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Seasonality in the reproductive phenology of *Ficus*: Its evolution and consequences

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Summary. Ficus can only reproduce if they are pollinated by mutualistic wasps that breed within the figs. Pollen-loaded wasps enter the figs when the female flowers are receptive. Several weeks later, their offspring load pollen within the fig and then emerge. As individual trees typically produce crops of synchronous figs at long intervals, the short-lived wasps have to move to another, receptive, tree. The wasp population can only survive, and hence the fig population reproduce, if there are trees fruiting all over the year. When only few trees are present within a population gaps in the flowering sequence may lead to the extinction of the local pollinator population. Two models are presented. One investigates the number of trees necessary in order to sustain a local pollinator population when the tree population has a seasonal pattern of fruiting. The second model investigates how such a seasonal pattern may evolve within a fig population as a result of individual selection on the trees. It is shown that pollinator populations are fragilized under seasonal conditions. Hence, the breeding system of *Ficus* limits their expansion into highly seasonal habitats. Seasonal habitats may also lead to seasonal adjustment of male versus female investments and to the evolution of dioecy.

Key words. Ficus; reproductive phenology; sex allocation.

Introduction

The relationship between *Ficus* and their pollinators constitute one of the best studied cases of obligate species-specific mutualistic pollination. *Ficus* have to be pollinated by tiny wasps that only breed within the enclosed inflorescence or fig. With few exceptions, each of the some 700 *Ficus* species has its own species of pollinator. Mated female wasps enter the figs when female flowers, up to several hundreds enclosed within each fig, are re-

ceptive. The wasps lay their eggs in some flowers, each larva developing at the expense of one seed, and pollinate other flowers that will produce seeds. In the absence of the pollinator no pollen penetrates the fig. Some weeks later, when adult female wasps are ready to leave the fig, the pollen is ripe. The females become pollen-loaded while leaving the fig. The females then search for a receptive fig of the right species in order to breed (for a detailed description see Galil[4] and Verkerke[12]). According to current knowledge the wasps survive for only a (very) short time outside the figs[7].

As a consequence of this peculiar pollination system, a population of figs can only reproduce if it is able to sustain a population of pollinators. Being capable of sustaining a population of wasps is therefore critical. This is, however, in most species, a property of the fig population and not of the individual tree. Although traits can be identified that would increase the chance that wasps can persist, these traits are not always the same ones that increase individual performance. It is therefore possible that under some local conditions, individual selection on the trees will lead to the local disappearance of the wasp and hence of the fig population. In the present paper we will focus on the consequences of seasonality on the persistence of a pollinator population.

The flowering phenology of a large number of Ficus species can be described as follows[3,6]. Each tree produces well-defined crops at irregular, long intervals; all the figs of a crop are visited during a few days and the crop ripens and releases wasps for a few days some weeks later. As the adult wasps are short-lived, the pollinators emerging from a tree cannot wait until the next crop of that tree is receptive: they have to find another tree bearing receptive figs at that time. This is possible because of among-tree asynchrony. If there is a period during which no receptive figs are produced within the population, all the wasps emerging during that period will die without leaving any offspring. When all the crops harboring wasps release them during such a period, the local population of wasps dies out, and as a consequence the fig population is no longer able to reproduce. A local wasp population can therefore only survive if there are crops produced throughout the year (see Bronstein[3]). As each tree flowers at long intervals, this can only be achieved via the among-tree asynchrony that has been observed in the field. The survival of the wasp population depends on there not being too many and too long periods during which no receptive figs are produced. The more trees that are present within the population the shorter and the rarer such periods will be: hence, the higher the number of trees, the less likely it is that the local population of wasps will go extinct.

The number of crops produced each year within a fig population is not the only factor determining the likelihood that the local wasp population will not go extinct. Another major factor is the year-round distribution of crops. If only very few crops are produced during one season, that season will be the most critical for the survival of the local wasp population as gaps in the flowering sequence will be more frequent and longer during that period. More trees will therefore be necessary to ensure the persistence of the local wasp population than if there had been no seasonality in crop production within the population.

Only very few thorough field studies are available on the phenology of Ficus species. But even in the two studies conducted in the rain forest[10,11], i.e., under the most homogeneous year-round conditions, the distribution of crops over the year was not uniform: although each tree apparently fruited at its own rhythm, independently of other trees, there were seasonal peaks and seasonal lows in numbers of trees fruiting. A general feature of figs is therefore year-round fructification within a population, but with seasonal peaks and lows in numbers of trees fruiting.

We first tried to determine, through simulations, the consequences of this general property of Ficus – a non-uniform year-round distribution of crops and independence among trees – on the number of crops that has to be produced each year within a fig population in order to allow the maintenance of a wasp population. We then examined how individual selection on figs may lead to the evolution of seasonal distributions of crops under seasonal conditions. It was then possible to predict when the result of individual selection on figs may lead to the disappearance of the pollinator, or, in other words, whether figs may be excluded from some habitats because conditions lead to a breakdown in stability of the fig-pollinator mutualism. It was also possible to predict when gender specialization should occur within fig species.

Effect of a seasonal fruiting pattern on wasp survival

The model

If a very large number of trees were fruiting within a population a smooth distribution of crops over the year would be observed. When the number of trees is reduced, some irregularities will appear due to chance events. When the number of trees is highly reduced, the irregularities may become so large that during a period of time there are no crops produced, and the population of wasps may die out.

The aim of our simulation model was to determine the consequences of such irregularities, for given numbers of crops per year, for the probability that the population of wasps will not go extinct over a period of time, i.e., the number of trees that have to be present for individuals within the population to be able to reproduce.

We assumed in our stochastic simulation model that, if the number of crops within the population were infinite, they would follow a temporal distribution that we defined a priori. We then assumed that an individual tree

did not know when other trees were fruiting. Therefore all the fructification dates within the population were supposed to be independent of each other. In order to obtain this, in the simulation model, for each crop of a year, we drew its date of pollinator receptivity at random within the predefined distribution (and not within a uniform distribution). In some simulations, for instance, a crop had twice as many chances of becoming receptive on date A as on date B. As a result, on average, there were twice as many trees receptive on date A as on date B, but, due to chance events, in some simulations there could be fewer trees receptive on date A than on date B.

For each crop we then determined when it would release pollen-carrying wasps. This was achieved by adding to the date of receptivity the duration of wasp development. As this duration is slightly variable, we also had to introduce some variance on this parameter. In all the simula-

tions we used a wasp development duration of 5 ± 1 weeks, a realistic value for some *Ficus* species (see for instance Michaloud[10]).

For a given number of crops and a given flowering distribution, dates of receptivity and dates of wasp emergences were thus determined for five successive years. It was then assumed that wasps were released during the first five weeks of the simulation so that early extinction, due to lack of initial establishment of the wasps, would not occur in the model. The model then determined the path followed by the successive generations of wasps among fig crops and tested whether the wasps had not gone extinct after five years.

It is assumed in the model that the wasps will emerge from a crop on a given week and that they have to find a receptive crop the same week in order to breed. Wasp success will be determined by three factors: the duration of wasps attractivity of a crop, the duration of wasp emergence and the life span of the wasp. Wasp emergence duration is easy to monitor and has often been observed; it is often less than a week. Duration of attractivity can only be determined experimentally, since failure of wasps to arrive on a tree can be due to unavailability of wasps as well as to non-receptivity of figs. Natural arrivals are most often only spread over a few days, but Bronstein[2], for instance, has demonstrated experimentally that wasps will enter figs before and after the period of wasp arrival in nature. Therefore, published data on wasp arrivals do not give a reliable estimate of duration of attractivity. Life span of a wasp can be determined only through observations that are almost impossible to do (but see Kjellberg et al.[7]). We believe, however, that the value introduced in our model is realistic. If the wasps emerging on a given week could visit crops receptive the same and the following week, fewer trees would be necessary to sustain a wasp population, but the qualitative results would probably not be modified.
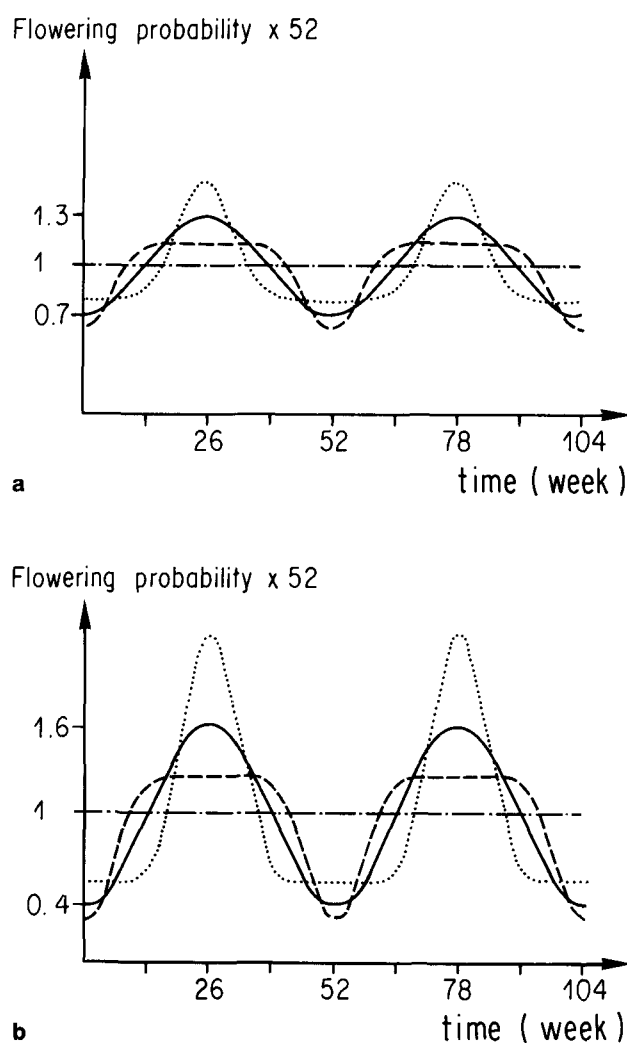
Flowering probability x 52

Flowering probability x 52

Figure 1. The distributions of flowering probability used in the models. ———, broad peak flowering period; · · · ·, short peak flowering period; ——, equilibrated flowering periods (sinusoid); — · —·, uniform flowering probability. *a* Twofold maximum among week difference of flowering probability. *b* Fourfold maximum among week difference of flowering probability.

The crop distributions

The general form of a seasonal distribution of crops within a fig population can be characterized by two aspects.

1) 'Shape': the relative length of periods of high and low intensity of crop production.

2) 'Intensity': the amplitude of the relative fruiting intensity variation (expected number of crops per week) during high and low periods, respectively.

Three shapes were used (fig. 1). One had a broad peak flowering period, one had a short peak flowering period and one was symmetric as high and low periods were of equal length (subsequently called equilibrated).

Two different values of relative intensity were used: a twofold difference and a fourfold difference (fig. 1a and b).

A uniform distribution was also used as a non-seasonal reference system.

The probability that a crop of a year will flower during that year is equal to one. In the uniform distribution, the probability for a crop to flower on a given week is therefore equal to 1/52 (fig. 1). It is also the mean weekly flowering probability of all the distributions of flowering probability. The part of the distributions lying above the 1/52 line corresponds to above mean expected numbers of receptive crops produced (fig. 1).

For each value of the parameters, the model was run one thousand times in order to provide estimates of extinction probabilities.

Results

The results are presented in table 1. Clearly more trees were needed to ensure wasp survival when there was seasonal variation in fruiting intensity within the population. In order to ensure the survival of the wasps over 5 years in 50% of the runs, 100 crops a year were necessary for the uniform distribution, 110 with the twofold variation in fruiting intensity and 140 with the fourfold variation in fruiting intensity. In order to ensure the survival of the wasps over 5 years in 95% of the runs, 120 crops were necessary for the uniform distribution, 140 for the twofold variation in fruiting intensity and 190–200 for the fourfold variation in fruiting intensity.

There was almost no effect of the shape of the seasonality curve on the number of crops necessary; only the intensity of flowering seasonality had a serious impact on numbers of crops necessary. This can be explained a posteriori by compensation between two factors. On one hand, when the period of low crop production is relatively long, there are automatically more crops per week during that period than when it is short, so that wasp extinction probability per unit of time during the low production period is lower; on the other hand, this period is longer. This is clearly apparent in figure 1, a and b. As an extreme, a distribution with a very short period of high (or low) fruiting is almost equivalent to a uniform distribution. The development time of the wasp may also be a critical factor here, as, if it is long, it can enable the wasp to bridge a period of very low fruiting intensity. The general impact of wasp development time and variance on this parameter will be investigated elsewhere for a non-seasonal system.

Discussion

Our work with the model has pointed out two important practical consequences. First, it is not critical to have a very precise description of a population's fruiting distribution, which would necessitate observing thousands of crops, in order to determine the yearly number of crops required to sustain a population of wasps. It is possible to use thorough field observations – on some hundred(s) crops – to predict the number of trees necessary to keep a wasp population going.

Table 1. Success of wasp persistence over a 5-year period according to the number of crops produced per year within the population and according to the crop distribution

a) Uniform distribution of flowering over the year

Number of crops per year	Number of failures	Number of successes	Proportion successes
60	1000	0	0.00
70	990	10	0.01
80	881	119	0.12
90	617	383	0.38
100	317	683	0.68
110	136	864	0.86
120	51	949	0.95
130	17	983	0.98
140	9	991	0.99
150	4	996	1.00
160	0	1000	1.00
170	0	1000	1.00
180	1	999	1.00
190	0	1000	1.00
200	0	1000	1.00

b) Twofold difference in numbers of crops produced between peak and low flowering periods

Number of crops	Proportion of successes		
	Short peak flowering	Equilibrated flowering	Broad peak flowering
60	0.00	0.00	0.00
70	0.00	0.00	0.00
80	0.04	0.04	0.04
90	0.17	0.18	0.24
100	0.40	0.43	0.45
110	0.64	0.62	0.64
120	0.80	0.78	0.82
130	0.93	0.89	0.89
150	0.95	0.96	0.95
150	0.98	0.96	0.97
160	0.99	0.98	0.99
170	1.00	0.99	1.00
180	1.00	0.99	0.99
190	1.00	1.00	1.00
200	1.00	1.00	1.00

c) Fourfold difference in numbers of crops produced between peak and low flowering periods

Number of crops	Proportion of successes		
	Short peak flowering	Equilibrated flowering	Broad peak flowering
60	0.00	0.00	0.00
70	0.00	0.00	0.00
80	0.00	0.00	0.00
90	0.01	0.01	0.04
100	0.02	0.03	0.11
110	0.10	0.13	0.21
120	0.21	0.23	0.36
130	0.34	0.38	0.47
140	0.53	0.50	0.60
150	0.64	0.65	0.70
160	0.77	0.74	0.81
170	0.83	0.82	0.86
180	0.91	0.90	0.89
190	0.94	0.91	0.93
200	0.97	0.94	0.94

Will fig reproduction often be constrained by pollinator survival? What part do population size and seasonal crop grouping play in such instances? The answer will very much depend on mean number of crops per year for individual trees, and number of trees present within a population. It is however clear that a population of figs

cannot breed if it is restricted to a few individuals, especially if there is a seasonal flowering pattern.

Another open question is how frequent local extinction of wasps can occur without leading to local extinction of the *Ficus* population. For instance, with a 95% probability of survival of the local wasp population over 5 years, there is a 50% probability of survival for 65 years (0.95[13]). Rare wasps transfers between adjacent populations may then be sufficient to counteract local extinctions and keep the system going. It is also probable that over such a long period of time, there will be some climatic accidents–beyond the scope of our model–that will affect the survival of the wasp population, such as the typhoons witnessed by Hill[5] in Hong Kong.

The evolution of crop grouping under seasonal conditions

The second question we address in this paper is, how will crop grouping evolve when some periods permit better seed and/or wasps production?

Although wasps and seeds are produced in the same organs, female flowers, and develop simultaneously within a fig, periods favorable for their production may be different. For instance, the presence of seed dispersers or good germination conditions have a major influence on the efficiency of seed production (number of seedlings produced per unit of investment) but not on wasp production. It should, however, be noted that as long as seed set is not limited by pollinator availability, the male fitness of a crop will not be determined by the absolute number of wasps emerging: it will be determined by the number produced relative to other crops releasing wasps at the same time. If conditions are bad, they will be bad for all those crops. It is therefore only during periods when pollen is limiting that the season quality for wasp production is relevant. We chose to restrict our simulation model to a situation in which there were periods of the year permitting at the same time higher seed and wasp production in a crop.

The model

A population of trees was supposed to be made up of several phenotypes, one flowering with a uniform probability all over the year, and three 'seasonal' phenotypes. Seasonal phenotype 'X' is characterized by a normal distribution of flowering probability, centered on week $X \pm 1.4$ of the year.

The parameters introduced into the model were:
– The peak flowering week of the seasonal phenotypes. In the following we will assume that each tree, whatever the phenotype, flowers once a year; otherwise it would have been necessary to define several peak flowering weeks for each seasonal phenotype and the general analysis would have been more difficult.

– The initial frequencies of the different phenotypes. Modifying the initial frequencies of the different phenotypes did not affect the final result so that most simulations were started with 5 trees of each seasonal phenotype and 385 non-seasonal trees. This corresponds to the invasion of a non-seasonal population by seasonal phenotypes.
– The number of trees present within the population (we chose 400 trees in our simulations, in order to have a number much larger than what was needed to sustain a population of wasps in the preceding model).
– The mean development time of the wasp (the same value was used as in the previous model, 5 ± 1 weeks).
– The number of crops at the female stage that could be fully fertilized by the wasps emerging from a standard male crop. We defined the standard male crop as a fully visited crop produced during the worst season.

The model was then run for six years without modifying the frequencies of the different phenotypes. The crops were drawn at random within the predefined flowering distributions and the development time of the different crops. It was assumed that a large number of wasps searching for figs were present during the first 5 weeks. The path taken by the different generations of wasp was then computed and their abundance each week was calculated.

Using this information, the female and male reproductive success of the different phenotypes was calculated. The female reproductive success was determined by summing the seed production of the different flowering episodes of that phenotype. Seed production of a crop is determined by the season quality curve and potential limitation of seed set due to insufficient pollination. The male reproductive success of a phenotype was determined by summing the number of seeds sired by the pollinators emerging from the different crops of that phenotype.

The first year of each simulation turned out to give significantly different fitness values from the following 5 years due to initial conditions. The five following years gave homogeneous results. Therefore only the five last years were used to calculate mean fitnesses. The mean fitnesses were computed for 20 different simulations. The initial frequencies of the different phenotypes were then modified according to the calculated fitnesses. The model was then rerun until either the mean fitnesses of all surviving phenotypes became equal or until the wasp population became extinct.

Values chosen for parameters investigated

Three forms of season quality were used, one with equally long good and bad seasons (sinusoid), one with a short good season and one with a very short good season, and two different amplitudes of the difference in season quality between bad and good season, 2 and 4 (fig. 3).

As the model only allowed the introduction of a limited number of seasonal phenotypes, we chose our three seasonal phenotypes to fall at 3 points separated by 5-week intervals, so that they could successively pollinate each other and hence frequency interdependence among them would be clear.

The peak of the good season was fixed at week 26. We made two sets of simulations, one with phenotypes '16', '21' and '26', and one with phenotypes '21', '26' and '31'. Two values for the number of crops a standard crop could fertilize, 100 and 5, were used. The first value suppresses pollen limitation, while the second one allows the consequences of pollen limitation to be seen.

Results

The results are presented in table 2. Some general features are clearly apparent. When seasonality is strong and the good season short, the high frequencies reached by seasonal phenotypes may lead to an excessive reduction of the number of non-seasonal trees. The baseline in figures 2 and 3 represent the number of non-seasonal trees expected to become receptive each week. When this number becomes too low, irregularities due to chance events will lead to the disappearance of the pollinator population as in the previous model. When seasonality is strong individual selection on figs to flower on the best dates may lead to extinction of their pollinators.
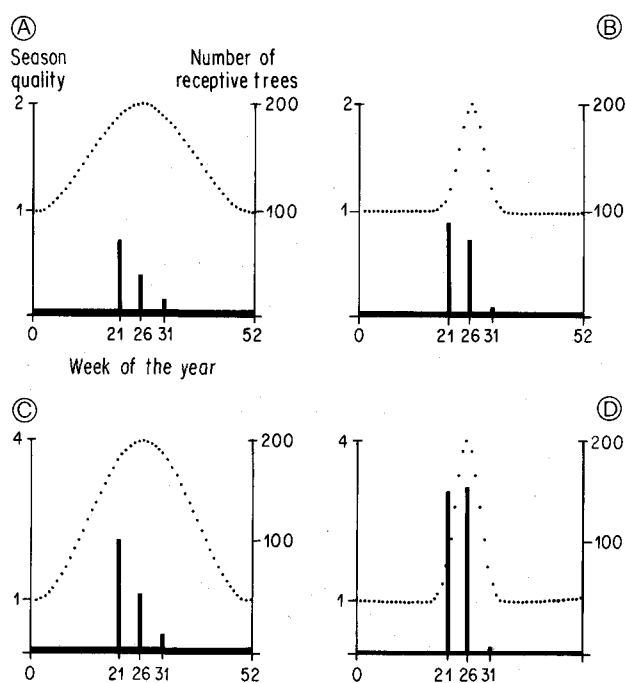

Figure 3. Season quality curves and equilibrium frequencies in the phenotype '16–21–26' simulations. Same legend as figure 2.

Figure 2. Season quality curves and equilibrium frequencies in the phenotype '21–26–31' simulations. Two shapes, sinusoid (A, C) and very short good season (B, D) and two amplitudes, 2 (A, B) and 4 (C, D) are represented. . . . ., season quality curve; ▮, equilibrium frequencies (the thickness of the baseline gives the mean number of non-seasonal trees receptive each week).
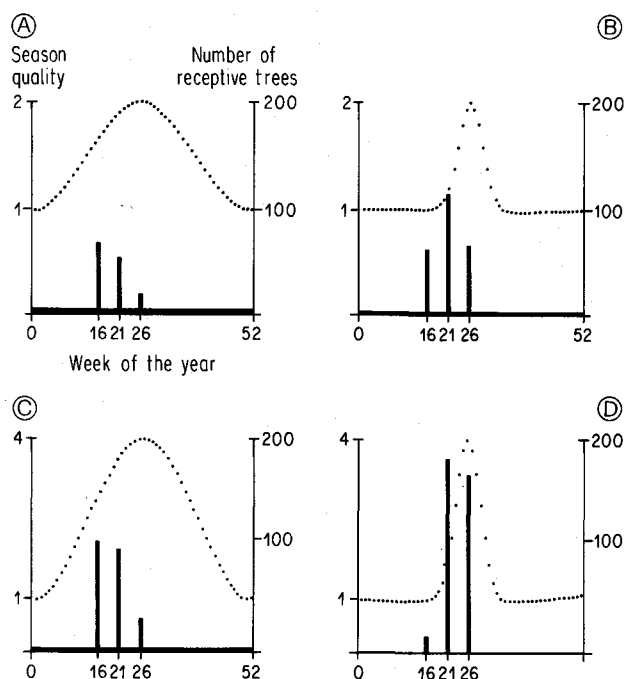
Phenotype '31', flowering 5 weeks (one generation of wasps) after the peak of the good season, always remains at very low frequencies. Phenotype '21' flowering 5 weeks before the good season, reaches higher frequencies than phenotype '26' flowering at the peak of the good season. The frequencies reached by phenotype '16' flowering 10 weeks (2 generations) before the peak of the good season were remarkably high. This seasonal phenotype was the most adundant in the equilibrated seasons simulations, although the flowering dates used in the simulations were not in its favor; it was always only pollinated by non-seasonal trees, and therefore could be constrained by insufficient pollinator visits.

The relative contributions of male and female function to the fitness of a phenotype varied (table 2, X-value). Early flowering phenotypes had higher male success and lower female success than the phenotypes flowering later on (phenotype '31' is abnormal in this respect because it remained at low frequencies and therefore could pollinate a proportionally non-negligible number of non-seasonal crops; in a more complete model, this number would be much lower). This effect increased with the shortening of the good season and with stronger season amplitude. There was no consequent difference in the male versus female fitness of phenotypes '21' and '26' between simulations made with phenotypes '16–21–26' and simulations with phenotypes '21–26–31', except that, when pollen was limiting, phenotype '21' in the '21–26–31' simulations was more efficient as a male.

Pollen limitation always made the first phenotype to flower relatively more efficient as a male. This is because

Table 2. Equilibrium frequencies and male success of 3 seasonal phenotypes according to season form (shape and intensity) in a population of 400 trees. Starting frequencies for each seasonal phenotype in each simulation were 5 trees.

	Season¹	Moderate intensity			Strong intensity		
		+/−	+	++	+/−	+	++
Non-limiting pollen	Phenotype	21/26/31	21/26/31	21/26/31	21/26/31	21/26/31	21/26/31
	Frequencies²	66/30/8	85/36/5	86/43/2	100(42/10	134/51/3	164/109/1
	X³	41/37/41	41/30/38	50/21/42	38/33/35	39/20/31	65/05/35
Limiting pollen	Phenotype	21/26/31	21/26/31	21/26/31	21/26/31	21/26/31	21/26/31
	Frequencies	62/34/9	78/51/5	85/71/3	97/50/11	155/157/12	151/155/1
	X	46/37/40	56/25/38	70/16/42	44/30/36	88/12/14	91/06/29
	Season	Moderate intensity			Strong intensity		
		+/−	+	++	+/−	+	++
Non-limiting pollen	Phenotype	16/21/26	16/21/26	16/21/26	16/21/26	16/21/26	16/21/26
	Frequencies	65/41/15	84/69/25	73/80/38	100/66/22	127/159/50!	75/180/106!
	X	48/40/37	56/38/28	59/48/18	50/36/30	77/32/07!	83/62/03!
Limiting pollen	Phenotype	16/21/26	16/21/26	16/21/26	16/21/26	16/21/26	16/21/26
	Frequencies	62/50/17	80(102/35	59/113/64	100/92/26	33/193/148!	17/187/172!
	X	56/38/37	77/37/22	77/56/12	63/30/27	?	87/83/03!

¹ Shape of season quality curve: +/− : sinusoid; + : short good season; + + : very short good season.
² Frequencies: number of trees of each phenotype at equilibrium (when followed by!, the number at which the population of wasps dies out is given)
³ X: percentage of the fitness of a phenotype due to male function (when followed by!, the fitness is measured a few generations before wasps collapse: the? means that frequencies were changing too fast to give a good estimate).

on one hand, it had to rely on few non-seasonal trees for pollination and therefore its seed production was limited, and on the other hand it always managed to fully pollinate the following phenotype.

Discussion

The first obvious conclusion of the simulations is that individual selection on fig trees to flower at times that maximize seed and wasp production may result in a breakdown of the pollination system; it leads to gaps in the year-round flowering sequence necessary to allow the pollinator population to reproduce locally. Therefore, the typical fruiting phenology of monoecious figs may limit the expansion of such species towards highly seasonal conditions. It may explain why *Ficus* are absent from temperate climates.

The second conclusion is that the relative value of male versus female investment for a tree depends on the week on which it is flowering. Sex allocation adjustment towards the production of either seeds or wasps is therefore expected. The result of such adjustments will affect the results obtained, through frequency-dependent mechanisms. For instance, individuals flowering on week 26 (the 'best' week) should allot more to female function. This should increase male fitness of the trees flowering on week 21. This should in turn shift the selected investment of trees flowering on week 21 towards wasp production, thus reducing the number of flowers to be pollinated, on week 21, by the trees that flowered on week 16. This in turn should decrease the frequency of those trees at equilibrium. As a result, the trees flowering on week 21 may be less well visited and therefore produce a more male biased investment. Here, introducing sex allocation adjustment further destabilizes the system. Selective shifts of the wasp versus seed production should be rather easy

in figs as the same organs, female flowers, ensure seed and wasp production and a simple change in style lengths would be sufficient.

As an extreme, under the most seasonal conditions, before the wasps disappear, the first trees to flower are, in a functional sense, virtually males and the last ones are virtually females. Highly seasonal conditions could lead (if the wasp could be maintained) to complete sexual specialization, one phenotype becoming male and another one female. A male seasonal phenotype that could produce a small crop 5 weeks earlier in order to multiply the pollinators would then be favored, by individual selection, if the wasp tended to remain on the tree on which they were born (this behavior of the wasps has been observed on *Ficus carica*[8]). If so, the male trees would become wasp breeders selected to maintain the wasps over the yearly cycle and hence individual selection under highly seasonal conditions would no longer lead to wasp extinction. The breeding system of such *Ficus* species could, however, still limit their reproduction under highly seasonal conditions due to developmental constraints on the wasps and on the figs[9].

In order to confirm and expand the results obtained, a less simplistic model, enabling adjustment of flowering intensity during all the weeks of the year and allowing for different allocations to male and female function, is needed. However, the similarity between the relative male to female success of a phenotype in the '16−21−26' and the '21−26−31' simulations tends to show that even a very simplistic model may give robust answers.

Conclusion

The breeding system of monoecious *Ficus* held to be typical by Janzen[6] − individual reproductive synchrony and population level asynchrony − is definitely problem-

atic under seasonal conditions. Populations in seasonal environments must produce many more crops in order to be equally viable.

Resource allocation to male and female function should also vary over time, the allocation to male function progressively decreasing over the good season. This conclusion should be rather easy to test. In order to do this, numbers of seeds and numbers of individuals of the pollinator species (including males) should be measured within fruits over the season, in *Ficus* species occurring in obviously seasonal environments. This would provide evidence on whether *Ficus* are capable or not of controlling the proportion of flowers allotted to pollinator production.

The models show that seasonal conditions may favor evolution towards functional dioecy in *Ficus*. Dioecious species may be more resilient to strong seasonality than monoecious ones because male trees may be selected, at the level of the individual, to maintain the pollinator over the bad season. As suggested by Berg[1], dioecious species may also be reproducing better under seasonal conditons as all the female function is expressed during the best period.

Why then has dioecy not evolved in American figs, even in seasonal climates? Field studies on American monoecious figs under such conditions are needed.

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