

Nutritional Dimorphism in New Guinea Dioecious Figs

George D. Weiblen¹

Bell Museum and Department of Plant Biology, University of Minnesota, 250 Biological Sciences Building, 1445 Gortner Avenue, Saint Paul, Minnesota 55108, U.S.A.

Silvia B. Lomascolo²

Department of Zoology, PO Box 118525, University of Florida, Gainesville, Florida 32611, U.S.A.

Ryoko Oono

Department of Plant Biology, University of Minnesota, 250 Biological Sciences Building, 1445 Gortner Avenue, Saint Paul, Minnesota 55108, U.S.A.

and

Elizabeth R. Dumont

Department of Biology, Morrill Science Center, 611 North Pleasant Street, University of Massachusetts, Amherst, Massachusetts 01003, U.S.A.

ABSTRACT

The life history of figs (*Ficus*, Moraceae) involves pollination by specialized insects and seed dispersal by vertebrate frugivores. This three-way interaction raises the possibility of conflict between pollinators and seed dispersers over fig resources. The conflict might be mediated in dioecious figs by the segregation of inflorescences with specialized male and female sexual functions, termed gall figs and seed figs, on separate trees. In dioecious figs, pollinators are intimately associated with gall figs, whereas vertebrate frugivores prefer seed figs and disperse the seeds they contain. Optimal foraging theory predicts that frugivore preference for ripe seed figs is associated with superior nutritional quality when compared to gall figs. We tested this prediction comparing nutrient and mineral properties of ripe figs in 12 functionally dioecious and two monoecious species from New Guinea. Analyses of variance indicated that gall figs contain more fiber and minerals, whereas seed figs contain significantly more carbohydrates and fat. Fruit bats, the primary dispersers of dioecious figs in New Guinea, prefer carbohydrate-rich diets, and from this perspective, seed figs offer a greater nutritional reward than gall figs. More nondigestible fiber in gall figs than seed figs would appear to discourage frugivory. Parallel differences between ripe gall figs and seed figs occur in each independent dioecious lineage whereas nutritional content in monoecious figs is more similar to seed figs. This suggests that sexual dimorphism in nutritional quality might be adaptive and associated with the maintenance of functional dioecy in figs.

Key words: dioecy; fig; frugivores; minerals; nutrients; Papua New Guinea.

FIG TREES (*FICUS*, MORACEAE) ARE HIGHLY DEPENDENT ON MUTUALISMS for the propagation of gametes and offspring. Seed dispersal involves vertebrate frugivores and pollination involves specialized seed-predating wasps (Agaoninae, Hymenoptera). Fig pollination is an obligate mutualism among the best-known examples of specialization in tropical ecology (Cook & Rasplus 2003, Herre *et al.* 2008). Each species of fig is pollinated by one to several species of fig wasp (Molbo *et al.* 2003). Female wasps enter the flower-filled receptacle through a small opening at the apex. In exchange for pollination services, some flowers are galled by ovipositing fig wasps. Each larval fig wasp occupies an individual fig ovule and mating occurs between adults occupying the same inflorescence. Females collect pollen from male flowers before flight and the search for receptive figs in which to oviposit, pollinate, and complete the cycle. In contrast to the specificity of fig–pollinator interactions, a broad range of vertebrate frugivores may disperse the

seeds of any fig species. Figs are important resources for herbivores and frugivores in tropical forests around the world (Basset *et al.* 1997), and are considered keystones in some ecosystems (Terborgh 1986, Kissling *et al.* 2007; but see Gautier-Hion & Michaloud 1989, Borges 1993). Despite the general attractiveness of figs as fruit, suites of characters including fig color, size, presentation, and odor attract different subsets of frugivore communities (Kalko *et al.* 1996, Korine *et al.* 2000, Shanahan *et al.* 2001).

The three-way interaction of figs, pollinators, and dispersers widens the potential for evolutionary conflict between pollination and dispersal (Dumont *et al.* 2004). For example, frugivore consumption of figs sheltering potential pollinators could negatively affect the male component of plant fitness thus selecting traits that discourage frugivores. The conflict between pollination and dispersal may be mitigated by either temporal or spatial segregation of pollen and seed dispersal according to the breeding system of the fig, whether monoecious or functionally dioecious.

Monoecy is the ancestral breeding system in *Ficus* and is pan-tropical in distribution (Weiblen 2000). Each monoecious fig produces seeds, galls, and pollen but the ripening associated with frugivory is delayed until the pollen-bearing fig wasps have emerged

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¹Corresponding author; e-mail: gweiblen@umn.edu

²Current address: IADIZA – CCT Mendoza, CONICET, Ave Ruiz Leal s/n, CC 505, Mendoza 5500, Argentina

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from their galls and exited the fig. In this way, the interactions of pollinators and seed dispersers with monoecious species are separated in time (Janzen 1979).

In functionally dioecious species, male and female sexual functions are segregated on separate plants known as gall figs and seed figs. Dioecy appears to have evolved at least twice in *Ficus* and is restricted to the Paleotropics (Weiblen 2000, Jouselin *et al.* 2003, Rønsted *et al.* 2008). The rearing of fig wasps is generally confined to gall figs, where potential pollinators feed, mate, and collect pollen before seeking receptive figs. Young figs of each sex emit similar volatile cues that attract pollinators to both seed figs and gall figs (Grison-Pige *et al.* 2001, 2002) although not always with equal frequency (Patel *et al.* 1995, Weiblen *et al.* 2001, Dumont *et al.* 2004). Bracts enclosing the fig entomb visitors to both types, and, whereas eggs laid in gall figs give rise to the next generation of pollinators, eggs deposited in seed figs fail to develop. Gall figs nourish pollinator larvae and produce pollen, whereas seed figs deceive their pollinators, lack functional stamens, and produce only seeds.

It has long been held that frugivores prefer ripe seed figs to gall figs (Corner 1940). Higher visitation rates by birds to seed figs than gall figs are known from the field (Lambert 1992) and choice experiments demonstrated a strong preference by fruit bats for the former (Dumont *et al.* 2004). Although gall figs are occasionally consumed by bats (Phua & Corlett 1989), they typically have low removal rates and often accumulate on the ground under the parent tree after the emergence of the fig wasps (Corner 1940, Lambert & Marshall 1991).

Frugivore preference for seed figs reduces potential conflicts between the relative fitness contributions of pollination and seed dispersal, as well as competition between pollinators and dispersers. Similarity of gall figs and seed figs at flowering time compared with striking dissimilarity in fruit could be products of opposing selection pressures imposed by pollinators and frugivores at different life history phases (Dumont *et al.* 2004).

Patel and McKey (1998) predicted that frugivore visitation to ripe seed figs is associated with characteristics that increase attractiveness. This is supported by Lambert's (1992) observation that ripe seed figs of three dioecious species in Malaysia were brighter, softer, smaller, and therefore accessible to a broad range of frugivores than were ripe gall figs. Dumont *et al.* (2004) reported that seed figs in *Ficus pungens* were larger, sweeter, fattier, more brightly colored, more fragrant, and lower in nondigestible fiber (NDF) than gall figs. Volatile compounds that attract mammalian dispersers to seed figs and repel them from gall figs have also been documented (Borges *et al.* 2008). Here, we examine the prediction that differences in nutritional quality between fig sexes are consistent with the attractiveness of seed figs over gall figs. We report differences in the nutritional quality of gall figs and seed figs in populations of 12 dioecious species and two monoecious species from the island of New Guinea (Fig. 1). This sample includes the ancestral monoecious condition and each *Ficus* lineage, subgenera *Sycomorus* and *Ficus*, in which dioecy evolved (Weiblen 2000, Berg 2003, Jouselin *et al.* 2003). This study is the first to identify predictable differences between ripe seed figs and gall figs in nutrient content and mineral composition. Although the precise conditions favoring

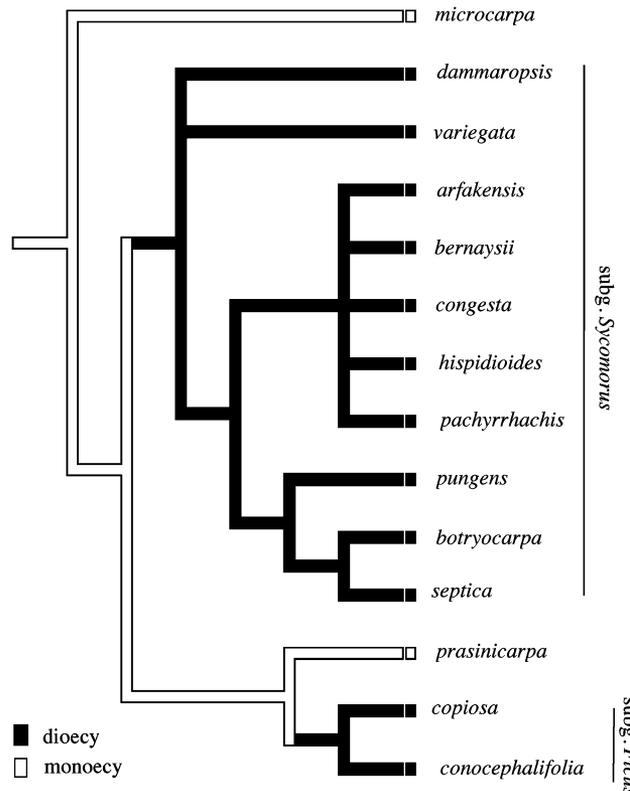


FIGURE 1. Molecular phylogeny and ancestral breeding systems of *Ficus* included in this study. Phylogenetic relationships are based on parsimony analysis of the internal transcribed spacer (ITS) region as described in Weiblen (2000). Monoecy is the ancestral condition in the genus and our sample includes two independent lineages of dioecious figs, the subgenera *Ficus* and *Sycomorus*.

the origin of dioecy may never be known (Harrison & Yamamura 2003), we argue that the observed differences are integral to the maintenance of dioecy in figs.

METHODS

Ripe figs were collected in primary and secondary lowland rain forests near the villages of Baitabag (5°08' S, 145°147' E) and Ohu (5°114' S, 145°141' E) (Madang Province, Papua New Guinea). Vegetation at these sites includes a diverse community of more than 40 fig species. Sampling included species from each of the two dioecious lineages, particularly *Ficus* and subgenera *Sycomorus*, and representatives of their monoecious sister groups, section *Conosycea* and section *Urostigma* (Fig. 1). Figs were judged to be ripe when they detached from trees with a gentle pull. Seed figs of most species soften but remain intact when ripe, whereas those of *Ficus conocephalifolia* and *Ficus dammaropsis* rupture at the apex and extrude the gelatinous drupelets through the opening (ostiole). Ripe gall figs included in this study have relaxed openings that are further widened by emerging pollinators. Figs were processed *in situ* or transported on the day of collection to the New Guinea Binatang

Research Center at Nagada Harbour (Madang) where they were refrigerated. In all cases figs were measured, cleaned, and dried within 24 h.

We measured fig mass to the nearest 0.1 g and diameter to the nearest 0.1 mm in the dimension perpendicular to the axis of the stalk. We also measured puncture resistance in g/mm^2 using an agricultural fruit pressure tester fitted with a 3.2 mm diam plunger (McCormick Fruit Tech, Yakima, Washington). Toughness is a key factor mediating animal dispersal because bite forces set physical limits on the range of food items consumed by animals (Aguirre *et al.* 2003, Anderson *et al.* 2008). The average of three measurements of puncture resistance from each fruit was used in subsequent analysis, except for *F. dammaropsis*, where the hardness of both gall and seed figs exceeded the upper limit of our instrument ($500 \text{ g}/\text{mm}^2$).

Fruit bats commonly press macerated figs against the roof of the mouth with the tongue, swallow the juice, and expel the fibrous portion. Sugar content in fig juice was therefore recorded using a refractometer (% of carbohydrates in juice). Juice samples from single figs were filtered with cheesecloth before measurement. Approximately five male trees and five female trees were sampled for each dioecious population. Whole fig samples were dried in separate paper bags in an oven at $40\text{--}50^\circ\text{C}$. Ninety-five percent of samples for nutrient analysis were from individual trees, but in the case of trees bearing small crops (*e.g.*, *Ficus copiosa*), it was necessary to combine figs of the same sex from different trees.

Nutrient analyses were conducted by the California Animal Health and Food Safety Laboratory at Davis and the Nutrition Department at the Wildlife Conservation Society (Bronx, New York). Crude fat, crude protein, and NDF content of dried samples were ascertained using techniques recommended by the Association of Analytical Communities (Jones 1984). Briefly, crude fat was determined through petroleum ether extraction. Kjeldahl nitrogen was determined by digesting samples in sulfuric acid using a copper catalyst followed by steam distillation. Nitrogen was converted to crude protein by a factor of 6.25. NDF was obtained by boiling samples in neutral detergent, and rinsing away the soluble fraction to isolate cell wall components including hemicellulose, cellulose, and lignins. Soluble carbohydrate was obtained by water extraction and phenol reduction followed by a spectrophotometric assay with a sucrose standard (Strickland & Parsons 1972). The percentage of each dietary constituent was calculated against the dry weight of the sample.

Mineral analysis was conducted at the Laboratory of Large Animal Pathology and Toxicology, University of Pennsylvania. Samples of 0.5 g were placed into TeflonTM vials and digested with 5.0 mL of concentrated nitric acid at 90°C for 12 h. The samples were cooled to room temperature and the final volumes adjusted to 25 mL with water. Following centrifugation, the clear supernatants were analyzed by inductively coupled plasma atomic emission spectrometry (ICP-AES) with a power input of 1.175 kW. A swine feed sample with certified mineral values from the Association of American Feed Control Officials (9932-AAFCO) was analyzed to verify accuracy of the instrument. The concentrations of four elements were determined simultaneously for each fig sample by

ICP-AES (GBC Integra XM2) with argon gas as a carrier. The wavelength (nm) of the emission peaks for the elements were as following: Ca at 612.222, K at 769.896, Mg at 277.669, and P at 213.618.

Variation in four fresh fig traits, four nutritional components, and four minerals among individual trees in populations of 12 dioecious and two monoecious species was analyzed. In the case of dioecious populations, nutritional differences between seed figs and gall figs were evaluated by two-way analysis of variance (ANOVA) with species and sex as factors. Sequential Bonferroni correction was applied to test results to control for the probability of erroneously rejecting null hypotheses (Rice 1989). In cases where a significant species-by-sex interaction was detected, sequential Bonferroni-corrected *t*-tests were conducted to evaluate sex differences in particular species. In recognition of the possibility that seeds or galls might pass undigested through the guts of frugivores, we examined their relative contribution to overall fig nutrient and mineral content by separate assays of seeds, galls, and pulp in *Ficus hispidooides*. The pulp fraction included the fleshy wall of the receptacle surrounding the drupelets of seed figs, but not the gelatinous mesocarp that adheres to each seed and is consumed along with the pulp. It was not feasible to separate the latter component due to the large number and small size of drupelets in each fig combined with the difficulty of separating the mesocarp from each seed.

RESULTS

Sympatric dioecious fig species differed significantly in mass, diameter, hardness, and sugar content of juice (Table 1). Gall figs and seed figs also differed significantly in diameter, hardness, and sugar content within species but the direction and magnitude of differences depended on the species (Fig. 2). For example, gall fig diameter was significantly larger in *Ficus botryocarpa* and *F. copiosa*, whereas seed figs were larger in *F. pungens* and *Ficus septica* (Table S1). On the other hand, the percentage of carbohydrates in juice as measured by field refractometry was consistently higher in seed figs for five out of 11 species (Table S1). A significant species-by-sex interaction (Table 1) was due to substantial variation in the magnitude of the difference. More precise comparisons of soluble sugars are based on nutritional analysis (Table S2).

Dioecious *Ficus* showed pronounced and consistent nutritional differences between gall figs and seed figs in carbohydrate, fat, and NDF content. Soluble carbohydrates were always more abundant in seed figs, often 80–90 percent more so than in gall figs (Fig. 2). The difference between sexes was statistically significant and independent of variation among species (Table 1). Crude fat varied among species but was consistently more abundant in seed figs than gall figs, which contained significantly more NDF than seed figs. Protein content varied significantly among species but not among sexes (Table 1).

Content of four minerals was significantly higher in gall figs than in seed figs with calcium having the greatest mean difference between sexes (Fig. 2). There was significant interspecific variation in calcium content but the direction of the difference between sexes was the same in all species. Magnesium and phosphorus also

TABLE 1. Two-way analysis of variance results for fig traits in 12 dioecious *Ficus* species. Degrees of freedom (df), sum of squares (SS), F-statistics, and sequential Bonferroni-corrected P-values are reported for each trait. In cases of significant interaction between species and sex, sequential Bonferroni-corrected t-test results are reported in Table S1.

	df	SS	F-statistic	P-values
Diameter				
Species	10	83,961.6	863.1	< 0.01
Sex	1	164.4	16.9	< 0.01
Species × sex	10	1887.7	19.4	< 0.01
Mass				
Species	10	181,209.2	367.8	< 0.01
Sex	1	142.5	2.9	NS
Species × sex	10	10,777.2	21.9	< 0.01
Hardness				
Species	10	2,776,725.7	62.6	< 0.01
Sex	1	350,391.6	78.9	< 0.01
Species × sex	10	232,040.3	5.23	< 0.01
Sugar in juice				
Species	10	207.6	14.0	< 0.01
Sex	1	1365.4	918.2	< 0.01
Species × sex	10	283.0	19.0	< 0.01
Crude fat				
Species	11	294.2	6.0	< 0.01
Sex	1	268.3	60.8	< 0.01
Species × sex	11	56.7	1.5	NS
Crude protein				
Species	11	138.6	6.3	< 0.01
Sex	1	16.2	8.2	NS
Species × sex	11	28.4	1.3	NS
Fiber				
Species	11	690.1	0.8	NS
Sex	1	4346.1	59.3	< 0.01
Species × sex	11	1530.8	1.9	NS
Carbohydrates				
Species	11	2795.5	2.3	NS
Sex	1	13,011.7	119.4	< 0.01
Species × sex	11	1914.6	1.6	NS
Mg				
Species	11	251,207,004	24.4	< 0.01
Sex	1	71,775,668	76.6	< 0.01
Species × sex	11	17,846,823	1.7	NS
K				
Species	11	1,933,049,655	1.7	NS
Sex	1	3,953,027,670	38.7	< 0.01
Species × sex	11	99,996,182	0.9	NS
P				
Species	11	18,492,789	6.2	< 0.01
Sex	1	10,198,744	37.8	< 0.01
Species × sex	11	6,033,703	2.0	NS
Ca				
Species	11	3,495,653,016	8.6	< 0.01
Sex	1	1,539,133,891	41.9	< 0.01
Species × sex	11	465,820,550	1.1	NS

differed between the sexes in spite of substantial interspecific variation. Only potassium lacked significant variation among species (Table 1).

Interpretation of these results in light of frugivore dietary preference and the potential for seed dispersal depends on the extent to which the whole fig traits we measured are attractive and nutritive. Given that fig seeds typically pass through animal guts intact, it can be argued that their contribution to the nutrient content of whole figs is inaccessible to frugivores. When we examined the relative contribution of seeds, galls, and pulp to whole fig nutrient content, we found that the presumably inaccessible fraction differed among components (fiber, fat, etc.) and between sexes. For example, most of the fiber in seed figs and gall figs came from seeds or galls, 68 and 58 percent, respectively. Fiber can therefore be attributed primarily to the seed coat and secondarily to the fleshy receptacle that comprises the pulp. The greater overall fiber content of gall figs relative to seed figs (Fig. 2) reflects a more fibrous receptacle.

Fat content in whole gall figs was evenly divided between galls and pulp (receptacle) whereas seeds contained 67 percent of the fat in seed figs, a difference that can be attributed to the presence of endosperm. The predominance of soluble carbohydrates in the receptacle of both sexes (58% in gall figs and 64% in seed figs) confirmed field measurements of juiced figs (Table S1). That most protein was found not in pulp, but in galls (65%) or seeds (57%), is consistent with the incomplete release of fig wasps from the former and the presence of fig embryos in the latter.

Minerals were predominantly in the pulp fraction of whole figs, except phosphorus, which was evenly divided between galls and pulp in gall figs, and 60 percent in seeds of seed figs. Magnesium and calcium were similarly distributed between the digestible and indigestible fractions, with 61 and 69 percent in pulp, respectively. Potassium content was highly skewed toward the pulp fraction (80%) in seed figs and gall figs alike.

How nutritional properties of dioecious figs compare with monoecious species is also relevant to the interpretation of these results. We sampled *Ficus microcarpa* representing section *Conosycea* and *Ficus prasinicarpa* representing section *Urostigma* (Fig. 1). Carbohydrate content of ripe figs from these monoecious species was more similar to that of seed figs than to gall figs of dioecious species (Table S2). The same was true for monoecious fig protein, fat, and mineral content whereas fiber content was relatively high and comparable to that of gall figs.

DISCUSSION

Dioecious fig species exhibit substantial variation in nutritional quality among individual trees (Tables S2 and S3). Some variation is associated with sexual dimorphism, but much is not, as evidenced by standard deviations and the lack of statistically significant differences between sexes in protein content (e.g., Table S3). Nutritional variation among trees in populations raises the possibility that extremely local differences in plant resource availability and allocation could facilitate dispersal by influencing foraging behavior. J. R. Winklemann and F. J. Bonaccorso (pers. comm.) note that fruit bats sometimes abandon fig trees with abundant ripe fruit and fly

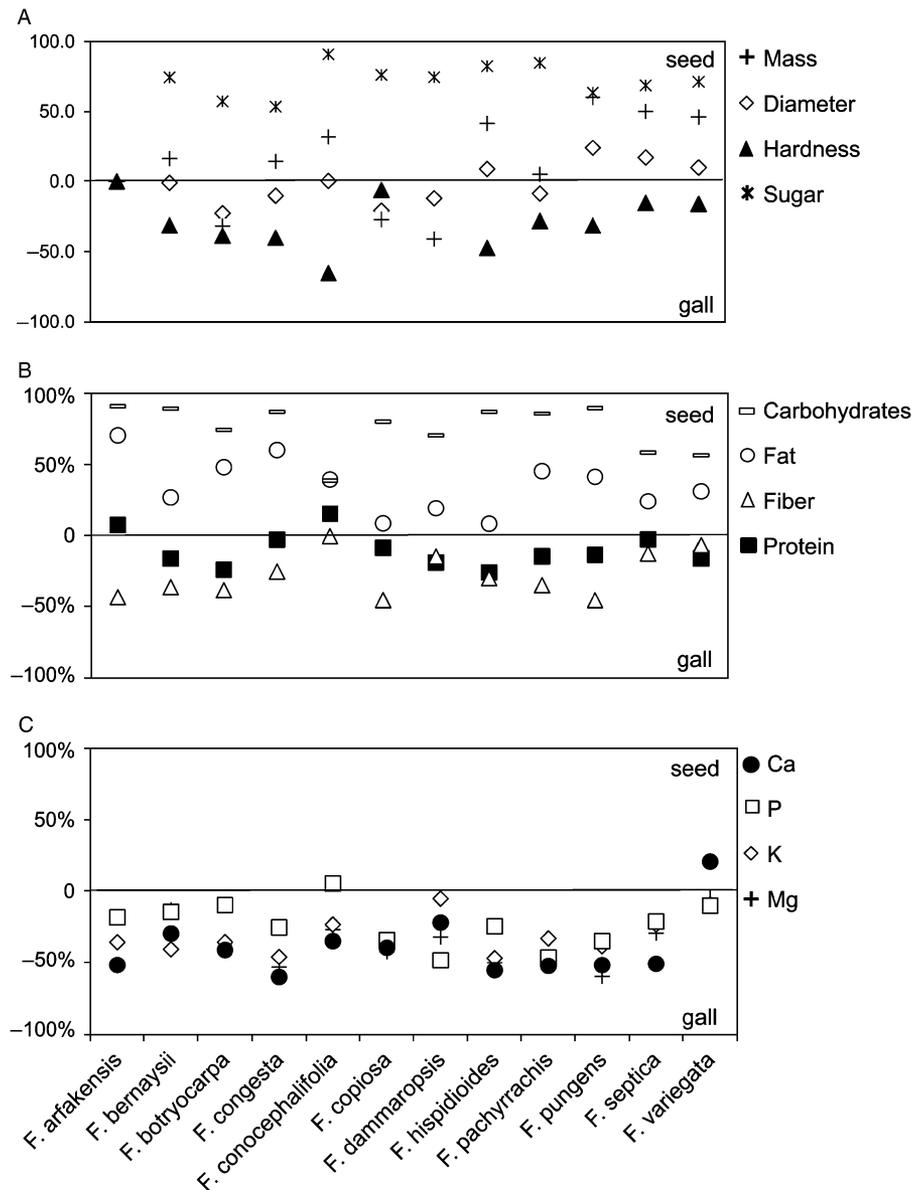


FIGURE 2. Relative differences between seed figs and gall figs in 12 species of dioecious *Ficus* for (A) physical measurements and sugar in juice, (B) nutrient content, and (C) mineral content. Percentages reflect differences between mean values for gall figs and seed figs relative to the larger of the two values. Positive percentages indicate higher mean values for seed figs whereas percentages less than zero reflect higher values for gall figs. Physical measurements were not available for *Ficus arfakensis*. Data are presented in Tables S1–S3.

several kilometers to other trees of the same species. Population genetic variation in nutritional quality and other attractive traits influencing rates of frugivore visitation and seed dispersal raises the possibility of adaptive trait evolution. We sampled too few trees per species to evaluate the significance of intrapopulation differences in nutritional quality of seed figs. Future investigation of the relationship between frugivore visitation to individual trees and nutritional quality would be intriguing, but here, we focus on evidence of sexual dimorphism.

Various bats, birds, and nonvolant mammals in New Guinea consume seed figs of the dioecious species we examined (Shanahan

et al. 2001, S. B. Lomascolo, pers. obs.). We set out to test the prediction that attractive and nutritional differences observed between the sexes in *F. pungens* (Dumont *et al.* 2004) are ubiquitous in dioecious figs. Whereas dioecious species vary substantially in many aspects (*e.g.*, fig diameter and mass), there is an overall sexual dimorphism between the greater soluble carbohydrate content of seed figs and the greater NDF content of gall figs. These differences are consistent with the relative attractiveness of seed figs to potential dispersers and they are observed in each of the two dioecious fig lineages (subgenera *Ficus* and *Sycomorvus*). That functional dioecy evolved only twice in *Ficus* (Weiblen 2000) renders a comparative

statistical analysis inappropriate, but at least we can say that the same nutritional dimorphism is observed in each independent dioecious lineage (Fig. 1).

Studies of bats and birds as obligate frugivores suggest that they have relatively low protein requirements and limited abilities to assimilate dietary lipids (Delorme & Thomas 1996, 1999; Korine *et al.* 1996; Bosque & Pacheco 2000; Dierenfeld & Seyjagat 2000; Levey & Martinez del Rio 2001; Pryor *et al.* 2001). In contrast, many frugivores exhibit physiological adaptations and preferences for foods that are rich in soluble carbohydrates, namely sugars (Witmer & Van Soest 1998, Levey & Martinez del Rio 2001, Dumont *et al.* 2004). Seed figs in all of the dioecious species that we sampled offered more soluble carbohydrates and thereby a greater nutritional reward to potential dispersers. It is noteworthy that the seed figs in our sample tend to contain higher proportions of soluble carbohydrates than reported for most monoecious figs (Conkling & Wrangham 1994, Silver *et al.* 2000, Wendeln *et al.* 2000).

Two of the dioecious species we sampled in which sugar content of juice was not significantly greater in seed figs, *F. conocephalifolia* and *F. septica*, are peculiar in other respects. The species we studied are predominantly cauliflorous, bearing figs of either sex on leafless branches located along the trunk or branches. Four of these (*F. conocephalifolia*, *F. copiosa*, *F. dammaropsis*, and *F. septica*) also bear figs in leaf axils, but *F. conocephalifolia* is the only species in which gall figs and seed figs are segregated in different positions on plants. Gall figs are hidden in the leaf litter at the base of the trunk whereas seed figs are borne exclusively and prominently in leaf axils. *Ficus septica* has distasteful latex with antibiotic properties (Baumgartner *et al.* 1990) that is especially copious in gall figs. The lesser sexual dimorphism in sugar content might be compensated by other traits in these cases.

Apart from the more substantial sugar reward of seed figs, high fiber content of gall figs may deter frugivores generally. Most of the frugivores in New Guinea are volant species for which additional weight increases the energetic cost of flight. Volant frugivores minimize the weight of indigestible food by physiological and behavioral means. Frugivorous bats and many frugivorous birds have relatively rapid gut passage rates (Tedman & Hall 1985, Richardson *et al.* 1987, Boon & Corlett 1989, Utzurrum & Heideman 1991, Levey & Martinez del Rio 2001; but see Shilton *et al.* 1999), which are adequate for the assimilation of soluble carbohydrates but also help to accelerate the elimination of indigestible fiber. Fruit bats are known to masticate figs, press the bolus against the roof of the mouth, swallow the juice, and spit out the fibrous fraction (Bonaccorso & Gush 1987, Dumont 2003).

Several recent studies have focused on the potential importance of mineral content in the diets of frugivores. In particular, calcium has been shown to influence foraging by frugivorous bats (Nelson *et al.* 2005), and may be a limiting resource because it is required by female mammals during lactation and by female birds during eggshell deposition (Barclay 1994). Moreover, it has been hypothesized that high calcium content may explain why figs are a keystone resource (O'Brien *et al.* 1998). In the dioecious species we sampled, gall figs exhibited higher concentrations of calcium than seed figs (Fig. 2), but frugivores invariably prefer seed figs

(Corner 1940, Lambert & Marshall 1991, Lambert 1992, Dumont *et al.* 2004). This apparent contradiction could be explained by the fact that calcium is present as oxalate in a layer of specialized, sclerid cells that contribute to hardness of the receptacle in some species (Berg & Corner 2005) and may actually be resistant to digestion. Sclerids, tough fibers, and unpalatable odors of gall figs could serve to repel frugivores in spite of their sometime greater calcium content. In any event, monoecious figs contain more calcium than many other tropical fruits, and in most cases, the mineral content of ripe seed figs falls within the range reported for monoecious species (O'Brien *et al.* 1998, Wendeln *et al.* 2000; this study). An exception to this pattern is the remarkably high potassium concentration in dioecious figs of either sex (Table S3). Although gall figs in some species contained more protein, calcium, and magnesium than seed figs, most of these nutrients were localized in galls that would be inaccessible to all but seed-cracking frugivores. The same can be said of the greater fat content in seed figs due to the presence of endosperm, which is largely inaccessible to frugivores and serves to nourish the embryo on germination.

In summary, across the functionally dioecious species we sampled, gall figs exhibit higher proportions of fiber and minerals than do seed figs, which are fattier and sweeter. Attractive and nutritional differences between ripe gall figs and seed figs in two independent dioecious lineages (Fig. 1) suggest that dimorphism in ripe fruits may be associated with the adaptive significance of functional dioecy. In support of Patel and McKey's (1998) prediction, carbohydrate differences between gall figs and seed figs serve as cues directing frugivores to consume seed figs preferentially.

The proximate mechanisms governing fig choice by frugivores are not fully understood but recent analyses of fig odors have shown volatile cues to attract mammalian dispersers to ripe seed figs and repel them from gall figs (Hodgkison *et al.* 2007, Borges *et al.* 2008). Chemical cues differentiating the sexes at the fruiting phase run contrary to cues that attract fig pollinators to both sexes during the flowering phase (Chen & Song 2008, Proffit *et al.* 2008). Differences in physical and nutritional properties between ripe gall figs and seed figs also lend further, albeit circumstantial, support to the idea that pollinating wasps and frugivores exert opposing selective pressure on functionally dioecious figs at different life history phases (Dumont *et al.* 2004). Similarity of receptive seed figs to gall figs results in successful pollination. In contrast, distinctions between gall figs and seed figs in nutritional value at ripeness may simultaneously encourage frugivores to select seed figs and discourage them from selecting gall figs. In addition to the spatial segregation of male and female sexual function in dioecious *Ficus*, predictable differences between ripe gall figs and seed figs in nutritional and attractive properties may serve to reduce the potential for conflict between pollinators and seed dispersers over fig resources.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Sample sizes, means, and standard deviations of ripe fig diameter, mass, hardness, and carbohydrate content derived from field refractometer readings of fruit juice.*

TABLE S2. *Mean crude fat, crude protein, nondigestible fiber, and soluble carbohydrates as a percentage of dry weight in ripe dioecious and monoecious figs from New Guinea.*

TABLE S3. *Mean fig mineral content in parts per million (ppm).*

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