species (Table 1). A positive parameter estimate (Table 1) indicates an increased likelihood of single-seededness in fruits with that character. With the effects of other variables controlled, indehiscent fruits are much more likely than dehiscent fruits to be single-seeded, while dry fruits are somewhat more likely than fleshy fruits to be so. Of the four dispersal syndrome categories, endozoochory is positively associated with single-seededness, while the pooled category of myrmecochory and synzoochory is less strongly negatively associated.

For the quantitative variables, a cubic function was fit to seed size:

$$3.65 \ (\text{seed size}) - 1.08 \ (\text{seed size})^2 + 0.05 \ (\text{seed size})^3$$

Table 1. Parameter estimates for best-fit model. Values in parentheses are for the model using only one species per genus

Variables	Magnitude	Standard Error	p-value
Intercept	−1.750 (−0.750)	0.494 (0.690)	0.001 (NS)
Categorical variables			
Dehiscence:			
Indehiscent	+1.751 (+2.030)	0.245 (0.398)	0.001 (0.001)
Dehiscent	−1.751 (−2.030)	0.245 (0.398)	0.001 (0.001)
Fleshiness:			
Fleshy	−0.478 (−0.049)	0.138 (0.230)	0.001 (NS)
Dry	+0.478 (+0.049)	0.138 (0.230)	0.001 (NS)
Dispersal syndrome:			
Anemo-/hydrochory	−0.600 (−0.446)	0.401 (0.524)	NS (NS)
Autochory	+0.113 (−0.329)	0.399 (0.547)	NS (NS)
Endozoochory	+1.504 (+1.157)	0.280 (0.418)	0.001 (0.01)
Synzoo-/myrmecochory	−1.017 (−0.383)	0.504 (0.602)	0.04 (NS)
Quantitative Variables			
Seed size:			
Seed size	+3.653 (+3.816)	0.613 (0.961)	0.001 (0.001)
(Seed size)^2	−1.084 (−1.301)	0.219 (0.361)	0.001 (0.001)
(Seed size)^3	+0.047 (+0.056)	0.011 (0.017)	0.001 (0.01)
Fruit Size	−0.795 (−0.944)	0.160 (0.243)	0.001 (0.001)
Seed size × fruit size	+0.213 (+0.288)	0.05 (0.087)	0.001 (0.001)

Table 2. Parameter estimates for different fruit size (cm) and seed size (cm) combinations, calculated by summing the values obtained after substituting the particular fruit size and seed size into the functions in Table 1. Superscripts indicate numbers of species with each fruit size/seed size combination

Ssize	Fsize									
	0.15	0.5	0.85	1.5	2.5	4.0	6.0	8.0	10.0	15.0
0.1	$+0.409^{2}$	$+0.142^{12}$	-0.125^{13}	-0.621^{12}	-1.384^{5}	-2.528^{4}	$-^{0}$	-5.581^{1}	$-^{0}$	$-^{0}$
0.5		$+1.217^{9}$	$+0.976^{28}$	$+0.529^{18}$	-0.160^{15}	-1.193^{14}	-2.570^{7}	-3.947^{1}	-5.324^{2}	-8.766^{1}
0.85			$+1.829^{12}$	$+1.429^{41}$	$+0.816^{17}$	-0.105^{18}	-1.333^{6}	-2.561^{4}	-3.789^{6}	-6.859^{13}
1.5				$+2.484^{30}$	$+2.009^{52}$	$+1.295^{48}$	$+0.344^{11}$	-0.607^{8}	-1.558^{4}	-3.935^{22}
2.5					$+2.428^{13}$	$+2.034^{34}$	$+1.509^{14}$	$+0.948^{14}$	$+0.459^{9}$	-0.853^{24}
4.0						$+0.472^{9}$	$+0.586^{5}$	$+0.700^{10}$	$+0.814^{6}$	$+1.099^{27}$
6.0							$-^{0}$	-3.198^{1}	-2.232^{4}	$+0.183^{9}$
8.0								$-^{0}$	$-^{0}$	-2.709^{2}
10.0									$-^{0}$	-5.345^{2}
15.0										$+3.832^{1}$

while a linear function, with a coefficient of −0.795, sufficed for fruit size. An interaction between fruit size and seed size ($p < 0.001$) introduced the term 0.213 × (seed size) × (fruit size) into the predicted logit (Table 1). One can calculate the contribution of a particular seed size, fruit size combination to the probability that a fruit is single-seeded by summing the cubic function of seed size, the linear function of fruit size, and the interaction term (Table 2). Although the effects of seed size and fruit size cannot be completely disentangled, the probability of being single-seeded generally increases with seed size and decreases with fruit size. The (seed size) × (fruit size) interaction apparently occurs because fruits with seeds larger than 4.0 cm are somewhat more likely to contain multiple seeds than the same-sized fruits with slightly smaller seeds. Interactions involving second and third order seed size terms did not improve the fit

significantly. With the inclusion of a (seed size) × (fruit size) interaction, no interactions involving other variables were significant, although (seed size) × (dispersal syndrome) was suggestive ($p = 0.055$). Overall goodness-of-fit of the model was excellent [maximum likelihood statistic = 168.25, 162 d.f., $p = 0.352$; see Everitt (1977)].

Running models from reduced data sets constructed by using only one species per genus or by deleting the six largest families resulted in two changes. The fleshy vs. dry fruit character and the synzoochory/myrmecochory dispersal category are not significant in either model. Otherwise, the parameter estimates for all the variables changed slightly. Since the two models from reduced data sets are nearly identical, only the model using one species per genus is presented in Table 1. The ANOVA performed to examine character variabilities revealed that only the fleshy vs. dry character and fruit size exhibit greater

Table 3. Percentage of variance contributed by taxonomic level calculated by nested ANOVA for all species in data set

Trait	Family (df = 62)	Genera (df = 210)	Species (df = 304)
Seed number	23 3	35 6	41 1
Dehiscence	25 5	65 4	9 0
Fleshiness	60 3	39 7	0
Dispersal syndrome	30 7	65 6	3 7
Seed size	25 0	53 1	22 0
Fruit size	52 9	27 1	20.3

variation among families than among lower taxonomic levels (Table 3). Apparently, no variation exists among congeneric species for the dry versus fleshy trait. Most variation in other characters occurs among genera, although variation below the genus level is underestimated for fruit size and seed size because size variation within species was not included

The analysis was also repeated using 25.0 cm as the midpoint of the largest fruit size class in order to test sensitivity to our original arbitrary choice of 15.0 cm. Again, parameter values changed but not trends or conclusions

Discussion

Our analyses indicate that indehiscence is the most important qualitative trait predicting single-seededness, corroborating the pattern recognized by taxonomists (Stebbins 1967; Cronquist 1968). One can imagine at least two evolutionary scenarios for this association. Indehiscence may have evolved first because the fruit developed into a specialized dispersal unit and/or because a thickened, mature ovary wall affords more protection than the seed coat alone. Single-seededness might then have evolved as a way of avoiding sibling competition resulting from more than one seed germinating in the same location (Cronquist 1968; Casper and Wiens 1981; Casper 1984). On the other hand, single-seededness could have arisen first, possibly as a trade-off with some other component(s) of seed yield, such as seed size (Adams 1967; Marshall et al. 1985), and indehiscence might have evolved secondarily. Even with the latter scenario, an indehiscent ovary wall could still serve an important protective function during and/or after dispersal.

That size attributes also contribute to the likelihood that a fruit is single-seeded is verified by our models. The parameter estimates for some combinations of fruit size and seed size add more predictive value than whether or not a fruit is indehiscent. Undoubtedly, these results in part reflect design constraints (e.g. small fruits cannot have many large seeds), but evolutionary trade-offs between seed number per fruit and seed size cannot be discounted.

Still, we believe that post-dispersal selective pressures are pervasive. Supporting this idea is the observation that among species with indehiscent, multi-ovulate ovaries,

ovule abortion typically results in mostly single-seeded dispersal units (Casper and Wiens 1981; Uma Shaanker et al. 1988). It is not clear why simple trade-offs with other components of seed yield should so often result in only one seed.

Although dispersal syndrome proved less important than dehiscence vs. indehiscence in our models, a positive correlation with one dispersal syndrome was consistently significant. Proportionately more endozoochorous fruits are single-seeded. This association probably indicates a large representation of drupes, and the stony endocarp could provide important protection during handling and ingestion by animals. Pulp to seed ratio might also be important in how frugivores choose fruits (e.g. Levey and Grajal 1991). About 35% of the endozoochorous species in our data set have dry fruits, but many of them dehisce to expose multiple seeds whose fleshy seed coats (testae), or dry mimics of fleshy seed coats, attract dispersers.

That endozoochory, which can result in the dissemination of seeds in clumps, is positively associated with single-seededness seems to weaken our argument that sibling competition is an important selective force in the evolution of the single-seeded trait. However, additional factors may reduce sibling competition in endozoochorous species. The extent that seeds from one or more than one fruit are deposited in clumps largely depends on the frugivore, and different frugivore species may handle the same fruits in different ways (Snow 1971; Howe 1986; Howe 1989; Loiselle 1990). Howe (1989) reports that small fruit-eating birds and bats often scatter seeds by regurgitation or defecation. He also concludes that non-flying mammals are more likely to accumulate seeds in their guts and, therefore, defecate them in clumps than are birds, who must minimize the mass of indigestible material they carry. Howe suggests that, in general, the probability of seed clumping increases with frugivore body size and decreases with seed size. Loiselle (1990) examined droppings of five frugivorous bird species in La Selva, Costa Rica, and found that among six different plant species, seed number per dropping correlated highly with seed number per fruit. Thus, even in endozoochorous systems, single-seededness may reduce the number of seeds per dispersal event. The ultimate density of seeds also depends on the amount of secondary dispersal by rain or other animals. While secondary dispersal seems likely, little information is available regarding just how much occurs. It would seem that seeds held together in an indehiscent fruit are far less likely to be scattered secondarily than those deposited in feces or regurgitated in clusters.

The lack of association between single-seededness and abiotic dispersal modes is also revealing. Dispersal by wind or water is not especially likely (or unlikely) to be achieved via single-seededness. Obviously, both entire fruits and individual seeds, with the appropriate morphology, can disperse by these means. Wind dispersal, for example, is achieved by flattened indehiscent pods in some members of the Papilionaceae but by individual seeds in the Bignoniaceae. Furthermore, we suggest that because the association between indehiscence and single-seededness is generally important, single-seededness in

wind-dispersed fruits is not necessarily related to increasing dispersal distance. Even in wind-dispersed species, single-seededness may serve primarily as a means of avoiding sibling competition following germination Field studies of wind-dispersed *Cryptantha flava* support this idea (Casper and Grant 1988; Casper 1990).

Comparative methods that analyze sets of species character values as this study does have been criticized on the grounds that species are not statistically independent (e.g. Felsenstein 1985): a group of taxa may share a trait, or combination of traits, because of common ancestry rather than because the trait is adaptive. Associations (interpreted as evidence for adaptive significance) of the kind sought in this study may, in certain data sets, be overcounted or even spurious as a result. A variety of techniques have been proposed to subtract the effects of phylogeny from patterns of character covariation (reviewed by Harvey and Pagel 1991; see also Huey and Bennett 1987; Maddison 1990). The complete phylogeny of the diverse taxa considered here is, of course, unavailable.

We chose to work directly with species values and examine the data for phylogenetic effects through other means. We deliberately selected a flora that encompassed a broad taxonomic range (63 families in 29 orders) because we felt that in such a data set it was unlikely any single clade could strongly influence the results. Associations resulting from phylogeny, unlike those due to adaptation, would be expected to be in different directions in different clades, and would be averaged out over many clades. The data set also averaged very few (2.1) species per genus which we thought should reduce inflation in error degrees of freedom. The high variation found at the species and genus levels for most traits suggests that phylogenetic constraints should not seriously affect the results. We looked for phylogenetic effects by examining changes in the model after deleting the six largest families and after using only one randomly selected species per genus.

The different approaches indicate that the dry vs. fleshy trait and the synzoochory/myrmecochory dispersal category are the only model parameters that might be seriously biased by phylogenetic effects. Dry fruits are positively associated with single-seededness when all 577 species are included in the model, but the trait makes no significant contribution when each genus is represented by a single species or when the six largest families are deleted. There is no variation among congeneric species for the fleshiness trait, which probably reflects its use as a taxonomic character. Together these results suggest that a few speciose genera (probably within the largest families) are responsible for the significant fleshiness trait in the full data set. Whether phylogenetic effects produce the negative association between synzoochory/myrmecochory dispersal category and single-seededness is less clear. This category was only marginally significant in the original model ($p = 0.04$), and the use of the reduced data sets resulted in its representation by small sample sizes (e.g. $n = 24$ for the second model presented in Table 1). These models constructed from reduced data sets also confirm that a strong association exists between single-

seededness and indehiscence, and that correlations with dispersal syndromes are less important

The finding that most of the variation in seed size occurs at the genus level contradicts observations of Hodgson and Mackey (1986) who describe less than expected intra-family variation in seed mass within a local flora in central England. They relate the pattern to taxonomically-linked constraints on variation in some other traits, including ovule number, and claim that the adaptive radiation of major taxa may have been restricted by these suites of characters. Clearly our studies differ. They considered only dicotyledons, excluding trees and shrubs greater than one meter in height, while we restrict our analysis to woody species. Mazer (1990), using selected genera represented in the flora of the Indiana dunes, found that genus explained significant variation in seed mass when ecological factors were also considered.

We also recognize predation on seeds as another potentially important factor in the evolution of seed number per fruit. Depending on the system, seed predators may select for either multi- or single-seeded fruits (Bradford and Smith 1977; Garrison and Augspurger 1983; Herrera 1984). While our data do not address seed predation, it must be considered when evaluating the importance of fruit seededness for any particular species.

In summary, we have interpreted the strong association between single-seededness and indehiscent fruits in our model as evidence that single-seeded dispersal units have evolved partly as a consequence of selective pressures operating during and after dispersal. We have argued that sibling competition is one of those factors. Nevertheless, the possibility of dispersal, especially endozoochory, resulting in clumped seed distributions despite the occurrence of single-seeded fruits deserves additional consideration. Several questions are immediately suggested: To what extent does secondary dispersal scatter intact seeds after the initial dispersal event? What proportion of clumped seeds germinate? As Howe (1989) suggests, are seedlings of some plant species better adapted to living in clumped distributions than others? And as a corollary, are seedlings generated by multi-seeded endozoochorous fruits more likely to end up and survive in clumped distributions than those from single-seeded fruits? Further examination of post-dispersal fates of seeds – across different dispersal modes – with the idea of pursuing possible selective pressures on seed number per fruit is obviously needed.

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