

PLANT KIN SELECTION

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ABSTRACT: The interaction of genetic relatives is a precondition for kin selection. Although many plants live in kin groups, no one has reviewed the possible impact of kin selection on plant evolution. Plant kin selection may operate to restrain competition, to promote altruism, and to regulate parent-offspring behavior.

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"The social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbors' fitness against his own according to the coefficients of relationship appropriate to that situation."

Hamilton (1964b)

"Birds do it, Bees do it...in Boston even beans do it."

Cole Porter

INTRODUCTION

Hamilton (1964a,b) developed the modern genetic theory of kin selection to explain the evolution of social behaviors that do not maximize individual fitness. He argued that one should consider, instead, the inclusive fitness: the sum of an organism's individual fitness and its effects on the fitnesses of all its relatives, with each effect multiplied by the respective coefficient of relatedness. Three important elements of inclusive fitness are the degree of genetic relatedness, the magnitude of benefit, and the magnitude of the cost (West Eberhard 1975). Helping a close relative would be selectively advantageous behavior if it raises an organism's inclusive fitness. Proposed examples of kin selection include helpers at bird nests (Brown 1974) and worker bee castes (Hamilton 1964b).

For at least part of their lives, many plants interact with conspecific genetic relatives (Harper 1967, 1977:239). The haploid gametophytes of mosses and ferns nourish diploid sporophytes. Sibling pollen grains may travel together in tetrads, pollinia, or viscin-held clumps (Willson 1979). Seeds in an ovary have the same maternal parent and may share the same pollen parent. Vegetative propagation and agamospermy establish populations of clones. Levin and Kerster (1974) reviewed the available data on gene flow in seed plants and concluded that effective population sizes are on the order of a few tens of meters. Six California grassland herbs have population sizes from 200 to 30 individuals (Jain 1976). Schaal (1975) discovered that *Liatris cylindracea* has a subdivided population of inbred neighborhoods. Since *Liatris* is an obligate outcrosser, the inbreeding is likely due to the mating of nearby relatives.

Despite the existence of plant kin groups, few persons (Hamilton 1964a,b; Seger 1976; Mirmirani and Oster 1978) have applied kin selection theory to plant ecology and evolution. This paper will explore the implications for plant populations of two behaviors predicted by kin selection: restraint of competition and altruism. Its purpose is to call attention to a new field for observation and experimentation, to synthesize isolated ideas in the literature, and to suggest alternative approaches for some biological problems.

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DEFINITION OF TERMS

A major obstacle to the demonstration of plant kin selection is the nature of plant behavior. How does one distinguish between competition, altruism, and parasitism? In all three situations one participant has a greater individual fitness than another. One plant is (+) with a higher fitness relative to one which is (-) with a lower fitness. Does the (-) plant "intend" to sacrifice its fitness to benefit the (+) plant?

Table 1

Changes in Fitness When Two Plants Interact

Interaction	(+) Plant	(-) Plant
	Individual Fitness	Inclusive Fitness
Competition.....	Lower	Lower
Parasitism.....	Higher	Lower
Altruism.....	Higher	Higher

However, distinctions are possible when fitness changes are compared (Table 1). If altruism occurs through kin selection, the (-) plant has a lower individual fitness but increases its inclusive fitness. In competition and parasitism the (-) plant has a reduced inclusive, as well as individual, fitness by interacting with the (+) plant. The (+) recipient plant in altruism and parasitism has a greater individual fitness when the interaction with the (-) plant occurs. Competing (+) and (-) plants, by contrast, both have lower individual fitnesses. Consider two plants and ask what happens when one is removed to grow separately. If each plant does better without the other, the two plants were competing. If not, the interaction was altruistic or parasitic. If when grown by itself the (-) plant declines in inclusive fitness, the relationship between the plants had been altruistic and not parasitic.

Although it restricts the prevalent notion of altruism, this paper uses the above definitions to avoid oxymorons like "forced altruism" to describe parasitism (Darlington 1978). A latter section of this paper treats the case of more than two conspecific individuals affecting each other's fitness. The evolution of plant behavior through group selection will not be considered.

RESTRAINT OF PLANT COMPETITION

Kin selection places a limited restraint upon intraspecific competition (Hamilton 1964a). A plant can reduce its inclusive fitness by competing too well against close relatives. As stated in the introduction, the effect of competition on inclusive fitness depends on the coefficient of relatedness, the fitness cost, and the fitness benefit. Seger (1976) constructed a kin selection model in which homozygosity is a measure of genetic relatedness. According to his calculations an allele for reduced competition (He called it "altruism.") when neighbors are homozygous can readily reach fixation. Mirmirani and Oster (1978) in a different model reached the opposite conclusion. Kin selection by itself could not limit competition.

Hamilton (1964b) hypothesized that seeds in an ovary of a wind pollinated plant are more likely to have several pollen parents than insect pollinated seeds. Pollen grains carried by an insect to a stigma have a greater chance of coming from the same plant than pollen blown by the wind onto the stigma. The clumping of pollen dispersal units like tetrads or pollinia (Willson 1979) also increases the number of full-sibling seeds in an ovary. Because wind pollination and singly dispersed pollen grains produce less closely related seeds in an ovary, the seeds should have less restraint upon competition for maternal nutrients compared to insect pollinated seeds.

Restraint of competition should tend to create an even distribution of energy among developing seeds.

Other areas for investigation of kin selection effects upon competition are pollen tube growth, plant self-thinning, intraspecific allelopathy, and attraction of pollinators or dispersers. In all these areas one needs to know if the intensity of competition varies inversely with the degree of genetic relatedness of the competitors. Studies (see Harper 1977) have been made of competition between genotypes but not at the level of siblings vs. cousins vs. unrelated individuals.

Some dioecious plant species may have a unique form of self-thinning. Natural populations of Thalictrum fendleri have an excess of males in drier sites and of females in wetter ones (Freeman, Klikoff, and Harper 1976). Differential mortality creates the unbalanced sex ratio since in Thalictrum sex is genetically determined. Maynard Smith (1978:163) speculated that kin selection could establish genes favoring the death of males in moist sites and of females in dry ones. A male seedling in a moist site would limit to the point of death its competition against its sisters. The fitness of the females in the moist areas would have to be high enough for inclusive fitness to compensate the male's sacrifice.

PLANT ALTRUISM

Plant altruism is an equally speculative prediction of kin selection. Indeed, Wilson's (1975:117) definition of altruism omits plants. This omission may not be necessary since one can suggest plausible forms of altruistic plant behavior.

A reproductive division of labor may signal altruism. Some plants would be able to do proportionately more of the reproduction because of those plants which concentrate their energy on other functions. The plant altruist pays a cost in individual fitness but aids close relatives which share and propagate some of its genes. Plant altruists could be intraspecific analogues to member species of plant defense guilds (Atsatt and O'Dowd 1976). Insectary species in a defense guild maintain the predators and parasites of herbivores that eat guild members. Repellent species of plants keep away and attractant species decoy herbivores from other guild members. By analogy within a species, a plant altruist could specialize in defensive functions against herbivores or in allelopathy against other species and thereby benefit close relatives.

Another plant function is the colonization of new areas. Pioneer altruists would devote themselves to aiding the successful establishment of genetically related seedlings. See Smith (1977) for a not well-understood situation in which albino Phyllostachys bambusoides seedlings appear to help their photosynthetic siblings against a competitor weed species.

J.L. Harper (pers. comm.) mentioned that root grafts among conspecifics may be altruistic. Govier (1966) showed that, when a suitable host species was not present, individuals within laboratory populations of the hemiparasite Odontites verna formed root connections among themselves and that one or two plants were then able to mature and produce seed although isolated individuals did not. Not enough is known about this case to determine whether or not the donor plants raised their inclusive fitnesses so parasitism is not distinguished from altruism.

An additional case is the late stage of root grafting in Pinus strobus (Bormann 1966). The dominant tree translocates food to the suppressed tree and helps it to survive. Perhaps, kin selection can explain this "noncompetitive relationship." Does the dominant parasitize less severely a close relative? Or is the dominant altruistic at this stage of the interaction? One must know the genetic relatedness of the white pines and the respective seed outputs.

Pollen production is not normally altruistic, but in some obligately apomictic angiosperms pollination is a prerequisite for seed formation even though the embryo receives no genes from the pollen parent. This is called pseudogamy (Grant 1971). Why should these plants expend energy to produce pollen? If an individual plant grows near members of its clone, it will raise its inclusive fitness by ensuring the

fertility of its genetic copies (Maynard Smith 1978:66). As a footnote, pollen cooperation in nonapomicts should be the result of kin selection.

Like the case in restraint of plant competition the necessary information on inclusive fitnesses has not been collected for a test of plant altruism.

MATERNAL PLANTS AND EMBRYO OFFSPRING

A developing seed interacts with its siblings and maternal parent. The interests of the participants do not coincide. If inbreeding depression is low or nonexistent and nutrients are limited, a maternal plant raises its inclusive fitness by favoring those offspring that share more of its genes and by aborting the less closely related. The kin selection guide of maternal choice may also apply to which pollen grains are allowed to fertilize ovules. Charnov (1979) examined some of the same issues from the perspective of male-female conflict. Double fertilization may be the pollen genome's way to counteract maternal choice or sibling competition and to ensure the genome's own survival. The zygote-sustaining endosperm shares genes with the pollen genome unlike other maternal plant tissues. Because of double fertilization the endosperm is more likely to feed the growing zygote formed from the union of the pollen and ovular genomes.

Sibling embryo competition reduces the parent's reproductive output. A maternal plant can minimize this competition by widely spacing the ovules in each ovary (Hamilton 1964b). The degree of spacing should increase as restraint of competition decreases, that is, when the seeds are more likely to be half-sibs than full-sibs. W.J. Kress (ms.) has found correlations among pollination syndromes, pollen unit size, and ovule number that follow the predictions of Hamilton.

The kin selection effects on maternal choice and sibling competition can contradict one another. Imagine a plant with ten developing seeds, not all of which can be brought to maturity. The pollen parent of two seeds is closely related to the maternal plant. The pollen parent of the other eight is not. Maternal choice prefers per capita the two seeds. The eight seeds restrain competition among themselves but not against the maternal choice. Such competition could be among seeds in the same ovary or between siblings in different fruits. An additional level of complexity comes after seed dispersal and germination when tree seedlings compete against their parents as well as their siblings (Alexander 1974:362-363).

CONCLUSION

The possibility of plant kin selection relies upon the existence of plant kin groups. The extent of kin groups at all stages in the plant life cycle has yet to be well documented, but, when plants do live in kin groups, kin selection as an evolutionary force will manifest itself in changes in plant behavior according to the components of inclusive fitness. Behaviors matching the predictions of restraint of competition and altruism are evidence for kin selection, but parental manipulation can create similar results (Alexander 1974), and adequate proof requires the measurement of inclusive fitness. This is not an easy task. The definitions of an individual plant are various (Harper 1977). Estimates of fitness and the coefficient of relatedness are often crude (Kurland and Gaulin 1979). Altruism, parasitism, and competition must be distinguished from each other. Several factors may cause the same behavior (West Eberhard 1975). Finally, theoretical work now goes beyond the simpler models of Hamilton (e.g. Craig 1979; Parker and Macnair 1979).

Nevertheless, one can set up artificial kin groups in the greenhouse and the field, and follow individuals in wild plant populations with markers. Plants are more amenable to such studies than animals. They have diverse breeding systems and population structures; they can be transplanted; they can be fertilized to start progenies of known genetic backgrounds. The idea that a plant is an organism interacting with its kin is the source of the suggestions and predictions in this paper. Plants

and their behaviors should provide a test of current ideas in sociobiology.

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