

Group selection in plant populations

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Summary. Several mechanisms have been proposed for group selection, to account for the evolution of altruistic traits. One type, Neighbourhood models, suggests that individuals react with those immediately around them, but with no recognition mechanism. The organization of plant populations seems especially favorable for this type of selection. The possibility of Neighbourhood selection was investigated by simulating a plant population. It was possible for an altruistic trait to evolve, though only under restricted conditions. The main requirement was gene flow only by very restricted pollen dispersal, and a high benefit : cost ratio in the altruistic relationship. Under conditions favourable for such evolution, the starting frequency of the allele, the initial pattern, and the population size, had little effect. Inbreeding tended to prevent the increase of the altruism allele, though this depended on the mechanism of selfing. Known ecological features of plants are discussed that could be considered altruistic and hence require some form of group selection for their evolution, and whether the benefit : cost requirements are likely to be met. Neighbourhood models of group selection are a possibility in plant populations, and we therefore cannot exclude the possibility of altruism in plants. However, Neighbourhood selection is weak force, unlikely to be effective in the face of opposing individual selection. It may be more important as reinforcement of individual selection.

Key words: Group selection – Kin selection – Neighbourhood selection – Altruism

Introduction

Many models have been produced of group selection (*sensu lato*: Wade 1978) in animal populations. This

paper considers its possible significance in plant populations.

Group selection (*s.l.*) is that subclass of natural selection in which gene frequencies change because of effects of the allele on the reproductive performance of neighbours and/or relatives, rather than on the individual itself. The importance of group selection is that it allows the evolution of traits that cannot evolve by individual selection because, whilst beneficial to a population as a whole, they are deleterious to the individual carrier (Wright 1945; Boorman and Levitt 1980). Such traits are usually called 'altruistic' (Eshel 1972). This study is concerned with the evolution of such traits in plant populations.

There is no basic distinction between group selection (*sensu stricto*) and kin selection (Michod 1982; Wilson 1983 b), and the same equations can be used. In both, the altruistic allele is locally at a disadvantage, but also exists in a genetically patchy environment. The important condition for group/kin evolution to occur is therefore non-random association between genotypes (Levin and Kilmer 1974; Michod 1982). The various models differ in the mechanisms proposed for this non-random association:

1. "Reciprocity selection" (Boorman and Levitt 1980), or "Greenbeard effects" (Dawkins 1976), where organisms show altruistic behaviour to individuals with a morphological marker. This model does not seem to apply to plant-plant interactions.
2. "Kin selection" (*sensu stricto*), in which the non-random interactions are caused by an individual's recognition of its own kin (Eshel 1972). It is difficult to see the applicability of such models to plant populations.
3. "Wrightian" group selection models (Wright 1945) or group selection *sensu stricto* (Boorman and Levitt

1980), which depend on spatial isolation between discrete groups of individuals differing by chance in their genetic composition (Maynard Smith 1964; Boorman and Levitt 1972; Wilson 1975; Matessi and Jayakar 1976; Mirmirani and Oster 1978). Early models postulated groups that were permanently isolated, with selection operating via differential extinction. Much of more recent theory has followed Wilson's (1975) "trait group" or IGS (Intrademic Group Selection: Wade 1978) model in which the groups are isolated only for a limited time, perhaps for part of the year. In these models, selection operates by groups with different genetic composition contributing different numbers of progeny to the following year's population. When the groups are based on kinship these models are essentially Kin models (Matessi and Karlin 1984; Fix 1985). When they are based on phenotypic recognition (Nunney 1985) they are essentially Reciprocity models (see above). Apart from these cases, there is considerable doubt whether such models can lead to the evolution of altruism (Charlesworth 1979; Darlington 1981). The basic problem is that they depend on the conflicting assumptions of low migration rates between groups but the ready replacement of groups that go extinct. Levin and Kilmer (1974) suggested that this might be resolved by a behavioural bar to immigration into an existing group, but this suggestion would not seem applicable to plants.

4. "Neighbourhood selection" (Nunney 1985) in which an individual benefits neighbours, irrespective of their genotype or relationship. However, with limited gene flow those neighbours have a good chance of being related to that individual, and bearing some of its own genes. Such low gene flow has been called viscosity (Murray and Gerrard 1984). Eshel (1972) suggests that a sufficiently high viscosity will ensure the fixation of any altruistic trait, a rather extreme comment. Like Reciprocity and Kin models, Neighbourhood models do not require any absolute discontinuities in the population breeding structure (Wade and Breden 1981), but like Wrightian models they need no recognition process.

Plants have all the characteristics to facilitate Neighbourhood models. They are sedentary. Gene flow in many plant populations is severely restricted (Levin and Kerster 1974). The population will therefore be highly viscous, and a plant's near neighbours will therefore tend to be fairly close relatives. This can be seen in the spatial distribution of novel genotypes (Gottlieb 1973), in genetic heterogeneity over short distances (Schaal 1975; Levin 1977; Linhart et al. 1981), and in crosses between near neighbours as higher embryo abortion (Levin 1984) and lower fitness (Schemske and Pautler 1984). Therefore, plants are

ideally suited for Neighbourhood models of group selection.

The purpose of this paper is to examine whether such Neighbourhood selection could occur under conditions realistic for plant populations, and if so what aspects of population structure facilitate its operation.

The model

A simple basic model was simulated. It comprised a 625-plant population with plants arranged at regular intervals in a square grid. A few simulations examined smaller populations. The plants of the basic model were assumed to be self-incompatible annuals, with non-overlapping generations. A few models examined the effect of self-fertilization.

The model involved a single two-allele locus with semidominance. The "wild type" allele produced some selfish behaviour in the plant. A selfish homozygote with neighbours of the same genotype was assumed to produce 25 pollen grains.

The 'altruistic' allele produced, when homozygous, altruistic behaviour. This increased the growth, and hence fitness as seen in pollen production, of the four immediate neighbours. This effect was fixed at five extra pollen grains per plant-to-plant benefit in all simulations. The altruist, in benefitting its neighbour, was assumed to suffer a 'cost-of-altruism', producing fewer pollen grains.

Thus the fitness of an individual, as seen in the number of pollen grains produced, was:

$$Y_i = 25 + \sum_{j=1}^4 5 n_{ij} - C s_i$$

where:

Y_i = the fitness of individual i

n_{ij} = if neighbour j of plant i is an altruist then 1, else 0

C = the cost-of-altruism (a value from 0 to 5)

s_i = if plant i is an altruist then 1, else 0

Pollen produced by each plant was in the basic model dispersed according to a 4-neighbour stepping-stone model (Levin and Kerster 1975), i.e. at random to the plant's four nearest neighbours on the grid, at the cardinal compass points. Other dispersal regimes examined were:

panmixia (pollen dispersal at random through the population),

8-neighbour stepping-stone (equal chance of dispersal to the eight nearest neighbours, N, NE, E, SE, S, SW, W and NW),

a leptokurtic distance distribution (Levin and Kerster 1975) with mean dispersal distance either 1.25 or 2.5

Table 1. Time to fixation (0.9 frequency) or loss (0.0 frequency) of the altruism allele

	Cost-of-altruism	Time to 0.9 frequency (generations)				Time to loss of allele (generations)			
		Three Runs		Mean		Three Runs		Mean	
Panmixia	1					46	48	50	48
	2					30	35	38	34
The basic model	0	82	112	114	103				
	1	162	175	211	183				
	2	239	303	306	283				
	3	750	799	885	811				
	4					175	250	488	291
Pollen dispersal 8-neighbour	0	258	290	342	297				
	1	438	740	755	644				
	2					63	156	212	144
leptokurtic (mean dist 1.25)	0	192	234	296	241				
	1	554	610	740	635				
	2					80	104	121	102
Initial corner pattern 4-neighbour leptokurtic (mean dist 1.25)	4					402	473	605	493
	2					120	268	499	296
Inbreeding Fixed	0	200	337	386	308				
	1	526	781	885	731				
Dispersal-dependent	0	495	611	744	616				
Seed dispersal	0	1,674				57	60		
Population size 25	1					4	5	19	
						30	34	36	21 ^a
100	1	129	165	222	172				
225	1	140	150	181	157				
[625	1	162	175	211	183]				

^a Mean of 6 replicate simulations

grid units, and random dispersal direction. The pollen grain was allocated to the plant nearest its landing place.

From the pollen landing on each plant, pollen allelic frequencies were determined. From this, and the ovule genotype, genotypic frequencies among the seed were calculated. In the basic model zero seed dispersal was assumed, since the interest was in very restricted gene flow. When seed dispersal was included, similar dispersal regimes were used to those described above. The genotype of the next-generation plant at each spot was determined at random from the genotypic frequencies in the seed landing, i.e. assuming no competitive selection.

Most simulations were started with a frequency of the altruism allele of 0.1. This can be assumed to have arisen by mutation or immigration, and circumvented the problem of chance elimination at very small frequencies. One model was examined with a starting frequency of 0.01. In most simulations the allele was

assumed to start randomly distributed through the population, with a Hardy-Weinberg ratio of genotypes. One model was examined with the altruistic allele present initially in a block of homozygotes in one corner. These models are essentially the "fixation" test of Karlin and Matessi (1983). Simulations were run until the frequency of the altruistic allele reached 0.9, or was lost from the population. Some runs were continued beyond 0.9, to check that the allele would be fixed, as indeed it was, but this happened too slowly for the simulation to be followed to fixation in all cases.

High computer requirements allowed only three replicates in most cases.

Application of the model

Panmixia

Neighbourhood selection assumes that a plant's neighbours will be more related to it than the population as

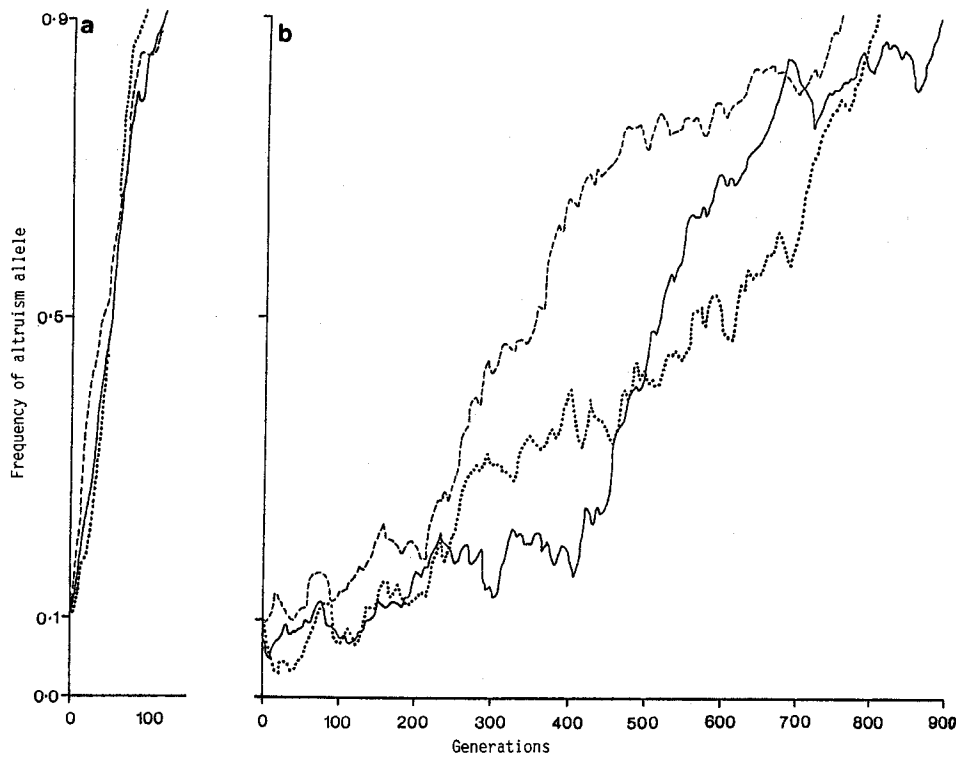


Fig. 1 a, b. Progress of evolution of an altruistic trait, with 4-neighbour pollen dispersal. There are three replicate runs. **a** With no cost-of-altruism. **b** With cost-of-altruism set at 3 (see text for details)

a whole. Panmixia, an assumption frequently made in population genetic models, prevents this. Under panmixia the altruistic allele was lost rapidly from the population (Table 1), even with the minimal cost-of-altruism (1).

The basic model

Under the basic model, with 4-neighbour pollen dispersal, fixation of the altruistic allele could indeed be very rapid (Fig. 1a, Table 1). When there was no cost-of-altruism, fixation of altruism was 90% complete in about 100 generations, and with very few reversals in the upward trend of frequency of the altruistic allele (Fig. 1a). A cost-of-altruism of 1 gave a somewhat slower rate of evolution, mainly because of a short lag at the beginning, and a tendency for reversals to occur when the frequency of altruism approached 0.9. With cost-of-altruism at 2 the initial lag was greater and reversals of the upward trend were more frequent. At cost-of-altruism 3 these setbacks became very frequent (Fig. 1b); whilst the maximal rate of substitution was again similar, it was never maintained for more than about 10 generations. At cost-of-altruism 4 fixation was never observed, though the allele remained in the population for up to 450 generations, much longer than with panmixia (Table 1).

A consistent feature of the simulations was the formation of 'knots' of altruists (Fig. 2). The type of knot formation depended on the parameters of the model. When the cost-of-altruism was low, so that the altruism allele was spreading fast, there were many small knots, in the order of 10 knots in the population in some simulations. Advantage was obtained even when the knots were small, knot formation was easy, and they did not readily disband. When conditions for the evolution of altruism were more marginal only the larger knots were stable. Even they sometimes disappeared. Knot disappearance seems to be the cause of the reversals seen in many of the simulations (e.g. Fig. 1b).

The subdivision of the area into knots of altruists amongst selfish plants resulted in a deficiency of heterozygotes in the population as a whole, typically in the range 0.3 to 0.5. Heterozygotes were naturally concentrated at the contact between the knots and the remainder of the population (Fig. 2).

The allele was usually slow to start increasing in frequency in the population (Fig. 1b). The simulations started with the altruists scattered randomly through the population at a low frequency. There is little advantage in being an altruist in these conditions. The frequency of altruism did not increase until knots formed.

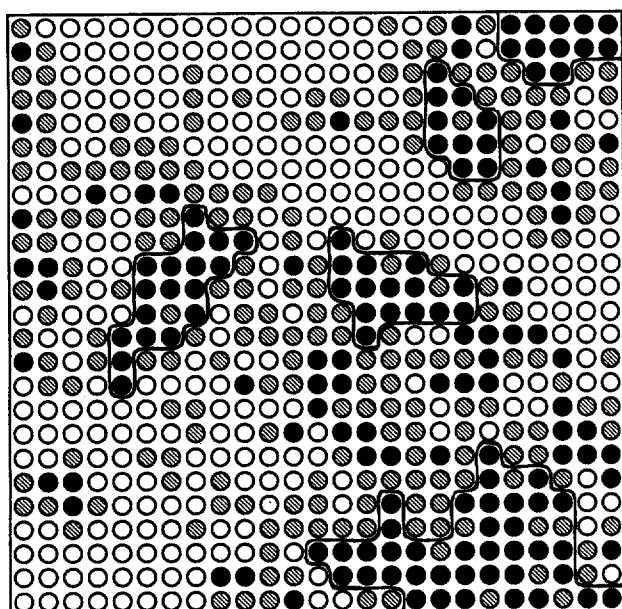


Fig. 2. The state of a simulated population, part way to fixation of an altruistic allele. Filled circle = altruistic homozygote; hatched circle = heterozygote; open circle = selfish homozygote. Lines highlight knots of altruists

Pollen dispersal

The 4-neighbour dispersal regime used as standard was very short-range dispersal, and so would be expected to be the most favourable for the evolution of altruism. In the current model especially, the four plants receiving pollen under a 4-neighbour regime are precisely those four that are assumed to confer benefits on the central individual when they are altruists. An 8-neighbour model was also examined, with pollen being dispersed to a plant's eight nearest neighbours, i.e. those diagonally adjacent too. This is still short-range dispersal, but pollen is dispersed to plants other than the 4 benefit-conferring neighbours. The results (Table 1) show that the altruism allele is still capable of being fixed when the cost-of-altruism is 0 or 1, although at a much slower rate. With the cost-of-altruism at 2, the allele is lost.

A more realistic pollen-dispersal model than either 4-neighbour or 8-neighbour is a leptokurtic model. Such a dispersal with a mean dispersal distance of 1.25 grid units (see Levin and Wilson 1978) was used. The results were similar to 8-neighbour dispersal (Table 1). Using a mean dispersal distance of 2.5 grid units, resulted in loss of the altruism allele from the population, even if there was no cost.

Initial pattern

Under most conditions the frequency of the altruistic allele increased only when knots of altruistic plants were present. Is the formation of an initial knot the limiting step? A simulation to investigate this took the case of

4-neighbour dispersal and cost-of-altruism 4, in which altruism was marginally unable to evolve, and started with the allele in the same starting frequency, 0.1, but present as homozygotes in a corner block. This is approximately the situation that would arise with seed immigration from one direction. Loss of the allele was slower than with a random-distribution start, but it occurred eventually in every simulation (Table 1).

With leptokurtic dispersal (mean dispersal distance 1.25) and cost-of-altruism 2, again a situation in which altruism was marginally unable to evolve, the loss of the allele was much delayed and a frequency of 0.28 was temporarily attained, but the altruism allele was eventually lost (Table 1).

Inbreeding

Breeding system has a great effect on many population genetic processes. Selfing was therefore examined to see whether it affected the possibility of fixing an altruistic allele. The pollen dispersal model used was leptokurtic with mean dispersal distance 1.25 grid units. Selfing was simulated in two ways:

- Fixed selfing: imposing a constant proportion of selfing,
- Dispersal-dependent selfing: In other models with leptokurtic dispersal, pollen landing in a position where the nearest plant was the pollen parent was discarded. For this type of selfing, it was added to the pollen parent's own pollen input.

The level used for Fixed selfing was 0.5. This meant that in any generation a plant had a 50% random chance of producing all self-fertilized seeds, and a 50% chance of producing seeds from alien pollen. The time to fixation (731 generations) was little different from that with self-incompatibility (635 generations, Table 1). Any difference was smaller than the difference between replicates. The small effect of selfing under this model could be because of the lack of seed dispersal. Normally one effect of selfing is to disperse seed of very similar genotype; with short seed dispersal distances this gives many near-identical neighbours.

Dispersal-dependent selfing (b) produced a much slower rate of increase in the altruism allele than did either outcrossing or Fixed selfing (Table 1). This is not because there was a greater proportion of selfing – the mean value was only 0.3. Consider an altruistic plant, A, surrounded by 4 selfish plants S:

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S
S A S
S

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Those S plants will impose a considerable alien (S) pollen rain on A. It will also receive a certain propor-

tion of its own pollen, of type A. However, because it has a cost-of-altruism, and all its neighbours are selfish and so will give it no benefit, that pollen production will be small. Therefore, a small proportion of its pollen rain will be its own, most will be of alien (S) type.

In the opposite case, a selfish plant surrounded by four altruists:

A
A S A
A

the altruistic plants will increase the growth of the central S plant and cause it to produce more pollen. It has no cost of altruism. Its own pollen will therefore constitute a greater proportion of the total pollen rain landing on it, and the chance of its ovules being fertilized by a pollen grain carrying the A allele will be less.

So whilst Fixed selfing guaranteed a certain proportion of selfing, Dispersal-dependent selfing gives the opportunity for neighbouring plants to affect a plant's degree of selfing, by affecting its pollen production. In both cases they do this in the direction of aiding the spread of the S allele at the expense of A.

The results of both types of selfing model confirm Craig's (1982) conclusion, obtained from a quite different model for social insects, that inbreeding does not necessarily make the evolution of altruism more likely. It contrasts with results from the model used by Wade and Breden (1981). Michod (1980) and Uyenoyama (1984) found that in most of their models inbreeding promoted the evolution of altruism, but in a few it retarded or prevented it, especially at low frequency of the altruism allele. Differences in conclusions from previous models, and between the two used here, show that the effect of inbreeding on group selection is not simple, but will depend on the population structure and the selfing mechanism.

Seed dispersal

Although pollen dispersal is typically longer-range than seed dispersal, it is of interest to see whether the altruistic allele could spread when dispersal is by seed instead of by pollen. The number of ovules produced by each plant was determined in the same way as the number of pollen grains, with additive benefits (5 seeds) from altruistic neighbours. There was no cost-of-altruism. Seeds were dispersed by the 4-neighbour schedule described above. These are the most favourable conditions possible for the spread of the allele. In three runs (Table 1) the altruism allele was lost twice, and was fixed the third time only after 1,674 generations.

There are two possible reasons for this. One is that with no pollen dispersal selfing will always occur (it

was necessary to assume self-compatibility for this simulation), and there will therefore be no heterozygotes. The second is that each dispersal event will disperse two genes. Gene flow was therefore double that with pollen dispersal.

Population size

The size of the population might be important for the fixation of an altruism allele. In a smaller population there will be fewer opportunities for knots of altruism to arise. There will also be more edge effect. Simulations were run with population sizes of 25, 100 and 225, to compare with the standard 625. The system chosen was 4-neighbour pollen dispersal, and a cost-of-altruism of 1. At a population size of 25 (Table 1) the altruism allele was always (6 out of 6 trials) lost. Over the other three population sizes the population size had very little effect on the rate of evolution.

Initial frequency

Although it is quite possible that an allele might reach a frequency of 0.1 in a small population through drift, founder-member effect or migration, this is unlikely in larger populations. The original altruism mutant will normally be in a minority. Could the altruistic allele increase in frequency if it started at a frequency of, say, 0.01? This is the "initial increase" test of Karlin and Matessi (1983).

Fifty simulations were run using the 4-neighbour pollen dispersal and cost-of-altruism 1, favourable conditions for increase of the altruistic allele. In 40 of the 50 simulations (80%), the altruism allele showed an eventual increase. The possibility exists for an altruistic allele to be fixed even when it enters the population at a very low frequency.

Discussion

There are two pre-requisites for the operation of Neighbourhood selection. Firstly, the plants benefitting from the altruistic behaviour of any individual must have a good chance of being related to that individual. Secondly, the benefit to those plants must exceed the cost to the individual with that trait.

Some authors have emphasised lack of mobility as a cause of neighbour relatedness (Eshel 1972), others the high group benefit and low individual cost (Wilson 1983a) and yet others population structure (Weigel 1981). All are important. The balance between them is seen in all these simulations. This is basically the balance between K and r in Hamilton's (1963) models.

The present model shows that the evolution of altruistic traits is possible under conditions that are realistic for plant populations. However, such evolution occurred only under favourable conditions, of very restricted pollen dispersal, no seed dispersal, and a total benefit:cost ratio of up to 20:1. Even then, evolution usually occurred slowly. This confirms the conclusions from other models (e.g. Bell 1978) that individual selection is a much more effective force than group selection when it can operate, and that the conditions under which group selection can override significant individual selection are very restricted (Levin and Kilmer 1974).

As in Bell's (1978) model, the altruistic gene increased at first in local groups that happened to have a high frequency of it. The altruism allele is of no advantage unless most of the neighbours are also altruists. It therefore tends to disappear except in such knots. The importance of knots is greater when the population structure and benefit/cost ratio make conditions marginal for the evolution of altruism. This is a form of frequency-dependent selection (Michod 1982). It results in a subdivision of the population into patches of different allelic frequencies, even in a homogeneous environment. The knots of altruism presumably start as chance aggregations of altruists. This is similar to the random difference between groups in other group selection models. Only rarely could the position of knots be related to the pattern of the initial randomization. They must have arisen by chance dispersal and pollination. Once formed, knots of altruism have higher productivity, as is essential to the operation of group selection (Michod 1982).

Since altruism can evolve under this model, it is appropriate to consider what characters in plants might be altruistic, and hence need group selection in order to evolve.

Most of the examples of plant population altruism in the literature have been of restraint in interference (Eshel 1972). Some cases have been of interference between different phases of the life cycle, or between seeds in one fruit, which are not applicable to the present model (Willson 1981; Kress 1981; Queller 1983; Nakamura 1980; Westoby and Rice 1982; Queller 1984; Law and Cannings 1984; Ellstrand 1984).

Since restraint in interference must always be altruism it must evolve by group selection, and hence cannot evolve unless the total benefit to the relatives is greater than the cost to the altruist, by a factor dependent on the relatedness. From the present model it seems that in plant populations this factor needs to be quite large. By definition of competition (Clements et al. 1929), what resource one plant gains the other loses. Therefore, the benefit in resources (e.g. soil nitrogen) cannot exceed the costs. However, the growth

response may be non-linear, so it is still possible for the benefit in growth to exceed the cost in growth. Givnish (1982) gives the example of forest herbs competing for light, where altruists would be short plants.

A high benefit/cost might be found in competition for pollinators. By attracting more pollinators a plant might gain a little in ovule fertilization rate or in seed quality. If the plant were to reduce its floral display, the same pollinator service released for its neighbours might have a much larger benefit for their fertilization rate. This would fulfil the condition of low cost and high benefit. However, there might be some individual advantage in not putting energy into pollinator attractants, visual, fragrant or nutritive, so individual selection might operate. Moreover, seed set is often considerably pollinator-limited (Zimmerman 1980).

Nectar production can also be altruistic, in that a pollinating insect will often be coated with pollen before it discovers whether nectar is present. If pollinators only remember which patches provide nectar, not which individual plants, a selfish nectarless plant in a patch of nectar producers has an individual advantage.

Mirmirani and Oster (1978) discuss the more indirect case of the time of switching to reproduction. A plant switching to reproductive growth later than the optimum time may achieve some competitive advantage, through increased root length, and plant height. However, a population of such late switchers will have a lower reproductive output than a population of plants that switch at the optimal time. It seems doubtful whether the benefit/cost ratio could be sufficiently large. In the real world, switching is not so sharp as in optimality theory (King and Roughgarden 1983).

Another possible application of group selection would be in the production of toxic exudates. It is unclear as to how widespread the phenomenon of allelopathy is (Harper 1977). Allelopathy is similar to competition in its evolutionary characteristics, but there are two important differences. Firstly, whilst intra-specific competition must be greater than inter-specific competition because the plants are occupying the same niche, some species show lower toxicity to themselves than to other species (Newman 1978). Secondly, it is common for the toxin producer to gain less than its neighbours suffer (Grummer and Beyer 1960). An altruist, not producing toxin, therefore has a cost smaller than the benefit to its neighbours.

Nakamura (1980) saw self-thinning as altruistic. Although self thinning can be seen as individually adaptive (Koyama and Kira 1957), it can also be seen as an inevitable result of competition when a competitive hierarchy appears (Ford 1975). Jones and Ramnani (1985) suggested lack of defence against herbivores as altruistic. Root grafts are another interesting suggestion

for altruism (Nakamura 1980), but it is hard to see how the benefit can be much greater than the cost.

Another type of altruism is restraint in resource use. Many plants that grow in adverse environments have low R_{\max} (relative growth rate in optimal conditions) (Parsons 1968). So long as reproductive effort is unchanged the evolution of low R_{\max} cannot be explained by individual selection. A plant with a higher RGR (or as Givnish 1982, puts it maximum carbon gain), when that growth rate results in offspring, will have an individual selective advantage. Low R_{\max} has been seen as an adaptation to prevent exhaustion of the resources of their environment. Since the resources used by neighbouring plants will overlap, this amounts to an appeal to group selection. The alternative explanation is that low R_{\max} is a by-product of adaptation to adverse environments (Grime and Hunt 1975).

Another possible example of restraint in resource use is limitation in uptake of "luxury" amounts of nutrients. Plants take up nutrients faster as the external concentration rises. There is a limit to uptake, but probably above that sufficient for maximal growth. Such behaviour could be explained as a result of saturation of the uptake mechanism, with no selective advantage to a plant in allocating more of its resources into the uptake of nutrient it does not need. Indeed, deficient plants do take up nutrients faster (e.g. de la Guardia et al. 1985). A second explanation is that a limit to uptake avoids toxic levels of that nutrient in the plant. A third possibility is that this failure to take up luxury amounts of nutrient may benefit the plant's neighbours, and if they are mostly of the same species, and are sufficiently related, Neighbourhood selection is possible.

Some aspects of breeding system might be seen as altruistic, such as self-incompatibility. Unless pollination is very readily achieved, the outcrosser must put a considerable effort into ensuring pollination, and/or have a lower seed set than the selfer. Yet the advantage of cross pollination is usually for the future success of the population. If environmental variation were frequent enough, outcrossing and consequent recombination might give sufficiently higher success for outcross offspring for an explanation in terms of individual selection to be possible (Mitchell-Olds and Waller 1985; Ellstrand and Antonovics 1985). The presence of recessive sub-lethals in the population (Levin 1984) might also give an advantage to an individual which was self-incompatible. If neither of these conditions prevail, self-incompatibility must be seen as altruistic, and group selection necessary.

Another breeding system case is the evolution of crossability barriers, such as a difference in flowering time, in a population subject to mal-adapted gene inflow. A mutant flowering earlier or later would have

the individual advantage that it could not be pollinated with pollen carrying the mal-adapted allele. It would have an individual cost of a lower availability of pollen. It is not clear to what extent flowering times are determined by avoidance of competition for pollinators (Ranta et al. 1981), and to what extent by optimal availability of pollinators. The general paucity of winter flowering plants is evidence that the latter is important. Either way, the "wild type" flowering time may have been optimized in evolution, and a mutant with a different flowering time may therefore incur a cost. It is therefore not clear whether the net effect to the individual will be benefit or cost, and therefore whether it should be regarded as altruism. In any case, the benefit is directly to its offspring, in fitness, and this might be seen as an extension of individual selection.

It is hard to see the production of pollen by pollen-triggered apomicts (pseudogamy) as anything but altruistic (Nakamura 1980), unless as a vestigial character, or having value for the occasional sexual reproduction that most apomicts show.

The discussion above shows that it is difficult to find clear cases of altruism in plants, compared to such animal characters as warning calls. This might reflect the only marginal opportunity for the evolution of altruism in plant populations, suggested by these simulations. It was once normal to see group selection as operative only for traits that could not be individually selected. Recently it has been argued that group selection may be operative for traits that, whilst conferring benefit on the group, also have some benefit for the individual (Michod 1982), and even that these are the situations where it will be found in nature (Wilson 1983 a; Fix 1984). The models here with no cost of altruism may be relevant, for in these models rates of evolution were relatively fast.

The results also make it clear that the conditions under which Neighbourhood selection can operate are very restricted. Previous comments on the effect of population viscosity as allowing the evolution of altruistic traits seem to have been made with animals in mind, though they have been phrased in general terms. That the force should be so weak and strict as to the conditions in which it can operate suggests that application of these models to the real world has been over-optimistic. Certainly Eshel's (1972) suggestion that given a sufficiently high viscosity any altruistic trait can evolve is unrealistic.

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