

Traits of Invasive Plants: Adaptation and Dispersal

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For weed risk assessment purposes, traits of invasive plants can be divided into roughly three major components: Undesirability, biogeographical, and biological. Undesirability components usually include traits that are undesirable to humans, for example, traits that cause allergies, toxicity, or physical harm. These traits may also contribute to a species' invasibility but the component is not usually defined in this context. The biogeographical component relates to the climatic match between the native and invaded site. This too may relate indirectly to invasibility traits but it is really the biological component that explicitly addresses the traits possessed by a species that contribute to its invasibility.

It is tempting to develop a single set of biological traits when assessing threat of invasion. To this end, lists have been devised to simplify the assessment process for governmental agencies. After considering groups of related woody species that were known to be invasive to those that were known to be non-invasive certain traits were significantly associated with the invasive group. The consensus list included small seed size, short juvenile period, low nuclear DNA content, short interval between large seed flushes, few seed dormancy breaking requirements, rapid vegetative spread and propagation. These lists were devised with a limited set of species, primarily *Pinus* species. Subsequently, dispersal opportunities were found to add significant discriminating power resulting in an assessment flow chart that may be used to detect invasive woody species (Table 1).

TABLE 1. Likelihood of an unknown woody species being invasive based on biological traits and the presence or absence of vertebrate dispersal opportunities where $Z=23.39-0.63\sqrt{M}-3.88\sqrt{J}-1.09S$ and M =seed mass (mg), J =juvenile period (yr), and S =interval between large seed crops (yr) (after Rejmanek et al. 2005).

		Vertebrate dispersal opportunities	
		absent	present
Z>0	Dry fruits, seed >3mg	likely	very likely
	Dry fruits, seed <3mg	likely (wet habitats)	likely (wet habitats)
	Fleshy fruits	unlikely	very likely
Z<0		not, unless dispersed by water	possibly

Growth analysis comparing known invasive and non-invasive groups of related species revealed that size-independent growth rate (relative growth rate) may be a mechanism by which

invasive species are more competitive than their non-invasive counterparts (Table 2). Specifically, the morphological allocation of biomass to the rapid production of many thin leaves contributed most to the superior growth rate. Further, photosynthetic efficiency as assessed by net assimilation rate (NAR) was found to not be significantly different among the groups.

TABLE 2. Growth differences of 29 known invasive, non-invasive, and unclassified *Pinus* species where RGR is relative growth rate ($\text{mg g}^{-1} \text{d}^{-1}$), NAR is net assimilation rate ($\text{mg cm}^{-2} \text{d}^{-1}$), LAR is leaf area ratio ($\text{cm}^2 \text{g}^{-1} \text{plant}$), SLA is specific leaf area ($\text{cm}^2 \text{g}^{-1} \text{leaf}$) and RLPR is relative leaf production rate (leaves produced per leaf present per day) (after Grotkopp et al. 2002).

	Non-invasive	Unclassified	Invasive
RGR	23b*	33a	37a
NAR	0.505a	0.559a	0.572a
LAR	50b	67a	73a
SLA	79b	101a	111a
RLPR	0.014b	0.022a	0.024a

* Numbers in the same row sharing a letter are not significantly different at 5% level according to Scheffe' Test.

Several of the significant biological traits associated with herbaceous invasive species were described over four decades ago in Baker's 1965 list of ideal weedy characteristics for agroecosystems. Long-lived seed with variable dormancy prevents an entire population from committing to a single germination event. In ephemeral natural environments especially those that are water limited, germination following precipitation could be catastrophic if subsequent precipitation events were widely separated. Successful invaders have been described as generalists because 1.) a broad native range correlates with a broad invaded range, 2.) germination requirements can be easily met in a variety of environments, 3.) ability to produce seed early that is dispersed through a variety of biotic and abiotic mechanisms. Many of Baker's ideal weedy traits match those that make alien ornamental plants invasive in natural settings. The matches illustrate the anthropocentric selection pressure that has resulted in creating our own problematic weeds following their escape into natural ecosystems.

Invasive plants in California provide many examples of exceptions to the "single set of traits" approach to predicting invasibility. There is a unique suite of ideal characteristics associated with each invaded ecosystem type in California. Finding moisture is the most significant challenge for any invasive species in California natural ecosystems. This is probably true for

invasive species in any state west of the 100th meridian. I have selected five representative ecosystems to illustrate some exceptional traits to those listed previously.

1. **AQUATIC:** Flotation devices such as the bulbous petioles of water hyacinth facilitate maximal photosynthesis in open air at the water surface where light and CO₂ levels are higher than under water. The plastic response to aerobic and anaerobic conditions exhibited by cultivated species may provide insight to how invasive species tolerate aquatic conditions. Examples include the large air-filled lacuna in the roots of submerged corn and the reduced matrix in the mitochondria of submerged rice obviate the need for the citric acid (TCA) cycle when oxygen is not present. These mechanisms of dealing with anoxic environments almost certainly exist in successful aquatic invaders. Hydrilla (*H. verticillata*) has no stomata and utilizes a C₄-like malate producing photosynthesis to concentrate CO₂ in low CO₂ environments, otherwise it utilizes the normal C₃ pathway, which does not expend the extra ATP when the advantages of C₄ photosynthesis are not necessary such as under high CO₂ conditions.
2. **OPEN CANOPY RIPARIAN:** Species that invade these habitats typically take advantage of the ecotone caused by seasonal flooding and drying which creates an opening between the aquatic and terrestrial environments. Giant reed (*Arundo donax*) is a species that can move into these ecotones and facilitate its own success due to its tolerance of a range of moisture levels. Its presence along waterways slows water flow along the water edge increasing sedimentation around shoot bases raising the water bed. This pushes water further up onto the stream bank allowing more giant reed to infest onto the bank and into the stream. As the waterway becomes shallower due to sedimentation and water is pushed up on the banks, giant reed eventually can infest from bank to bank. This species is not known to produce viable seed in California, and relies on a large rhizome that fragments and can survive submerged conditions for extended periods for dispersal.
3. **CLOSED CANOPY RIPARIAN:** Species invading these environments must be shade tolerant to be successful especially during the initial infestation stages. Tree species such as tree of heaven (*Ailanthus altissima*) spread short distances by prolific suckering and long distances by producing wind dispersed seed. The vine-like growth habit of cape ivy (*Delairea odorata*) allows this species to climb existing trees as if they were a trellis. Even though this species produces seed, it propagates primarily by fragmentation and subsequent establishment downstream.
4. **FOOTHILL GRASSLANDS:** Having a high water use efficiency (WUE, mol CO₂ fixed per mol H₂O transpired) is one way to be superior in water limited environments. Plants utilizing C₄ photosynthesis notoriously have a high WUE. Between 10-50% of summer grasses in California exhibit C₄ photosynthesis. However, annual exotic grasses that comprise much of the primary productivity in California grasslands are C₃ winter annuals that germinate,

establish and set seed quickly in response to the relatively short rainy season typical of California. Preemption of resource space seems to be the most successful strategy for these grasses. Yellow starthistle (*Centaurea solstitialis*), however, is adapted to efficiently extract water that becomes spatially separated from the shallower root systems of its competitors in the summer. It establishes early in the winter and remains a rosette while many of its grassy counterparts are producing seed. Starthistle develops a very deep tap root during the winter and spring months which will facilitate its success later in the summer when everything else has died and water is restricted to the deep soil layers. The success of these grass and thistle species is perpetuated by their adaptation to disturbances that characterize the foothill grassland ecosystem: fire, grazing and perhaps nutrient pulses associated with air pollution. The latter two (and perhaps the first) are associated with human.

- 5. COASTAL:** Brooms, dune grasses, pampas/jubata grass, Eucalyptus, and iceplant illustrate unique traits of a successful invader in these ecosystems. Gorse and the brooms (primarily French, Spanish, and Scotch) are typically found just inland from and northerly along the California coast. These species possess traits that were attractive to the horticulture industry. They belong to the *Fabaceae* family and as such produce seeds with very hard seedcoats that contribute to their longevity and dormancy. Spatial dispersal of seed is associated with ants, birds, and rodents. The *Cortaderia* species, pampasgrass and jubatagrass, were propagated originally for ornamental purposes. They are prolific seed producers that establish readily in freshly disturbed soil combined with the trait of a shallow fibrous root system that perpetuates soil erosion and thus their continued success. The dune grasses, European beachgrass (*Ammophila arenaria*) and veldtgrass (*Ehrharta calycina*) were also propagated for human interests: dune stability and forage for grazing. Strong vertical and horizontal growth has resulted in the complete displacement of dune natives at some locations. Eucalyptus (*E. globulus*, Tasmanian bluegum) was also propagated for human associated interests but also possess characteristics that are well adapted to invade California coastal ecosystems. However, its capacity as a primary invader is questionable because it seems to require human assistance in the form of soil disturbance to displace natives. Its putative allelopathic properties may simply be due to a mulching effect from fallen leaves and bark. Its wind dispersed seed may be a more significant invasive characteristic. Highway iceplant (*Carpobrotus edulis*) was also planted originally for human interests, this time as a roadside soil stabilizer and ornamental. Its spread is attributed to vegetative fragmentation and to fruit-eating mammals.

SUMMARY:

The traits that have lead to the most successful invaders in representative California ecosystems originated with human activities and interests. After that, traits that confer an ability to be successful across a broad range (i.e. generalist), strong vegetative growth and temporally unpredictable reproduction seem to be ubiquitous among successful invaders. There are many

exceptions in California and they center on being able to efficiently acquire water when and where it is available.

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