

Ecological and Population Genetics of Locally Rare Plants: A Review

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Abstract—Plant species with limited dispersal ability, narrow geographical and physiological tolerance ranges, as well as with specific habitat and ecological requirements are likely to be rare. Small and isolated populations and species contain low levels of within-population genetic variation in many plant species. The gene pool of plants is a product of phenotype-environment interaction. The effects of inbreeding mating systems, geographical ecotypes, phenotypic plasticity, microhabitat differentiation, and stochasticity on genetic variability in locally rare plants are considered. The emphasis of this review paper is on recapitulation of original data and conclusions of results from a variety of research studies that approach locally rare plants from ecological and population genetics perspectives.

Introduction

Temporal and spatial variations in plant population sizes are detected both within and among species. Some plant species occur in wide ranges (cosmopolitan), while others are restricted to only a specific habitat (endemic). This variability is the result of complex interactions among the life history features of populations, local environmental conditions, and ecological and physiological requirements of particular species (Barnett and Kohn 1991). One often assumes that rare and endangered species occur in small populations that are geographically isolated from one another. Rare plants may be locally common but occur in only a few places because their habitat is geographically restricted (Kruckeberg and Rabinowitz 1985). Rare plants may be locally scarce but geographically widespread. They may also be both scarce and geographically restricted, reflecting specific adaptation to habitats that are rare (Rabinowitz 1981). The ecological and evolutionary processes that give rise to rarity are so complex that one cannot assume all locally rare plants exhibit the same patterns (Kruckeberg and Rabinowitz 1985). Likewise, some locally rare plants appear to be genetically depauperate due to their relatively small population size. It may be premature to assume that this is a universal feature of all locally rare species (Stebbins 1980; Griggs and Jain 1983).

The distribution and amounts of genetic diversity within and among populations of locally rare plants depend on whether a species is naturally rare or whether it has

recently become rare as a result of stochastic events. Stochastic events may be environmental or anthropogenic. Plant populations that are naturally small may show genetic systems adjusted to close inbreeding, as well as adaptations that offset the disadvantage of rarity, as opposed to species that have experienced severe reductions in population numbers owing to habitat destruction, fragmentation, or degradation through anthropogenic activities (Barnett and Kohn 1991).

The role of ecological and population genetics in locally rare plants has been increasingly appreciated in recent years. This paper reviews and discusses some of the genetic and evolutionary consequences of small population size and the ecological significance of genetic diversity in locally rare plants.

Genetic Consequences of Mating in Small Populations

Differences in survivorship are detected between progeny from selfed and outbred matings within a population (Barnett and Kohn 1991). They (1991) further state that some plant species are capable of exhibiting both cleistogamous and chasmogamous flowers. Outcrossed offspring are expected to be more genetically diverse than the progeny of self-fertilization. A significant reduction in survivorship is found for selfed progeny in normally outcrossed plants (Schoen 1982). Similarly, differences in the relative fitness of sexually produced offspring versus vegetative (asexually) produced progeny have also been observed. An intense exploitation and interference competition would favor sexual offspring (Case and Taper 1986). Under changing environment, the competitive advantage obtained by the occasional rare genotype would give the sexual groups competitive dominance over the asexual (genetically identical) group, despite the initial advantages of asexual reproduction (Case and Taper 1986).

Heterozygosity seems to have a fitness advantage, and is often affiliated with increased growth rates and survivorship in many plant species. Although heterozygosity may not be advantageous with superior performance when environmental conditions remain relatively stable, heterozygosity may provide the ability to cope with fluctuating environments, and may play such a buffering role (Grant 1981).

Genetic Variation

Inbreeding

The frequency and intensity of inbreeding are often far greater in plants than in most animal groups. Unlike most

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animals, mature plants are sessile organisms. Seeds, pollen, and vegetative dispersal structures (for example, rhizome and stolon) are the only motile stages in the life cycle of a higher vascular plant. Because of limited gene flow through pollen and seeds, offspring plants usually germinate and establish fairly close to the parent, creating small neighborhood sizes. Populations structured into small neighborhoods appear to be inbred and contain low levels of within-population genetic variation compared to those in larger neighborhoods (Barnett and Kohn 1991). The level of inbreeding in a plant population increases over time at a rate dependent on the effective population size, and populations become inbred more rapidly when they are small in size (Barnett and Kohn 1991).

In plant breeding, it is often useful to know how rapidly the inbreeding coefficient increases when propagating by a regular system of mating, such as repeated self-fertilization, sib mating, and half-sib mating (Hartl 1988). Among the three mating systems, self-fertilization leads to an extremely rapid increase in the inbreeding coefficient (fig. 1). As expected of highly self-fertilizing species, each individual plant is highly homozygous for alleles (Hartl 1988). Some population geneticists propose that self-fertilizing in locally rare species contain fewer deleterious recessives than do outcrossing species, presumably because the increased homozygosity permits harmful recessives to be eliminated from the population by natural selection (Hartl 1988).

Alternatively, other population geneticists argue that the potential consequences of inbreeding in locally rare species include a significant reduction in genetic variability (decreased heterozygosity) and a significant increase in the frequency of lethal or highly deleterious recessive alleles.

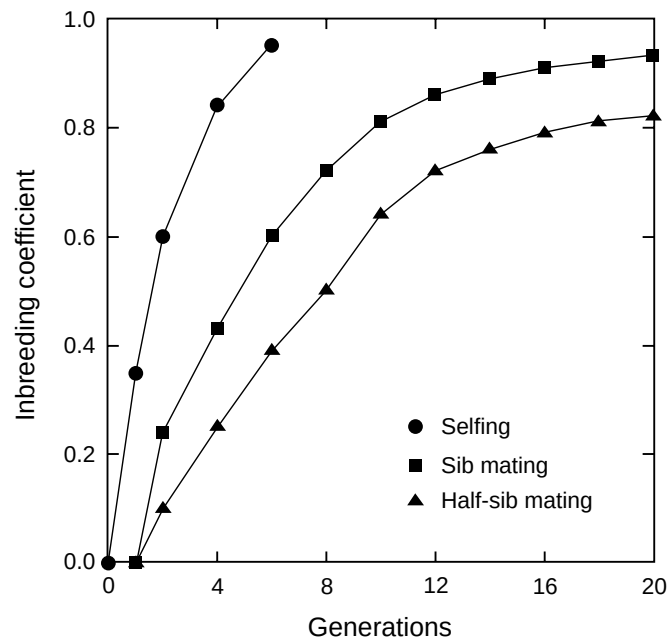


Figure 1—Theoretical increase in inbreeding coefficient F for regular systems of mating: selfing, sib mating, and half-sib mating (redrawn from Hartl 1988).

Mating patterns are prime determinants of the levels of inbreeding in both large and small plant populations (Barnett and Kohn 1991). In an outcrossing population, these are maintained by the balance between mutation and selection. Nevertheless, when an individual self-fertilizes or inbreeds with a relative, these alleles are often homozygous, resulting in inbreeding depression (Barnett and Kohn 1991). Plant populations with a long history of inbreeding due to specific adaptations to selfing, leading to small population sizes, would be expected to show a relatively little inbreeding depression (Templeton and Read 1984). In theory, inbreeding depression usually occurs in normally outcrossing plants, leading to a substantially lower yield and relative fitness (fig. 2). Conversely, inbreeding depression is less severe in species that are partially self-fertilizing, and may be absent altogether in species that are highly selfed (Wright 1977). In some cases, plant species may be adapted to further inbreeding (Huenneke 1991). Alternatively, inbreeding depression may occur even in species with a history of selfing or inbreeding (fig. 3), yet is difficult to accurately determine the level of inbreeding that a species is likely to suffer or sustain.

Although plants growing under optimal conditions in a greenhouse or botanical garden tend to show little or no inbreeding depression, the effects of inbreeding depression may be more severe when seeds are released back into the wild. Seeds produced under uncompetitive conditions may have relatively low “ecological value,” and small samples of locally rare plants maintained in botanical gardens may be inbred and of inferior genetic quality (Barnett and Kohn 1991). For this reason, conservation of wild plants growing in greenhouses or botanical gardens may lead to unintentional

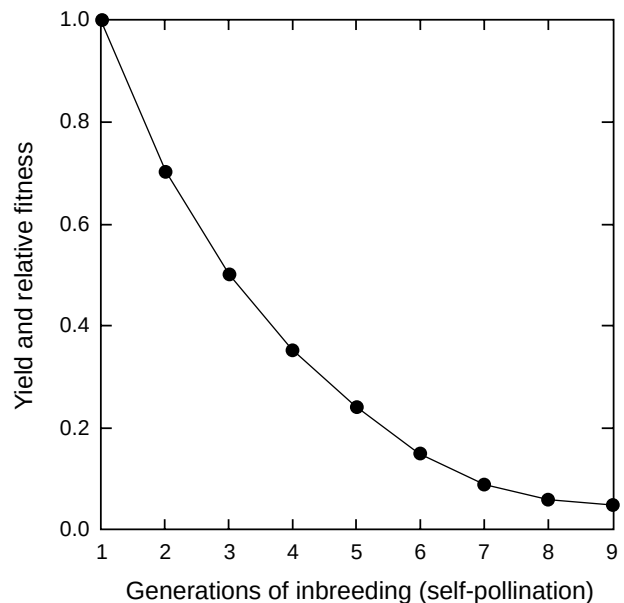


Figure 2—Characteristic loss of yield and relative fitness associated with inbreeding in a normally cross-pollinated plant species. This phenomenon of yield and relative fitness loss typically occurs with each successive generation of inbreeding (redrawn from Kaufmann 1989).

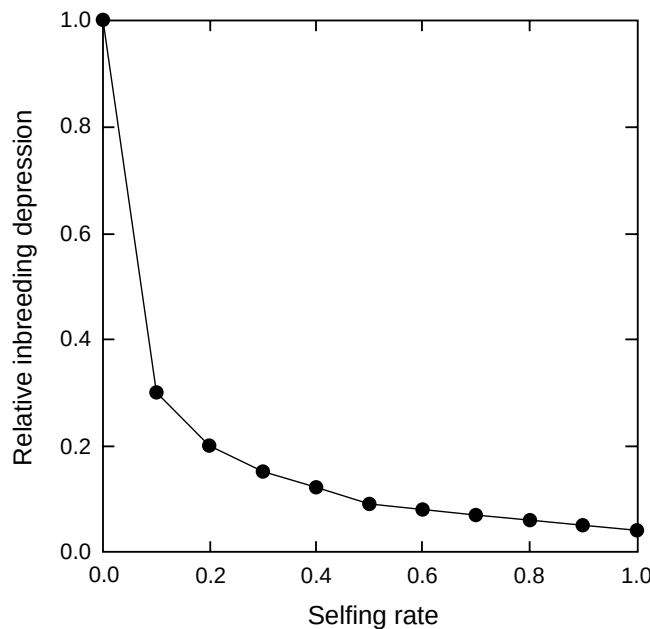


Figure 3—Relationships between inbreeding depression and the selfing rate assuming lethal or highly deleterious recessive alleles in a normally cross-pollinated plant species (redrawn from Barrett and Kohn 1991).

“domestication,” particularly if many sexual generations under optimal conditions are allowed to occur (Barnett and Kohn 1991) at the expense of losing some genetic diversity.

Geographical Ecotypes

Plant species occupying a wide geographical range are frequently associated with environmental and ecological conditions. In general, plant species with a wide geographical or ecological range exhibit considerable genetic heterogeneity and phenotypic plasticity (Jain 1979).

Distinct ecotypic variations in growth form have been observed in plants that are geographically widespread. Distinct ecotypes presumably represent discontinuous genetic variation, relating to specific habitats. Local ecotypes, varying in morphology or physiology with environmental conditions, reflect genetic differences among populations (Huenneke 1991). Each plant population is a unique realization of the phenotype-environment interaction (Schwaegerle and Bazzaz 1987). In many plant populations, ecological performance associated with genetic differences exists; such differences are often responses to unusual edaphic, climatic, geomorphic, or other specific ecological conditions (Huenneke 1991). For instance, metal tolerance ecotype is ubiquitous in mine populations, but is nearly absent in adjacent populations growing on non-mine soils. Despite some gene flow across the abrupt environmental boundary, ecotypic variation is maintained by natural selection (McNeilly and Bradshaw 1968). In general, plants would have lower growth rate and survivorship than their “resident” ecotypes if they were transplanted to considerably different environments (Huenneke 1991). Hence, genetic

differentiation among and within populations is frequently tied to variation in environmental factors, as well as to geographical and ecological ranges.

Response to Microhabitat Differentiation

Plants experience fine-scale microhabitat differentiations. Environmental variation influences population parameters, such as rates of mortality, growth, and reproductive output among individuals and among populations (Huenneke 1991). Microsite variation acts to buffer populations from environmental stochasticity, and is especially important for seeds, seedlings, and small plants (Huenneke 1991).

Some seedlings establishing several meters from their parent plant may have lower mortality and more rapid growth than seedlings establishing only 50 m from the parent (Huenneke 1991). Genetic variability may allow more efficient exploitation of a heterogeneous and changeable environment than would be possible for a genetically uniform population. However, not all plant species can utilize multiple microsite types efficiently and be buffered from environmental stochasticity. Such multiple microsite types require a higher genetic variation or phenotypic plasticity.

Response to Stochasticity

Stochastic occurrences play a vital role in determining the viability of small plant populations. These occurrences may be genetic or environmental. In general, great heterozygosity characterizes species establishing in variable environments (Beardmore 1983; Loveless and Hamrick 1984; Brown and Burdon 1987).

Genetic uniformity of a plant population may make the population highly susceptible to negative biotic interactions, such as herbivory and invasion by insects, pathogens, parasites, and exotic species. Populations may maintain genetic polymorphism in defense against biological invasions (Bremermann 1980). Variation in resistance to particular herbivores, pathogens, parasites (biological invasions) appears to be an important evolutionary response to promote genetic variation. The existence of a range of genotypes in a population may result in the survival of a few individuals after insect or pathogen attack (Bremermann 1980). The presence of genes for resistance or tolerance within a population may determine the chance of persistence in the face of insect outbreaks or other herbivory episodes (Bremermann 1980).

However, some stochastic events act on members of a plant population regardless of their genetic composition. Major catastrophic disturbances, such as fire, tornado, hurricane, typhoon, avalanche, landslide, earthquake, tsunami, and volcanic eruption, may be devastating to all genotypes in the population. Nevertheless, if disturbances are more moderate in intensity, genetic variability may lead to the survival of at least a few individuals in the population (Huenneke 1991).

Phenotypic Plasticity

A clear distinction between genetic variation and phenotypic plasticity of plants in nature are often difficult to

determine. Plasticity allows a single genotype to succeed in a range of environments, and may conceal the true extent of genetic differentiation (Huenneke 1991). Plasticity has a genetic basis that varies among individuals and among populations (Huenneke 1991). Perhaps as a consequence of being restricted to microsites, plants have evolved remarkable levels of phenotypic plasticity (Schlichting 1986). Plasticity presumably buffers populations from stochastic environmental conditions and enhances population viability. Patterns of phenotypic plasticity in individual species appear to have adaptive significance, and plasticity can be responsible for a significant amount of life-history diversity and is often a vital product of life-history evolution (Real 1994). Phenotypic plasticity accounts for some of the natural variation in life history, but the site-origin interactions indicate an extensive array of genetic variation in the actual sensitivity and response to environmental effects (Real 1994).

Although phenotypic plasticity with little genetic heterogeneity would retard the rate of evolution, abundant plasticity has permitted successful germination and establishment of many plants whose principal mode of reproduction is vegetative (clonal) propagation. Whether phenotypic plasticity can fully compensate for low genetic variability of a plant species establishing in a heterogeneous environment is difficult to determine. However, when a species does not possess phenotypic plasticity or when a species periodically experiences environmental stochasticity, genetic variation can promote population viability.

General Conclusions and Ecological Implications

It is imperative to determine to what extent local plant populations are genetically differentiated, whether such differences have adaptive value, and whether the mixing of gene pools from different populations would increase or decrease successful establishment and long-term survival. Most plant populations are genetically differentiated from one another. However, population ecologists and geneticists are unable to make accurate predictions on whether such differences would be of adaptive value in the face of changing environments, or how new genetic combinations are likely to fare in nature.

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