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An overview of studies on a community of Panamanian figs

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Abstract. Findings from long-term studies of eighteen monoecious fig species and their associated pollinators, parasites, and seed dispersers from a lowland tropical forest community in Panama are summarized. Studies of evolutionary genetics confirm the suggestion from earlier morphological studies that pollinator and non-pollinator wasps, as well as parasitic nematodes, are generally species-specific. Further, phylogenetic reconstructions suggest that these systems are predominated by strict-sense co-evolution among several trophic levels of fig-associated organisms. Studies of population genetics show that fig wasps routinely disperse pollen over surprisingly great distances. Moreover, both the number of individual fig trees constituting a breeding population and the area that they occupy (>100 km²) are among the largest for any plant species known. Studies of factors influencing reproductive success

of both the figs and their pollinators indicate that, for any given species, many factors (e.g. number and size of pollinators, resource availability, parasite loads) interact in complex but systematic ways to affect the production of seeds and pollinator wasps. Across species, there are repeated patterns of associations among characters such as average number of pollinators per fruit, pollinator sex ratios, nematode virulence, fruit size, fruit colour, physiological properties of the fruit, taxa of associated seed dispersers and degree of synchrony of fruit ripening that imply causal, adaptive linkages and trade-offs among these characters. Collectively, these studies suggest the critical role for comparative work of many species, preferably at many sites, in the understanding of this complex mutualism.

Key words. Monoecious fig species, pollinators, phylogenetic reconstructions, Panama, mutualism.

INTRODUCTION

In this paper, an overview of many recent findings on different aspects of the biology of the fig community in Panama is given. These findings extend discussions found in the useful reviews of several different aspects of fig and wasp biology (Corner, 1940; Ramirez, 1969, 1974; Galil, 1977; Janzen, 1979; Wiebes, 1979; Berg, 1989; Herre, 1989; Berg & Wiebes, 1992; Bronstein, 1992; Compton, 1993), and help serve as a framework for discussion of the results of the many researchers working on other species and sites. Although the Panamanian fig species are all monoecious, and show other marked differences compared with some of their Old World counterparts (e.g. Kalko *et al.*, this issue), there is no fig community that has been studied in the same depth (Bronstein & McKey, 1989). Specifically, studying the same set of morphological, developmental, physiological, phenological and reproductive characters across a series of fig and wasp species in one locale gives insights into the interrelations among those characters than can not be attained by focusing on only a few characters of one species at one site. Further, by studying many different aspects of the biology of the monoecious fig systems, it is more likely that the patterns found in the relatively more complex dioecious systems can be placed in context and understood.

Indeed, the variety of approaches, sites and species discussed by the various contributors to the Bergen symposium (this issue) highlights the fact that many different aspects of the basic biology vary from species to species (Kjellberg *et al.*, 1987; Herre, 1989; Compton, 1993a; Patel, Hossaert-McKey and McKey, 1993; Michaloud, this issue; Smith, this issue) and from site to site (Smith, this issue; Damstra, this issue), underscoring the point that generalizations can not be safely made concerning many aspects of the interactions from studies of single species at single sites. This may be particularly true if the site is at the edge of the species' latitudinal or elevational range (Smith, this issue).

The pattern emerging from the studies of the Panamanian, as well as other, species clearly suggests that many characteristics of the fig and wasp interaction are deeply and causally interconnected, and that viewing any character outside the context of the other characters is likely to result in misinterpretation. For example, neglecting the fact that fruit productivity can be the result of interactions among several factors (such as resource availability, the proportion of a fruit crop pollinated, and the number of pollinator wasps per fruit (foundresses)), and concentrating on only one factor (e.g. the average number of foundresses per fruit) easily leads to misinterpretation (Herre, 1989; and see below). Another example comes from attempts to understand the biology of a given species of the non-pollinating wasp fauna, and the effect that it has on pollinator or seed production. If simple correlations are

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taken, then often there is no clear relationship (e.g. Bronstein, 1991). However, by statistically controlling the confounding variables (such as between tree effects, and numbers of foundresses per fruit), then the nature of the relationship emerges (West & Herre, 1994; West *et al.*, this issue). It becomes clear that some species of the non-pollinator wasps (e.g. *Idarnes*, *Critogaster*) are competing with the pollinators for oviposition sites and often negatively affect the pollinator production. Indeed, one of the symposium's opening talks posed the question: 'Why are the results of fig-wasp interactions so variable?' The answer, almost certainly, is that there are many potentially confounding factors that interact in complex ways to influence the outcomes of the ecological processes that take place in any particular instance between the figs and the wasps. However, by studying many characters in many species, it is possible to see that these complex interactions nonetheless have many systematic aspects to them (Herre, 1989; West & Herre, 1994; see below).

I will begin with a summary of recent findings concerning the physiology of figs, specifically photosynthesis, energy balance and water relations. This will be followed by a discussion of the phenologies of fruits and leaves. Emphasizing the previously unappreciated role of resource availability and its interaction with pollinator availability, I will discuss what is known about the factors that affect the development of the flowers, the production of viable seeds and pollinator and non-pollinator wasps, and link this to the present understanding of how the long-term stability of the fig-wasp mutualism is maintained, followed by discussion of population genetics and gene flow via seed and pollen dispersal and our current understanding of evolutionary genetics and phylogenetic relationships among the groups of figs and wasps. Finally, the abundant opportunities for future research will be considered.

Throughout, the fundamental importance of the mechanisms that underlie the patterns observed in the outcomes of fig-wasp associations, and necessity of understanding the interactions among them, will be discussed. Without that foundation, we risk generating little more than empty metaphors that only serve as facades for ignorance. Where possible, studies of several species at single sites, single species across a range of sites, or several species at many sites is clearly the best way to proceed. Fortunately, both individually and collectively, this is increasingly taking place.

PHYSIOLOGY (PHOTOSYNTHESIS, ENERGY BALANCE, WATER RELATIONS)

Photosynthesis

The photosynthetically active tissues of the leaves and the fruits are the source of all the fixed carbon that comprises the fruits, the seeds, the pollen and the wasps. In a very real sense, the entire system can be said to flow along with the carbon dioxide fixed in the leaves. Interestingly, the photosynthetic rates of the leaves of several fig species are among the highest of any plant measured in a natural setting (Zotz *et al.*, 1995; Melcher & Herre, unpublished). The

nitrogen content of leaves is correspondingly high, probably owing to nitrogen's presence in presumably abundant photosynthetic proteins (Herre, unpublished). (This observation may help explain why figs, in the New World, are relatively rare components of tropical communities that grow on extremely poor soils.) Although the fruits are also photosynthetically active (at least in the species with fruit that develop with a green colour), they do not cover the costs of their own production, and are a net producer of CO₂. For example, in medium sized fruits, photosynthesis only reduces CO₂ loss by roughly 50%.

Photosynthetic activity in adjacent leaves appears to contribute to the dry weight and to the proportion and number of wasps and seeds developed by a given fruit. This inference is based on the observation that in many species, fruit growing at the base of larger leaves show higher productivity of seeds and wasps (see Fig. 1). It is confirmed by the observation that radiolabelled CO₂ fixed in a leaf is translocated almost entirely to adjacent fruits (see Fig. 2).

However, several observations strongly suggest that concurrent photosynthesis by adjacent leaves cannot account for all of the fixed carbon in fruit. First, several species can produce their fruit at times that they have dropped leaves (S.G. Compton, pers. comm.; Damstra, this issue). Secondly, many species produce fruit on specialized, leafless branches (e.g. many in the Old World *Sycomorus* group). Thirdly, dry weights of fruit rise dramatically just after pollination (Herre, unpublished). This rapid gain is too great to be accounted for by the photosynthetic production of the attendant leaves alone. Together, these patterns suggest the mobilization and translocation of stored or current photosynthate from both a distal (tree trunk or branch), as well as a local source of carbon during the maturation and growth of the fruit (see below).

Energy balance of fig fruit

The figs and their wasps have understandably been the source of much mystical and religious inspiration, and are justifiably venerated by many groups of enlightened people. However, they also live in a world in which objects usually obey the somewhat more predictable laws of physics. The importance of those laws is demonstrated by energy balance studies of fig fruits. The wasps are very sensitive to heat and die at temperatures only a few degrees above ambient. Such temperatures are expected and observed in objects exposed to full sunlight, as fig fruits frequently are. In detailed field and experimental studies of eleven species of Panamanian figs with fruit ranging from 5 mm to 50 mm in diameter, both the relative and absolute contribution of transpiration to maintaining non-lethal internal fruit temperatures increased with fruit size (Fig. 3). Small and large fruits, respectively, reached temperatures of 3 and 8 degrees C above ambient air temperature in full sunlight when transpiration (and therefore cooling associated with it) was prevented by covering the fruit surface with clear grease. The temperatures reached by large, non-transpiring fruits was sufficient to kill their pollinators. In contrast, control fruits which transpired reached maximum temperatures only 2–3 degrees C above ambient, regardless

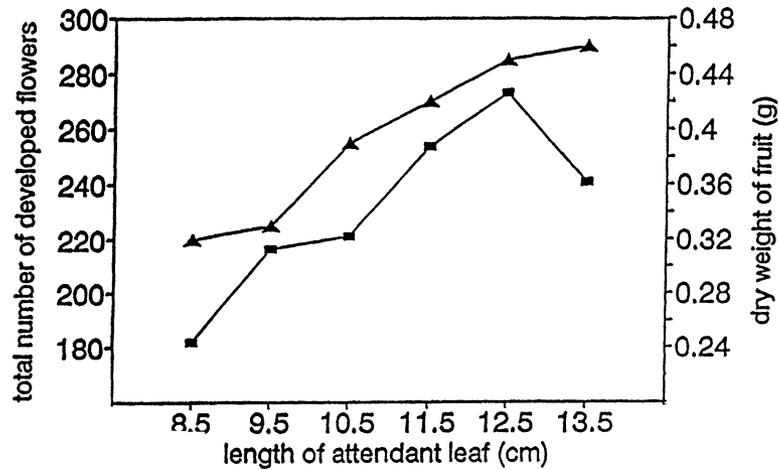


FIG. 1. The number of developed flowers (total number of viable seeds plus wasps, ■) per fruit and the dry weight (▲) per fruit plotted against the length of the attendant leaf for a crop of *F. yoponensis*. Each point represents the mean flower development and dry weight of ten fruits. Fruit at the base of larger leaves develop a larger number of flowers and reach greater dry weights at maturity. This result suggests a highly localized translocation of resource from leaves to their attendant fruits that is relatively larger from larger leaves (see text).

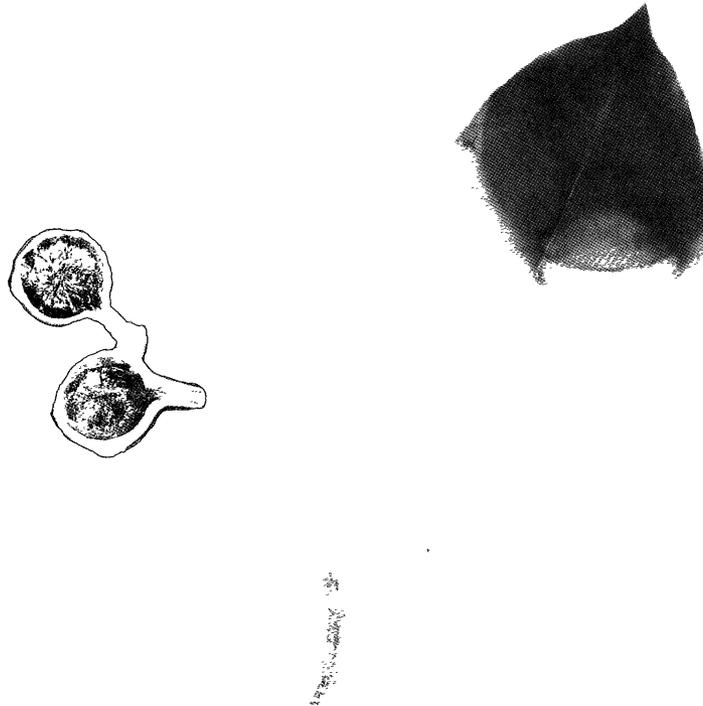


FIG. 2. Autoradiograph showing radioactivity labelled CO_2 uptake by leaf and its translocation to the attendant fruit (see text).

of size or exposure to sunlight. An analysis of the solar energy budget of fruit revealed that large fruits must transpire to maintain tolerable temperatures for the wasps because heat diffusion from fruit to air was too low to balance net radiation in sunlight. By contrast, small fruits do not need to transpire in order to maintain tolerable temperatures for the wasps (Patiño, Herre & Tyree, 1994). Therefore, fruit size has important physiological consequences and, as has been emphasized before, fruit size

is linked to a number of other aspects of the ecology of figs and wasps (Herre, 1989; see below).

Water relations

Figs exhibit a relatively high capacity to conduct water per unit cross section of wood compared to other tropical trees that have been studied (Patiño *et al.*, 1995). This property of fig wood perhaps underlies the additional observation

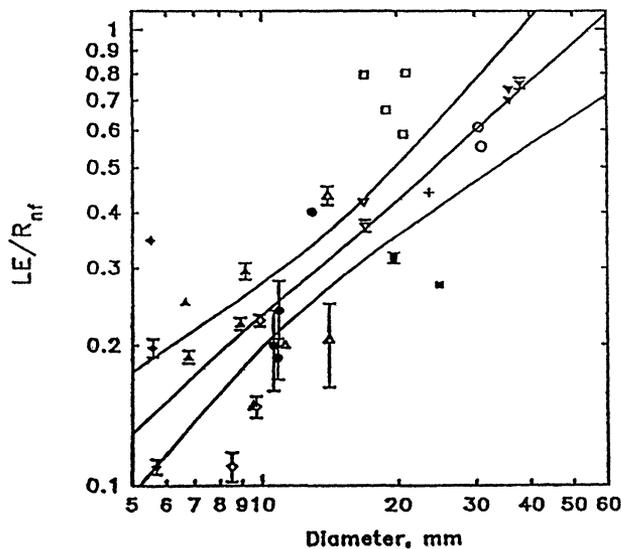


FIG. 3. The fraction of radiant energy dissipated by evaporation (LE/R_{nf}) plotted against the diameter of the fruit for eleven species of figs. Larger fruits must transpire considerable amounts of water in order to maintain internal temperatures that are low enough to permit the developing pollinator wasps to survive. In contrast, smaller fruits do not need to transpire in order to maintain tolerable internal temperatures (see text).

that figs exhibit relatively low wood cross-sectional area per unit leaf area, interesting when the high rates of photosynthesis are considered. Among the figs, free-standing species exhibit more wood per leaf area, slightly more conductive wood (at smaller branch diameters) and, consequently, greater water conducting capacity per leaf area than stranglers (Patiño *et al.*, 1995). This would appear to fit with their ecologies because higher capacity for conducting water is normally associated with greater sensitivity of the plant to damage from water stress. Also, we might expect deep-rooted, free-standing trees to be less subject to water stress than the stranglers that often spend large portions of their juvenile lives out of contact with the ground. Further, the fact that the stranglers are effectively structural parasites of other trees is undoubtedly connected with their relatively low investment in wood. Extending the energy balance studies of the fruits as well as the physiological comparisons between the free-standing and strangling species studied in Panama to those fig species growing in relatively dry habitats offer a series of interesting opportunities to link physiology with other aspects of the figs' ecology (see below).

PHENOLOGY (LEAVES, FRUITS, WASPS AND BEYOND)

Most plant species show fairly clear and regular seasonal patterns in leafing, flowering and fruiting patterns. However, most figs are not like most species, at least in this respect. Generally, fruit production in figs is synchronous within individuals, but very asynchronous across individuals in a population and in most species, fruit can be found at any

time of year. Not surprisingly, the production schedules of fruit and leaves have been the focus of a tremendous amount of work by a large number of researchers working on many different species (Milton *et al.*, 1982; Kjellberg & Maurice, 1989; Windsor *et al.*, 1989; Milton, 1991; Bronstein, 1992; Bronstein & Patel, 1992; Compton, 1993a; Anstett, this issue; Michaloud, this issue; Weiblen *et al.*, this issue; Damstra, this issue; Smith, this issue). Many researchers have been interested in fig phenologies primarily because fig fruits and leaves are a basic component of the diet of many tropical frugivores (Janzen, 1979; Foster, 1982; Milton *et al.*, 1982; Terborgh, 1983; Milton, 1991). Therefore, figs often function as 'keystone' species, and their importance in the conservation of many tropical forest communities is becoming increasingly recognized (Terborgh, 1983, 1986; McKey, 1989; Thomson *et al.*, 1991, but see Gautier & Michaloud, 1989). Other researchers have been interested in the relationship between fruiting phenology and the maintenance and dynamics of the pollinator wasp population (Kjellberg & Maurice, 1989; Bronstein, 1992; Anstett, this issue). Less appreciated are the consequences that patterns of leaf and fruit flushing will hold for physiological processes of the fig itself (e.g. water loss in relatively dry regions or seasons, and energy balance of the fruit) (Damstra, this issue). Therefore, phenology has consequences at several levels of the interactions among figs and their associates.

It is clear that different species produce leaves and fruits according to different schedules. In Panama several species produce leaves in flushes, whereas others produce leaves more or less continuously. The pattern of leaf flush is potentially important because many fig species live in seasonally dry environments and must be able to minimize water loss in order to tolerate droughts. Several fig species that live in extremely dry regions drop their leaves during dry periods, but still produce fruit (Compton, 1993a; Damstra, this issue). It is becoming increasingly clear that the connection between fruiting and leafing is quite plastic across species. Further, this flexibility in phenological patterns exists even within species, both across different sites, and at different times of the year in one site (Milton *et al.*, 1982; Windsor *et al.*, 1989; Milton, 1991; Bronstein & Patel, 1992; Cook, this issue; Damstra, this issue; Smith, this issue).

In several Panamanian and African species, active stem growth that is associated with leaf flushing occurs at different times from fruiting (Herre, pers. obs.; S.G. Compton, pers. comm.). This suggests an energetic constraint that imposes a trade-off between vegetative growth and reproduction. In one Panamanian species, *F. citrifolia*, fruiting is predictably followed by leaf loss which, in turn, is followed by the production of new leaves combined with rapid stem elongation. Then comes a period of relatively low growth, followed by fruiting, after which the cycle repeats itself (Herre, unpublished). This pattern is consistent with an accumulation of resource that is stored in the trunk or stems which reaches some critical level at which hormonal signals shift, the buds that develop into the fruit are activated (or cease being suppressed) and fruiting is initiated. The observation that broken branches frequently initiate fruit

just before dying suggests that there is a signal inhibiting fruit initiation that originates in the trunk, possibly the site of the stored resources. In any case, the system of hormonal signalling and the factors that influence whether resources are stored or are mobilized towards the growth and production of new leaves, or whether resource is mobilized and translocated to the support of a new crop provides an interesting opportunity to link studies of plant developmental physiology with ecology.

The interrelated questions of the effect of differences in tree phenological patterns and of the number of trees needed to maintain viable wasp populations has received considerable theoretical attention (Kjellberg & Maurice, 1989; Bronstein, 1992; Anstett, this issue). At a population level, several models suggest that the temporal pattern of fruiting phenology will have a great influence on wasp population densities. In general, the models suggest that increased periods of receptivity and release of wasps, increased asynchrony within the crowns of individual trees, decreased intercrop intervals, and decreased seasonality to fruit production increase the opportunities in overlap of fig flowering phenologies and, therefore, reduce the number of adult fig trees that are needed to maintain the wasp populations over time.

Earlier versions of the models are implicitly group arguments, and are most properly aimed at conservation: how many trees with such and such properties are needed to maintain wasp populations? More recent modelling efforts are considering the different question of what are the selective advantages to individual trees of producing crops according to any particular pattern, and are more evolutionarily relevant (Anstett, this issue). The findings of regular and effective long distance pollen dispersal (Nason & Herre, this issue) and the flexibility of phenological patterns (Smith, this issue) will be important considerations to integrate with future modelling efforts. Further, it will be necessary to appreciate that an increased pace of fruiting will come at the expense of vegetative growth.

In most cases, monoecious fig trees show within-crown synchrony and relatively random patterns of population wide fruiting with respect to season, although this appears to be less true at higher latitudes. Nonetheless, under such conditions, the proportion of the total number of adult trees in any given area that are either producing or receiving wasps at any one time is small (roughly 4–5%). In these cases it is estimated that the number of adults needed to maintain wasp populations is over 100. However, given these theoretical predictions, how do we test them?

Although fig wasps are small and apparently short-lived some observations suggest that, at least on occasion, they are capable of long-distance dispersal (Compton, 1993b; Thornton & Compton, this issue). Further, wasp populations apparently can rebound very quickly after natural disasters such as Hurricanes in Florida (Hossaert & Bronstein, pers. comm.). The wasps must be coming from somewhere, but how far? Electrophoretic results from Panama indicate that wasps are routinely dispersing several kilometres. Further, individual trees are almost invariably pollinated by wasps from many different sources. All available data suggest that the breeding populations of figs

may consist of several hundred individuals despite their typically low densities (Nason, Herre & Hamrick, this issue).

In general, New World species in which the seeds are primarily bat dispersed usually produce ripe fruit relatively synchronously within crowns, while those with fruit that are primarily bird dispersed produce and ripen fruit much less synchronously (Belice, Mexico, Guatemala, Costa Rica, Panama, Peru, E.A.H, pers. obs.; Brazil, S.V. Mikich, pers. comm.; Colombia; M.J. Quiñones, pers. comm.; and other parts of South America, C.C. Berg, pers. comm.). A possible explanation for this tendency may lie in the observation that the cues used by New World bats and birds to detect fruit are fundamentally different. Bats require a scent which can be detected over distance in the relative darkness of night (Kalko *et al.*, this issue). The fruits of the fig species that normally attract bats tend to be larger than those taken by birds. They tend to be green when ripe and produce a scent that is easily detected by even a relatively insensitive human nose. It is likely that simultaneous ripening of many fruit in a crop produces a correspondingly much stronger scent that is detectable over much greater distances. Indeed, large fruit crops attract flocks of bats from great distances, often several kilometres (Handley & Kalko, pers. comm.). On the other hand, birds are primarily visually orientated. Accordingly, the fruits of fig species that are primarily eaten by birds tend to be small and they ripen bright red or purple, and produce no scent detectable to the same admittedly insensitive nose. In this case, no amount of synchrony in the production of the visual signal will be effective outside line of sight. It is likely that the within-tree synchrony of initiating and ripening fruit observed among fig species is as affected by seed dispersal as it is by pollination, and that if only the latter is considered, important considerations are being overlooked.

FIG-WASP INTERACTION AT THE FRUIT LEVEL (WHO GETS THE SEEDS?)

Two intertwined questions are what factors affect seed and wasp production, in particular fruit crops or particular fruit, and what maintains the long-term stability of the system? The first question is essentially a matter of how physiological and developmental processes of the fig and wasp interact with ecological contingencies to affect seed and wasp production for any particular fruiting event. The second question is motivated by the recognition that the mutualistic interaction clearly contains antagonistic elements that, if unrestrained, would lead to collapse of the system; and essentially boils down to a search to identify the mechanism(s) that prevent the wasps from consuming all of the seeds and developing flowers. Although the answer to the first gives insight into the answer of the second, neither question can be completely answered outside the context of the other. There is, as yet, no completely satisfactory answer to the latter question.

The patterns of seed and wasp production profoundly affect the reproductive success of both fig and wasp and lie at the centre of the mutualism. Figs are completely dependent on the foundress wasp(s) for the pollination of flowers and, therefore, the production of viable seeds (i.e.

'female' function). It is true that, of the potential seeds that may develop, roughly 50% or more may be eaten by the offspring of the foundress wasp(s). However, the fig is also dependent on the female offspring of the foundress wasp(s) to carry its pollen off, and use it to pollinate other figs (i.e. 'male' function). The fig-pollinating wasps, in turn, depend completely on the fig to provide them with sites to lay eggs and complete their life cycle.

Despite some exceptions (see below), foundresses generally do not escape from the fruit in which they oviposit and their lifetime reproductive success may often be determined unambiguously, and then be related to a series of factors (e.g. foundress size, fruit size, parasitic wasp infestation of the fruit, nematode infection, etc.) with relative ease. Consequently, each fruiting event produces very strong selection on the individual wasps; they have only one opportunity. On the other hand, determining the lifetime reproductive success of a fig is nearly impossible. Most trees produce thousands of fruit per fruiting episode and individual trees may live scores of years and produce hundreds of fruit crops. The consequences of any one fruiting event are therefore relatively less important to the individual fig.

Factors affecting seed and wasp production

Within any given crop of fruit, many factors appear to interact in their influences on the productivity of the crop as a whole and the per fruit productivity of the seed and wasps in particular. At the level of the crop, fruits that are not pollinated are usually aborted, and the proportion of the initiated fruit that are matured in any one crop can be quite variable, depending on the local availability of pollinators following fruit initiation. At the level of individual fruit, there is strong evidence indicating that the number of foundresses per fruit (and therefore pollen availability per fruit), the amount of resource available and the incidence of non-pollinator (parasitic) wasps are all capable of affecting the seed and wasp production of fruit (Herre, 1989; West & Herre, 1994). All these observations emphasize the importance of taking many considerations into account and the need to synthesize information across many different levels of organization (see Fig. 4).

The proportion of receptive flowers that develop within a fruit depends on the availability of pollen and resources, and in any given case either the former or the latter can be limiting (Herre, 1989; Bronstein, 1992). In some cases, the per fruit productivity of seeds and wasps is inversely related to the proportion of an initiated crop that was pollinated and retained by the tree, strongly suggesting tree wide limits to resource availability (Bronstein, 1988a, b, and see below). Within crops, the dry weight of fruit, as well as the number of developed flowers, viable seed and wasps also increases in some species with the size of adjacent leaves, implicating local resource translocation (Figs 1 and 2, unpublished data). Further, the proportion and absolute number of flowers that develop generally increases with the number of foundresses, strongly suggesting the presence of within-fruit pollen limitation in many cases (Herre, 1989). Moreover, both across and within species, physically larger wasps

usually are associated with greater development of flowers, suggesting size-related differences among wasps in the capacity to carry pollen (Herre, 1989; F. Kjellberg, pers. comm.).

Of those flowers that are pollinated, some develop as intact, viable seeds whereas others are eaten by the developing wasp offspring. The number of eggs available for oviposition in a fruit clearly depends in part on the number of foundresses. Further, there are even subtle effects associated with the size of foundresses; the largest foundresses usually produce the largest number of eggs (Nefdt, 1989; Compton, 1993a) and offspring (Herre, 1989; and unpublished data). Specifically, in *Ficus obtusifolia*, the increasing numbers of pollinator offspring associated with increased foundress size often come at the expense of viable seeds, producing negative correlations between wasps and seeds (Herre, in prep.).

The effects of nematodes

All species of fig wasps that have been examined in the New World possess species-specific parasitic nematodes of the genus *Parasitodiplogaster* (Poinar & Herre, 1991; R. Giblin-Davis, pers. comm.). In all cases studied the infection rate is variable, and both infected and uninfected individuals can be found. By comparing the numbers of offspring associated with infected as opposed to non-infected foundresses, it is possible to estimate the effects of having a nematode infection on wasp lifetime reproductive success. Interestingly, in the wasp species in which there are normally large numbers of foundresses per fruit (providing abundant opportunities for horizontal transmission of the nematodes), the nematodes are relatively virulent and have a pronounced negative effect on their host's reproductive success. In contrast, in those species in which there are normally few foundresses per fruit (providing relatively restricted opportunities for horizontal transmission) the nematodes are relatively benign, and have little effect on their host's reproductive success (Herre, 1993). However, in most fig species the presence of nematodes seems to depress wasp reproductive success.

The effects of non-pollinating wasps

Of the wasps born in a fruit, both pollinators and non-pollinators are usually present. Although there are some Old World exceptions, all non-pollinators described from the New World oviposit from the outside of a fruit. There are many different species of non-pollinating wasps, belonging to many different genera (Gordh, 1975; Bouček, 1988, 1993; Bronstein, 1991; Compton & Hawkins, 1992; Bouček *et al.*, 1981; Compton *et al.*, 1994; Compton & van Noort, 1992; Hawkins & Compton, 1992; Compton, 1993a; Cook, this issue; Machado *et al.*, this issue). Some are much larger than the pollinators and tend to emerge from large galls that are derived from fruit wall or other material (e.g. *Idarnes* (incerta), *Aepocerus*). Some are clearly parasitoids of these gall formers. Others are similar in size to the pollinators and appear to develop from flowers or developing seeds that appear indistinguishable from those

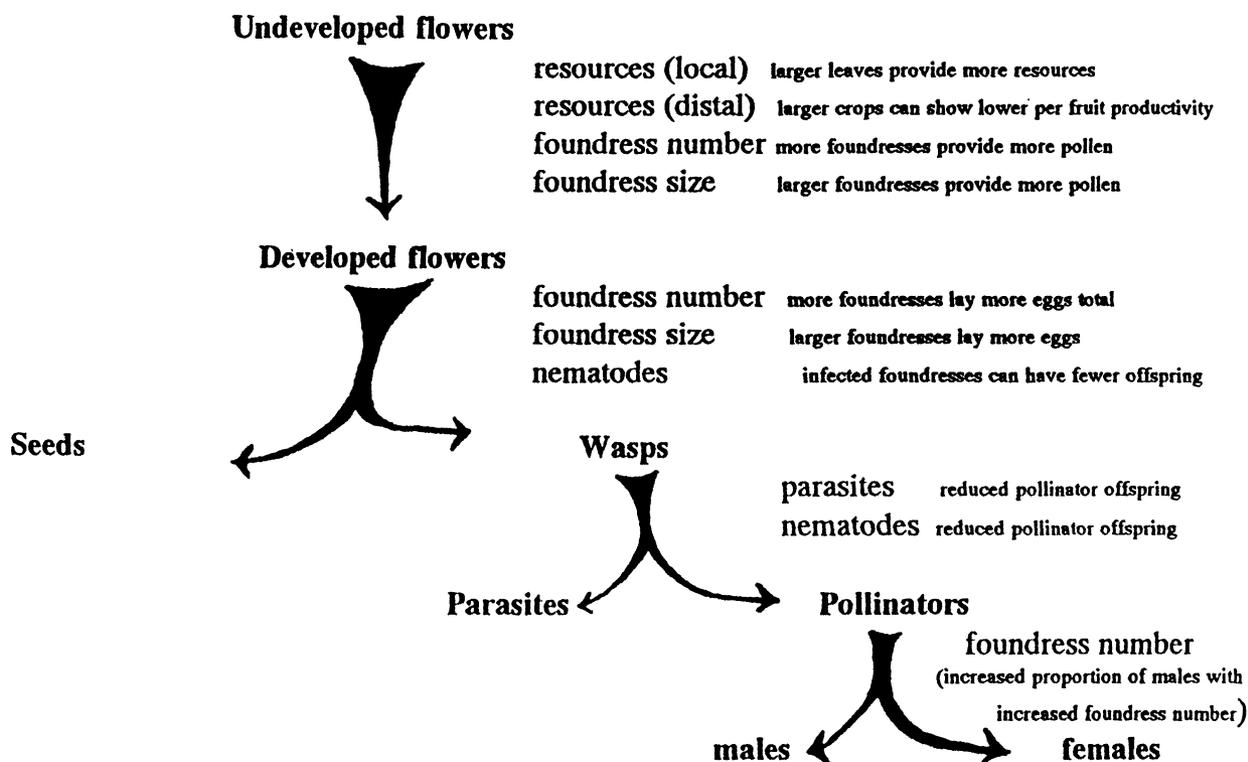


FIG. 4. The diagram identifies factors that influence the production of different products (seeds, pollinator or parasitic wasps, etc.) found in fig fruits, and describes the relationships among them. Each of the products (seeds and female pollinator wasps) that contributes to the reproductive success of the figs can be viewed as the result of a series of processes and their interactions. Several studies have identified the factors which influence each step in the series (see text). Only by the recognition that many factors interact in complex, but systematic ways to influence the productivity of fruit can the patterns of seed and wasp productivity begun to be understood.

in which the pollinators develop (e.g. *Critogaster*, some species of *Idarnes* and, possibly, some species of *Sycoscapter*, and *Philotrypesis*) (West & Herre, 1994; Cook, this issue; West *et al.*, this issue; Machado *et al.*, this issue).

In the New World species that have been studied carefully (*Idarnes* and *Critogaster*, that are, respectively, associated with *Urostigma* and *Pharmacosyceae*), these smaller wasps appear to be competitors with the pollinators for available oviposition sites. Further, the *Idarnes* wasps are not true parasitoids but, rather, appear to be in direct competition with the pollinator wasps for the same pool of flowers in which the larvae of either group can develop (West & Herre, 1994). On the other hand, the larger gall formers appear to cause reductions not only in pollinator production of the fruit in which they develop, but apparently seed set as well, possibly through a general draining of resources that would be allocated otherwise in their absence (West *et al.*, this issue).

The number and proportion that the non-pollinators comprise of the total wasps born in a given fig fruit is extremely variable. In some locales and some species, the proportion of non-pollinators is very low (Herre, 1989), in others they form the majority of the wasps produced (Bronstein, 1989a, b). The presence of non-pollinators can therefore obscure the functional relationships among the other products of fig fruits (e.g. relationships between

pollinator wasps and seeds). For example, as mentioned above, it is likely that the presence of the large galling wasps will mimic the effects of resource limitation by reducing the development rate of flowers (unpublished data). Indeed, in an experimental study of the relationship of foundress number to pollinator sex ratio, the fruit were bagged in order to avoid the possible confounding effects of the non-pollinators on host brood sizes and, possibly, sex ratios (S.A. Frank, 1985, pers. comm.).

The effects of foundress number

As is the case with most animals, some of the pollinators develop as females and others as males. Unlike many other animals, the brood sex ratios of the pollinators are generally very female biased. The degree of female bias is usually very sensitive to the number of foundresses contributing eggs to a shared brood in a fig fruit, with greater female biases associated with fewer foundresses. The shifts in sex ratio appear to be a response to differences in the intensity of local mate competition (Hamilton, 1967) and average level of inbreeding in the population (Herre, 1985, 1987; Frank, 1985). Because only the female wasps are capable of pollen dispersal, each male wasp produced represents an uncompensated loss for the fig tree. Therefore, the sex ratio shifts away from an extreme female bias with increasing

foundress numbers are definitely not in the fig's interest (Herre, 1989; Herre *et al.*, 1996).

It is clear that foundress number can influence seed and wasp production at many levels, and that having this information gives useful insight into mechanisms. However, in some species (*F. carica*, and particularly several of the dioecious figs (F. Kjellberg, and Anstett, pers. comm.)), foundresses regularly escape. In others (Hamilton, 1979; Janzen, 1979; Herre, 1985, 1987, 1989, 1993; Bronstein, 1998a, b; S. Compton, L. Chou, J. Cook, W. Ramirez, pers. comm.), they usually do not. In some cases there appears to be variation among individuals within species in the tendency for foundresses to escape. This variation within species appears to be related to the number of bracts that overlay the ostiole. Both within and across species, those fruit with a higher number of more rigid bracts are less likely to have their foundresses escape (pers. obs.). Nonetheless, protein and molecular analyses of seeds and pollinator offspring can be used to confirm foundress number counts in the species in which the foundresses remain in the fruit, and could be extended to those species in which they do not (Nason & Herre, unpublished).

The potential for confusing interactions among the factors influencing fruit productivity is clearly demonstrated by an interesting series of studies on *Ficus pertusa* in Monteverde, Costa Rica (Bronstein, 1988a, b, 1991, 1992). In twenty-two fruit crops, the proportion of initiated fruit that was pollinated and retained, the average number of foundresses per retained fruit and the productivity in seeds and wasps of individual fruits within crops were determined. Trees that received pollinators in a large proportion of their crop tended to have a high average number of foundress per fruit. Nonetheless, the fruit crops that had the highest foundress numbers also showed dramatically lower per fruit productivity (twenty-four seeds, and four pollinators per fruit), when compared with the crops with the lowest foundress numbers (eighty seeds, and fifty-one pollinators per fruit) (Bronstein, 1988b). In this case, if crop averages of seed and wasp production are plotted against crop averages of foundress number (e.g. Bronstein, 1992), then the relationship appears negative, the opposite of the relationship usually found within fruit crops of the Panamanian species (Herre, 1989; Frank, 1985, 1989). Unfortunately, only tree averages for foundress number were collected in the Monteverde samples, and direct comparisons of the effects of foundress number within crops cannot be made.

In the Monteverde samples, if crop means of seed number are plotted against crop means of wasp number, then the relationship appears to be positive (Bronstein, 1992), the opposite to what is frequently observed within crops from Panama (Herre, 1989, see Table 1). A probable explanation is that, in those cases in which the trees retained a lower proportion of their initiated crop, there was more resource available for the development of the pollinated flowers that produce either seeds or wasps in individual fruit that remained. This pattern appears similar to the case of *F. carica* in which per fruit dry weight increases when crops are artificially thinned after pollination (F. Kjellberg, pers. comm.). Indeed, it is the fruit in the Monteverde *F. pertusa*

trees that had the lowest proportion of their crop developed that showed the highest seed and wasp development per fruit. Therefore, in this study population, there appears to be an interaction between resource availability, number of foundresses per fruit and proportion of the fruit crop retained. If the nature of this interaction is not taken into account by carefully separating effects that occur among trees from those that occur among fruits within trees, it easily can lead to the generation of a number of plausible, but fallacious conclusions (Herre, 1989; West *et al.*, this issue).

Finally, in the Monteverde samples, the relationship between pollinator production and *Idarnes* production shows no trend overall. However, in the samples in which there is relatively high per fruit development rate of flowers (and lower overall retention rate of initiated fruit), the pollinators are negatively related to parasite presence (J.L. Bronstein, pers. comm.), as they are in the Panamanian species (West & Herre, 1994; West *et al.*, this issue).

As a whole the Monteverde population of *F. pertusa* seems to demonstrate the effects of resource limitation relative to the populations of several of the Panamanian species. Further, none of the related Panamanian species showed similar magnitudes of crop to crop variation in per fruit seed and wasp productivity (a three-fold difference in seeds and a nearly ten-fold different in pollinators, respectively). One possible explanation is the much higher incidence rate of parasitic wasps, particularly the gallers, found in the Monteverde trees (Bronstein, 1988a, b; Herre, 1989). The effects of the gallers can mimic the effects of resource limitation (West *et al.*, this issue) and, as mentioned before, resource limitation tends to obscure the functional relationships among seeds, wasps and parasites. Fortunately, this is a case in which observations from several species at several sites help to interpret the patterns. Without comparative data, correctly identifying the processes that underly the patterns would be almost impossible. Although it is important to distinguish between controlling factors (either statistically or experimentally) in order to understand mechanisms and the causal links among those factors, as opposed to describing the frequency with which different factors interact in any given way to produce any particular pattern of seed and wasp production, the 'take home' message is fairly clear. Many factors, particularly resource availability and foundress numbers, interact at many different levels of biological organization to influence seed and wasp production, and if particularly influential factors or the interactions among them are overlooked then the probable result is misinterpretation.

Evolutionary stability of the system

A question that has attracted a great deal of interest has been what are the factors that help to maintain the stability of the fig-pollinator mutualism itself? Despite the fact that the figs and wasps depend completely on each other, for the continued sexual reproduction of the former and the completion of the life cycle of the latter the reproductive interests of the two partners are not identical. The fig has an interest in the development of seeds both as viable seeds

TABLE 1. The correlation between the number of seeds and the number of agaonid wasps produced in fruit from twenty-eight crops sampled from seven species collected in Panama. Although the sign and magnitude of the correlation is variable, the majority of crops samples (twenty of twenty-eight) show a negative relationship between the number of wasps and the number of seeds that are produced in the fruit of these species.

Species	Crop sample	Sample size	Correlation coefficient	Sign of relationship
<i>F. bullenei</i>	1	12	0.42	Negative
<i>F. bullenei</i>	2	29	0.73	Negative
<i>F. bullenei</i>	3	25	0.75	Negative
<i>F. citrifolia</i>	1	17	0.04	Positive
<i>F. citrifolia</i>	2	22	0.20	Negative
<i>F. citrifolia</i>	3	39	0.14	Positive
<i>F. citrifolia</i>	4	29	0.24	Negative
<i>F. citrifolia</i>	5	55	0.50	Negative
<i>F. citrifolia</i>	6	68	0.32	Positive
<i>F. citrifolia</i>	7	21	0.01	Positive
<i>F. citrifolia</i>	8	18	0.14	Negative
<i>F. colubrinae</i>	1	23	0.25	Negative
<i>F. colubrinae</i>	2	10	0.50	Negative
<i>F. nymphaefolia</i>	1	21	0.10	Negative
<i>F. nymphaefolia</i>	2	48	0.05	Negative
<i>F. nymphaefolia</i>	3	34	0.07	Positive
<i>F. nymphaefolia</i>	4	17	0.14	Negative
<i>F. nymphaefolia</i>	5	14	0.53	Negative
<i>F. nymphaefolia</i>	6	32	0.02	Negative
<i>F. nymphaefolia</i>	7	24	0.24	Negative
<i>F. obtusifolia</i>	1	58	0.14	Positive
<i>F. obtusifolia</i>	2	40	0.14	Negative
<i>F. obtusifolia</i>	3	50	0.04	Negative
<i>F. obtusifolia</i>	4	25	0.28	Negative
<i>F. obtusifolia</i>	5	50	0.14	Positive
<i>F. paraensis</i>	1	37	0.10	Negative
<i>F. pertusa</i>	1	29	0.22	Positive
<i>F. pertusa</i>	2	26	0.14	Negative

per se, and as a means for supporting the development of the female offspring of the foundress wasps that are essential for dispersing its pollen. On the other hand, the pollinating wasp only benefits directly from the fig's production of seeds that are eaten by its own offspring. The tension resulting from this incongruence of reproductive interests is inherent in the relationship of all figs and fig-pollinating wasps, and why the wasps do not evolve ever-higher fecundities to the ultimate ruin of the fig's production of viable seeds is a fascinating question that has generated a host of hypotheses.

For example, it is possible that the foundress wasps do not produce enough eggs in order to exploit all of the seeds that might potentially develop. However, in many cases, the foundress wasps which pollinate the fig fruits carry more than enough eggs to saturate all of the female flowers within a syconium (Herre, 1989; Compton, 1993a). Another possibility is that the ovipositor lengths of the wasps constrain their access to the uniovulate flowers, the ovules of which are positioned at different distances from the oviposting wasps because of differences in style lengths. However, style length within the fruit of monoecious figs is distributed unimodally and not into short- and long-styled classes, and the ovipositors of the wasps are long enough to oviposit in a much larger proportion of flowers than actually develop into wasps (Kjellberg *et al.*, 1987; Bronstein,

1988a, b; Verkerke, 1989; Compton, 1993, and submitted). Further, the observation that species of non-pollinating wasps in several different groups of figs are apparently ovipositing on the same subset of flowers as the pollinators although they oviposit from opposite side of the fruit wall suggests that the basis for preserving some of the flowers to develop as viable seeds is not a direct result of spatial position of the ovaries, or style length (West & Herre, 1994; West *et al.*, this issue).

Apparently there are two populations of flowers, accessible and non-accessible, and accessibility to exploitation by either pollinator or non-pollinator wasps does not depend on ovule position *per se*. Nonetheless, there is as yet no generally applicable mechanism that has been demonstrated. Intriguing possibilities that merit thorough examination include physical differences in the flowers themselves, possibly due to differences in style width or toughness of the ovary wall (Verkerke, 1989). Another possibility might be histological, or physiological differences in which some flowers do not respond to 'galling' substances injected by the wasps, or are for some reason incapable of supporting the development of the wasp larvae. Nevertheless, all of these proposed explanations raise the question of why wasps would not have 'learned' over evolutionary time how to bypass these mechanisms (also see Thompson, Pellmyr & Huth, 1994).

POPULATION GENETICS (POLLEN AND SEED DISPERSAL)

Protein electrophoretic studies of some species of strangling figs have shown that what appear to be individual trees may in fact turn out to be 'mosaics', fusions of two or more distinct genetic individuals (Thomson *et al.*, 1991). From developmental, ecological and conservation perspectives, this phenomenon holds several potentially important implications. However, despite the fact that these 'mosaics' do occur and, therefore, that researchers should be aware of this possibility, further work has shown that mosaics constitute less than 10% of the individuals in most of the Panamanian populations studied (Nason *et al.*, unpublished).

On the other hand, an extension of the electrophoretic work on eleven species has shown that figs in general possess exceptionally high levels of electrophoretically determined genetic variability when compared with all other plant and animal groups that have been examined (Nason, Herre & Hamrick, this issue; Nason *et al.*, submitted). This result has also been found in populations from Florida and India (Nason & Hossaert, unpublished).

The high levels of variability coupled with the opportunities presented by the natural history of figs allows the identification of full sibling families, thereby allowing the exact reconstruction of paternal genotypes. Paternity reconstruction in four Panamanian species reveals large numbers of donors contributing pollen to each fruit crop (Nason, Herre & Hamrick, this issue). This observation combined with estimates of the densities of the host trees strongly suggests that the pollinator wasps routinely cover distances up to 10 km or more (but see Michaloud *et al.*, 1985; Michaloud, this issue), and that both the numbers and the areas covered by the individuals constituting interbreeding populations of the Panamanian figs are among the largest that have been described for any plant species. Given this demonstrated capacity for long distance gene flow via pollen, it is not surprising that there is no evidence for genetic structure of the Panamanian fig populations, even at large spatial scales (Nason, Herre & Hamrick, this issue). This lack of genetic structure at large spatial scales also appears to be the case in French populations of *Ficus carica* (Valdeyron *et al.*, 1985; Valizadeh *et al.*, 1987).

Although the vertebrate seed dispersers are not even remotely as species-specific as the wasps appear to be, nor are they not complete generalists. In Panama, there are consistent differences between the fruit preferred by birds and bats (see below). Further, the different bat species show some degree of specificity or preference for the fruit of particular fig species (Kalko *et al.*, this issue). This preference, in turn, appears to have consequences for the dispersal of seeds. Generally, larger species of bats prefer fig species with large fruit. Also, despite the fact that most New World bats drop many seeds, unswallowed, close to a source tree in feeding roosts, and despite the fact that gut passage times of swallowed seeds can be short, larger bat species range over much larger areas than the smaller species. Therefore, the larger species of bats present the opportunity for relatively longer range seed dispersal to the trees whose

fruit they eat (Kalko *et al.*, this issue). However, regardless of the seed disperser, pollen dispersal distances in figs are routinely very large, even with respect to seed dispersal.

EVOLUTIONARY GENETICS

With the co-operation of several colleagues who have supplied fig and wasp material from many parts of the world (C.C. Berg, S.G. Compton, J. Cook, L. Chou, M. Hossaert, D. McKey, A. Patel, F. Kjellberg, W. Ramirez, J. Tolsma, J.T. Wiebes), the phylogenies of fig species that represent each of the major recognized subgenera, and their corresponding pollinator taxa (*sensu* Berg, 1989) have been estimated using molecular data. The fig phylogenetic reconstructions are based on analysis of sequence from *rbCl* (chloroplast), *tRNA* spacer genes (chloroplast). The phylogenetic relationships among many species of both pollinator and non-pollinator wasps have been estimated by analysing mitochondrial *COI*, *COII* and *12S* genes (Herre *et al.*, this issue; Machado *et al.*, this issue). Despite the fact that the number of taxa sampled is far from complete, and that there were not a large number of phylogenetically informative sites in the *rbCl* and *tRNA* spacer regions used to estimate phylogenetic relationships among the figs, some inferences could nonetheless be made.

At a high taxonomic level, the phylogenetic relationships suggested by the molecular data differ in some respects from previous morphologically based phylogenies (Corner, 1958; Ramirez, 1974; Wiebes, 1979, 1982; Berg, 1989; Berg & Wiebes, 1992). First, there is no simple monoecious-dioecious split among the recognized subgenera of figs, as has often been proposed. The monoecious New World *Pharmacosycea* are more genetically distinct from all of the other groups of figs (subgenera *Ficus*, *Sycomorus* and *Urostigma*) than any of those are from each other. Further, the Old World monoecious *Oreosycea* do not appear to be a sister group to the *Pharmacosycea*, as has been proposed, but rather are most closely allied with the monoecious, pantropical *Urostigma*. Indeed, the New World *Urostigma* (mostly strangling species) appear to be more closely related to Old World dioecious species than they are to the New World monoecious *Pharmacosycea*. Although portions of the high level phylogenies of both the figs and their pollinators are poorly resolved, congruent phylogenies and the implied strict-sense co-evolution appear to present the best working hypothesis (Herre *et al.*, this issue; see Fig. 5). Because most of the variable sites occur along the branches leading to the representatives of the different subgenera rather than at the base of the branches separating them, it appears that the recognized subgenera of *Ficus*, along with their pollinators, radiated very rapidly and then persisted, accumulating changes independently.

Further, the clear separation of the lineage leading to the New World *Pharmacosycea* from the rest of the figs holds several interesting implications. One possible scenario to account for present distributions would be separation of New (*Pharmacosycea*) and Old (the rest) World fig lineages followed by a 'colonization' of the New World by what became the *Americana* section of *Urostigma*. Additional

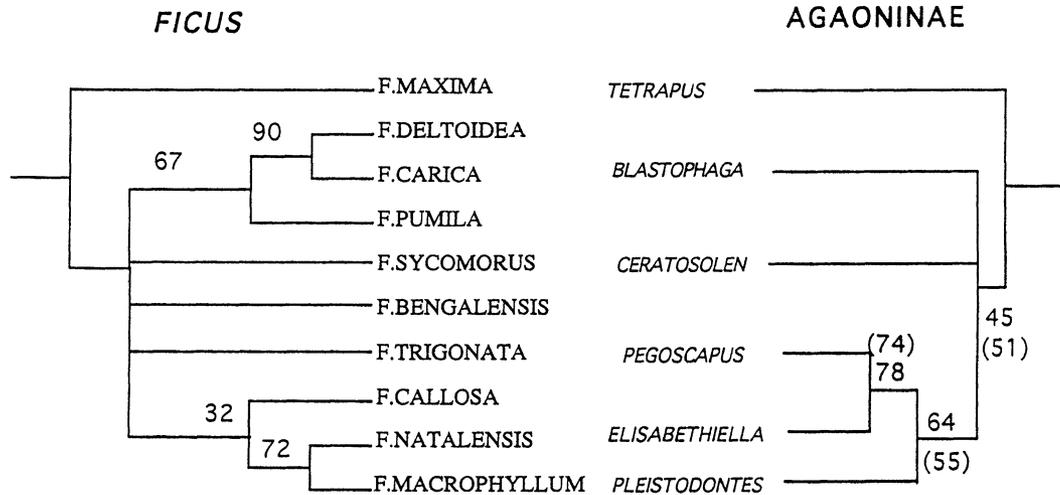


FIG. 5. The association between the consensus phylogenetic reconstructions among species representing the major recognized subgenera of the figs from different parts of the world (based on sequences of chloroplast *rbCl* and *tRNA* spacer genes) and the associated genera of pollinator wasps (based on mitochondrial 12s and COI–COII sequences). Although there are unresolved portions of the reconstructed phylogenies, the pattern is consistent with a predominance of strict-sense co-evolution (see text).

information that would be potentially useful for reconstructing biogeographical histories can be obtained from the relationships among the non-pollinator wasp fauna (Machado *et al.*, this issue), as well as the other dipteran and coleopteran groups that are associated with the figs their pollinators (Lachaise *et al.*, Perrin *et al.*, this issue).

Although the diversity of the wasp taxa for which molecular data are available is still somewhat limited, with the exception of true parasitoids, all the pollinators and non-pollinators (such as *Idarnes*, *Sycoscapter*, *Philotrypesis*, etc.) associated with fig syconia appear to constitute a monophyletic group (family Agaonidae, *sensu* Boucek). This finding strengthens the idea of a single origin for the pre-agaonid, and providing a solid foundation for understanding the origin of the mutualism. Apparently, an initial diversification between pollinating and non-pollinating wasps was then followed by speciation and ecological radiation, particularly among the non-pollinators. Given that pollinators and non-pollinators are sister groups, an appropriately calibrated molecular clock could be used to estimate the time since initiation of the fig–wasp system as it is presently constituted (e.g. date of the closure of the syconium, when one lineage of wasps remained within the structure as pollinators and the other remained outside as parasites).

At a fine scale, the molecular work supports the generalization that distinct species of pollinator wasps are associated with distinct fig species. Similarly, each fig wasp has its own species-specific nematode species (Poinar & Herre, 1991; Machado *et al.*, in prep.). Further, each fig species has a distinct suite of non-pollinator wasps (Machado *et al.*, this issue). With few exceptions in the taxa sampled thus far, the phylogenies of the pollinators, the nematodes and the non-pollinators show very similar

patterns across a fine (species) scale (Fig. 6). Thus, co-speciation seems to dominate across at least three taxonomic levels. This pattern seems reasonable given the dependence of the nematodes on their host pollinators for transportation and the fact that the attractants to the pollinators are apparently similar to the attractants for at least some species of the parasites (Van Noort, Ware & Compton, 1989; Compton, 1993a, b; Ware *et al.*, 1993; Hossaert-McKey, Gibernau & Frey, 1994, this issue). Our tentative conclusion is that at almost all levels the dominant theme is co-speciation and co-evolution, with only occasional colonization events. These results imply the predominance of coupled, long-term evolutionary interactions among several different taxa (pollinator, non-pollinator, nematode and host plant). However, the generality of these conclusions will be tested by broadening the base of the species sampled. Specifically, unresolved questions of high priority include determining the frequency of colonization events and establishing their importance in providing the opportunity for reticulate evolution to take place. Also, the capacity of long-distance dispersal by the pollinators calls into question the mechanisms of speciation in these extremely speciose groups.

DISCUSSION

If the patterns suggested by the molecular information are correct, then there are many different implications for the types and rates of character evolution that is possible. On one hand, some unrelated taxa show very similar morphologies. For example, the characters that have been considered to unite the *Oreosyceae* and the *Pharmacosyceae* are likely to present a case of convergence. Similarly, this

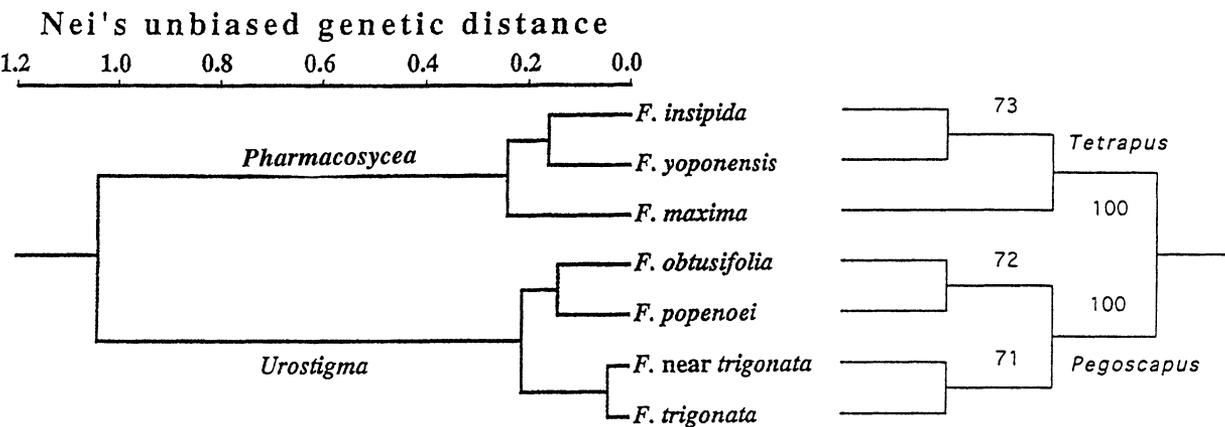


FIG. 6. The association between the phylogenetic reconstructions of seven species of Panamanian figs (based on a distance analysis of fourteen isozymes) and their respective species of pollinator wasps (based on parsimony analysis of mitochondrial COII gene sequences). These fig species and their pollinators show a pattern of strict-sense co-evolution (see text).

may also be true of the pollinator wasp taxa (*Pleistodontes*, *Tetrapus*, *Elisabethiella*, etc.) that have been joined in some phylogenetic reconstructions. Moreover, Van Noort (1991 this issue) has shown that even very distantly related pollinator and parasite taxa may converge on similar head morphologies. All of these observations are consistent with the idea that even morphological characters of fundamental functional importance may nonetheless be relatively evolutionarily flexible.

On the other hand, some relatively closely related taxa may show very different morphologies and ecologies. For example, related non-pollinator species, all in the genus *Idarnes*, show substantial divergence in the morphologies and behaviours of their males. The same is true for the species in the genus *Critogaster*, strongly suggesting a general lack of constraint in characters such as presence or absence of wings and the tendency to engage in lethal combat (Hamilton, 1979; Vincent, 1991; Machado *et al.*, West *et al.*, this issue). Additionally, even the ecologies of the *Idarnes* species can be strikingly different, with smaller species competing with the pollinators for oviposition sites in the figs' flowers, and larger species forming distinctive, large galls (Machado *et al.*, West *et al.*, this issue). Interestingly, an independent radiation the Old World genus, *Sycoscapter*, appears to have produced a similar pattern of ecologies among its member species (see Cook, this issue; L. Chou, pers. comm.). Detailed histological and developmental studies exploring the mechanisms underlying the different types of wasp exploitation of fig fruits across these different taxa would be particularly valuable.

The aforementioned examples of convergence and divergence suggest the capacity for flexible evolutionary change in both figs and the wasps. However, most of these examples have concerned the evolutionary malleability of single traits considered essentially in isolation. Returning to the theme of the importance of interactions among characters it is worth re-emphasizing that few, if any, characters function and evolve in isolation from others. For example, the potential relationships among fruit size,

TABLE 2. Summary of BCI species ecology. The suites of characters that tend to be associated with fig species that possess either large or small fruit (see text).

Small fruit	Large fruit
Small leaf	Large leaf
Fine branching architecture	Coarse branching architecture
Ripens red	Ripens green
Bird dispersed	Bat dispersed
Visual cues	Scent cues
Asynchronous fruit ripening	Synchronous fruit ripening
Air cooled	Water cooled
Few stomates on fruit surface	Many stomates on fruit surface
Few foundresses	Many foundresses
Seed poor	Seed rich
Wasps female biased	Wasps less female biased
Avirulent nematodes	Relatively virulent nematodes

physiology, wasp reproductive success and seed dispersal of the *Urostigma* species that have been studied intensively in Panama have all been mentioned during the course of this overview. Indeed, these species show some fairly consistent associations among suites of characters that suggest functional, adaptive linkages (Herre, 1989; see Table 2). Further, the pattern observed in the local Panamanian *Urostigma* species is generally repeated across other members of the group found across South America (C.C. Berg, pers. comm.). This suggests that there are usually multiple consequences for any evolutionary change in most characters. Therefore, only through comparing combinations of character states across many species is it likely that the interactions among the characters, and their consequences, can be understood.

As mentioned earlier, the size of fig fruits influences the relative importance of evaporative and diffusive cooling in full sunlight, with larger fruits requiring greater rates of transpiration in order to maintain internal temperature that

will sustain the developing pollinators (Patiño *et al.*, 1995). Additionally, fruit size has been implicated by several other studies as a correlate of other phenomena important in the fig and wasp interaction. In general, fig species characterized by larger fruits are pollinated by more foundress wasps per fruit (Herre, 1989). Further, the species that are characterized by higher numbers of foundresses harbour more virulent species of host-specific nematodes (Herre, 1993). In short, from the point of view of water lost, the proportion of female pollinating wasps produced and the inefficiencies associated with increasingly virulent nematode parasites of the wasps larger fruit would appear to present a less efficient packaging than do small fruit. Earlier studies suggest (Herre, 1989), and later studies confirm (Kalko *et al.*, this issue) that larger-fruited fig species, which tend to be relatively seed-rich, are dispersed preferentially by larger species of bats that generally are capable of dispersing seeds greater distances. Therefore, it appears that the apparent disadvantages of increased fruit size might be balanced in nature by an increased capacity to disperse seeds.

Essentially the small, red, primarily bird-dispersed fruits studied in Panama do not produce detectable scents nor do they have porous fruit surfaces which exhibit high stomatal densities. Without a porous surface, evapotranspiration and its associated cooling becomes less feasible. Fortunately a small object, such as these fruit, does not require evaporation to avoid overheating and therefore does not require a porous surface; nor do these small fruit photosynthesize at appreciable levels, a process that might require a substantial investment in photosynthetic enzymes. Interestingly, the protein content of the larger, porous-surfaced, transpiring, scent-producing, green, photosynthesizing fruits that are preferred by bats tend to be much higher (Kalko *et al.*, in prep.; Wendeln, in prep.).

In providing an overview of studies of the Panamanian figs and their associates I have emphasized the ecological and evolutionary importance of multiple levels of interactions among different fruit and wasp characters. This perspective is most strongly suggested by the recurring patterns observed among the suites of fruit characteristics of these Panamanian species. These relationships also seem to be generally representative of New World figs as well. Further, I have provided a series of functional hypotheses to account for those observed patterns. Old World figs often show patterns that are not consistent with these observations (e.g. the existence of fig species with large red fruits). Although the Old World fig species have not been studied with these functional hypotheses in mind, comparisons between well-studied fig systems in both New and Old World (e.g. Compton, 1993a; and Compton, this issue) will be especially valuable. For example, appropriately designed studies will be able to determine what the associations of fruit characteristics are in Old World figs, and to test whether there are consequences that the perceptual and behavioural differences in the respective assemblages of frugivores have for the fruit that they eat (Kalko *et al.*, this issue). All of this emphasizes the point that studying many characters in many species at many sites is clearly the best way to proceed. Fortunately, both individually and collectively, this is increasingly taking place.

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