CHARACTERISTICS OF INVADING PLANT SPECIES

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ABSTRACT

We have little synthetic understanding of the characteristics of successful plant invaders, *i.e.*, those that become naturalized. I will make, however, three observations about the characteristics of these species: 1) If considered collectively, their morphologic, genetic, and ecological characteristics in many regions (including Hawai'i) are as diverse as the characteristics of the native vascular plants. 2) Despite this extreme diversity, many local floras worldwide share the same naturalized species. Consequently, successful invaders may indeed share traits, although not necessarily the traits often suggested. 3) The opportunity exists through comparative studies of congeners to determine the characteristics that allow successful invasions.

INTRODUCTION

Naturalized plants in Hawai'i aptly illustrate diversity in the characteristics of successful invaders. Prominent or conspicuous invaders in Hawai'i range from annual grasses (Glenwood grass, *Sacciolepis indica*) and herbs (Beggar's tick, *Bidens pilosa*) to tussock grasses (fountain grass, *Pennisetum setaceum*) and turf grasses (Hilo grass, *Paspalum conjugatum*) to shrubs (lantana, *Lantana camara*) and vines (banana poka, *Passiflora mollissima*). Even ferns (*e.g.*, blechnum fern, *Blechnum occidentale*) have become naturalized. Alien trees are particularly prominent and diverse in life form, including pines (Caribbean pine, *Pinus caribaea* and cluster pine, *Pinus pinaster*) and many angiosperms, for example, *koa haole (Leucaena leucocephala)*, firetree (*Myrica faya*), and strawberry guava (*Psidium cattleianum*) (Smith 1985). Vines and aquatic free-floating plants may have the fewest biological restrictions to their invasion, and some of the worst future invaders may be expected to come from these groups.

Genetic Characteristics of Invaders

Genetic attributes and breeding systems among invaders worldwide are also diverse. Examples of aggressive invaders with little genetic variation are at least as common as those with high variability (Barrett and Richardson 1986). Genetic variability is probably not of paramount importance even for invaders with such variability in their natural ranges; little of this variation would usually be expressed in a small founder population. Whether this population bottleneck in natural selection commonly hampers an invasion is unknown.

Among both natives and aliens, generalists usually have more genetic variation than specialists. But many successful invaders are cleistogamous, *i.e.*, the flowers are self-fertilized in the bud, and these plants show little or no isozyme variation. Several invaders, such as cocklebur (*Xanthium strumarium*) in Australia and cheatgrass (*Bromus tectorum*) in the U.S., show clear heritable variation among populations in ecologically important traits, yet they display little or no electrophoretic variation (Barrett and Richardson 1986; Novak and Mack, unpub. data). Isozyme variation is, however, only a crude gauge of overall genetic variation. Two genetic "main options" are most often invoked as the explanations for persistence of an invader: polymorphisms and phenotypic plasticity. Some invaders, such as cheatgrass, apparently evolved with both options.

Sexual recombination is not a prerequisite for a successful invader. Some of the most successful invaders either display sexual reproduction infrequently (*e.g.*, water hyacinth, *Eichhornia crassipes*) or are sterile (*Salvinia molesta*); their populations may possess just a few genotypes that persist through vegetative propagation (Barrett and Richardson 1986). Other widely successful invaders may display vivipary, such as Mauritius hemp (*Furcraea foetida*) in Hawai'i (Smith 1985). Dioecism (having male and female organs in separate plants), as seen in Brazilian peppertree or Christmas berry (*Schinus terebinthifolius*), also does not restrict the spread of some invaders (Loope and Dunevitz 1981).

Invaders are often polyploids, but this condition is probably more an expression of the high percentage of polyploidy among vascular plants than a trait advantageous in colonizing new habitats (Stebbins 1985; Barrett and Richardson 1986; Gray 1986). Furthermore, interpretation is clouded because polyploidy includes a wide range of conditions, from the simple doubling of the same chromosomes (autopolyploidy) to the possession of sets of chromosomes from genetically differentiated populations (allopolyploidy). There may be little or no advantage in the simple genomic multiplication of autopolyploidy (Gray 1986). Perhaps the only conclusion that can be drawn currently about the genetic traits of successful invaders concerns the lack of requisite traits. Successful invaders do not necessarily share high genetic variability, high polyploidy, or high levels of heterozygosity, and they may have wide variation in breeding system.

Demography of Invaders

The demographies of few invaders have been evaluated anywhere. The demography of cheatgrass in the interior Pacific Northwest is one of the few documented records. This grass, a native of arid Eurasia, is now prominent in western North America and temperate South America. It displays weak dormancy (Hulbert 1955); seeds can germinate within two months after leaving the parent in late spring. In the northern hemisphere its seedlings can emerge after rain any time from late August until early May. Even though mortality may be extensive over winter, some plants from these multiple cohorts always survive and produce seeds in late June (Mack and Pyke 1983). Furthermore, these seeds are viable even before seed filling is complete (Hulbert 1955).

Characteristics of Successful Invaders

Statements about diversity in the characteristics of plant invaders conflict, however, with an observation. Many of the same species recur among the lists of naturalized species in local floras, as reflected in the list of the 20 worst weeds worldwide (Holm *et al.* 1977). Do these species have extraordinary opportunities for dispersal, superior traits for invading, or both? The opportunity provided by their introduction leads to the first of the three categories of characteristics I consider important for a successful invader (Table 1).

Several questions arise from such a compilation of characteristics. Are the traits held in common by successful invaders associated more with enhancing their dispersal than with their ecological tolerance of the new range? Have the features that aid in dispersal become more varied through time? For a plant to make a transoceanic immigration without human intervention, possession of a floating seed is important, if not essential. In the age of sailing ships, successful dispersal was dependent on the immigrant's ability to survive as a seed or dormant stem or root (or a potted plant) during a long voyage. Today the chief criterion in dispersability may be only the plant's commercial (including ornamental) value; hardiness in transit is no longer essential. But once the alien arrives, how important to a successful invasion is the escape of the species from its predators, etc. in the natural range?

These questions and observations suggest a tool little employed in the search for common characteristics among invaders: detailed, simultaneous examinations of closely-related congeners in the same range. Such investigations could compare the performance of either several alien congeners in the same new range, or one alien with one native congener. The examination should ideally begin with a determination of the genetic variation in the species soon after alien entry. The demography of the species should be closely monitored for consecutive generations. Comparisons should also be made of the autecology of the species and their biotic interaction (predators, parasites, pollinators, competitors). All the invasions followed in this manner may fail. But tracking the epidemiology of aliens that never become prominent may nevertheless be instructive in deriving an understanding of why some invasions fail while others succeed. The Hawaiian flora offers many opportunities for such study, as in the alien congeneric pairing *Schinus molle* and *S.*

terebinthifolius, and the pairing *Myrsine salicina* (alien) and *M. lessertiana* (native). Other opportunities occur in the alien genera *Hedychium* (gingers), *Psidium* (guavas), *Rubus* (berries), and *Senecio* (groundsel). Only after these and other examples worldwide have been thoroughly investigated will predictions of future plant invaders and the sites of their invasions reach a level meaningful for control.

Table 1. Characteristics of successful invaders.

I. Possess characteristic(s) allowing the opportunity for dispersal (at any spatial scale).

Deliberate: the species is considered useful as:*
- forage
- food
- fiber
- medicine
- ornamental

Accidental: the species is dispersed:
- as a seed contaminant
- with animals (attached to or within)
- in contaminated goods (e.g. ballast)

*Plants not considered useful by humans or not associated with useful plants, and confined to the centers of continents, have little opportunity for dispersal. The importance of the species' other features then becomes moot.

II. Dispersal coincident with leaving predators, competitors, parasites, and pathogens behind in the home range.**

**Seeds usually leave behind all but surface fungi and viruses. Escape from predators, etc. is presumed to be essential but needs to be verified on a quantitative basis.

III. Ability to tolerate the new range beyond the point of entry.***

***For example: the alien may never leave a ballast heap if it requires well-drained soil but arrived in a region with only clayey soil.

The expression of morphologic, genetic, and most ecological characteristics of the invader arises under III. But the importance of these features is moot unless I and probably II are satisfied.

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