

1 **Principles for ecologically-based invasive plant management**

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23

24 **Abstract**

25 Land managers long have identified a critical need for a practical and effective framework to  
26 guide the implementation of successful restoration, especially where invasive plants dominate.  
27 A holistic, ecologically-based invasive plant management (EBIPM) framework that integrates  
28 ecosystem health assessment, knowledge of ecological processes, and adaptive management into  
29 a successional management model has recently been proposed. However, well-defined  
30 principles that link tools and strategies managers typically use to ecological processes that  
31 needed to be repaired have been slow to emerge, thus greatly limiting the ability of managers to  
32 easily apply EBIPM across a range of restoration scenarios. The broad objective of this paper is  
33 to synthesize current knowledge of the mechanisms and processes that drive plant community  
34 succession into ecological principles for EBIPM. Using the core concepts of successional  
35 management that identify site availability, species availability and species performance as the  
36 three general causes of plant community change, we detail key principles that can link  
37 management tools used in EBIPM to the ecological processes predicted to influence the three  
38 general causes of succession. While we acknowledge identification of principles in ecology has  
39 greatly lagged behind other fields, and recognize that identification of ecological principles and  
40 the conditions in which they hold are still being developed, we demonstrate how current  
41 knowledge and future advances can be use to structure a holistic EBIPM framework that can be  
42 applied across a range of restoration scenarios.

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47 **Introduction**

48 Land managers long have identified a need for a practical and effective framework for achieving  
49 restoration goals (Cairns 1993; Clewell and Rieger 1997). Accordingly, much research in  
50 restoration ecology has focused on developing frameworks and conceptual models linking  
51 ecological theory to various restoration approaches for degraded systems (Westoby et al. 1989;  
52 Aronson and LeFloch 1996; Whisenant 1999; King and Hobbs 2006). One major area of  
53 advancement is centered on the movement toward ecologically-based invasive plant management  
54 (EBIPM) (Mangold et al. 2006; Sheley et al. 2006). The broad goal of this framework is to  
55 move management away from strategies focused exclusively on controlling the abundance of  
56 invaders and towards strategies focused on repairing damaged ecological processes facilitating  
57 invasion. While small plot studies have demonstrated compelling evidence supporting EBIPM  
58 as an effective and sustainable approach to managing invasive plants (Mangold and Sheley 2008;  
59 Sheley et al. 2009), a lack of an easily applied, holistic framework that synthesizes ecological  
60 knowledge into a useful format has prevented adoption and implementation of EBIPM by land  
61 managers.

62         Development and wide-spread adoption of a general EBIPM framework requires  
63 integration of several key components including methods to assess ecological processes leading  
64 to degradation, a conceptual framework based on ecological principles that allows managers to  
65 identify appropriate tools and strategies that alter ecological processes and mechanisms that  
66 allow plant communities to change in a favorable direction, and a method to measure level of  
67 success and adjust management strategies accordingly (Hobbs and Norton 1996; Hobbs and  
68 Harris 2001). Substantial advances in ecosystem health assessment and adaptive management  
69 have been made and a general conceptual basis for EBIPM, based on successional management,

70 has been developed (Pyke et al. 2002; Mangold et al. 2006; Morghan et al. 2006). However,  
71 well-defined principles on which to base application of tools and strategies managers typically  
72 use in EBIPM have been slow to emerge, mostly due to the exceedingly complex nature of  
73 biological invasion (Williamson and Fitter 1996; Daehler 2003). To be useful, EBIPM will  
74 require that our understanding of the mechanism and processes directing plant community  
75 change be complete enough to create general principles on which managers can base their  
76 decisions (Werner 1999).

77 The need to develop conceptual frameworks for restoration and invasive plant ecology based  
78 on ecological principles has been widely recognized (Hastings et al. 2005; Young et al. 2005).  
79 Identifying principles in ecology, however, has greatly lagged behind other fields such as  
80 physics, causing some question about the ability of ecology and associated applied disciplines in  
81 becoming a predictive science (Berryman 2003). Despite these concerns, some sub-disciplines  
82 in ecology, such as population ecology, have made substantial progress in identifying general  
83 principles capable of predicting dynamics of populations under specific sets of conditions  
84 (Berryman 2003). In addition, principles associated with disturbance, as well as spatial and  
85 temporal scaling that influence ecosystem function have been described (Dale et al. 2000). Most  
86 recently, major advances in understanding evolutionary constraints and tradeoffs associated with  
87 plant ecological strategies as well as ecosystem characteristics influencing invasibility have  
88 emerged, allowing some principles related to the ecology of plant invasions to be identified  
89 (Davis et al. 2000; Wright et al. 2004). While the specific sets of conditions in which these  
90 various principles hold are only beginning to be understood, advances have been sufficient to  
91 start using these principles as a basis for a holistic EBIPM framework.

92 A holistic framework for EBIPM has been recently proposed but principles to support this  
93 framework have not been developed (Sheley et al. submitted, Figure 1). The broad objective of  
94 this paper is to synthesize current knowledge of the mechanisms and processes that drive plant  
95 community succession into ecological principles for EBIPM. For the purposes of this paper, we  
96 define ecological principles as likely fundamental causes that link ecological processes to the  
97 relative abundance of desired and invasive species. Therefore, principles identified in this paper  
98 indicate a magnitude and direction of change that a management strategy likely will have on the  
99 dynamics of invasive and desired species. Implicit in this definition is the notion that in many  
100 situations we have an incomplete understanding of the conditions in which any particular  
101 principle holds, meaning there is a significant but unknown probability of any particular  
102 principle holding in a given situation. We first briefly outline the proposed holistic EBIPM  
103 framework then follow with a detailed discussion of key principles that provide the conceptual  
104 basis for the entire framework.

105

### 106 **A holistic framework for EBIPM and a need for principles**

107 The core framework for EBIPM is based on the successional management model developed by  
108 Pickett et al. (1987) (Figure 1). This hierarchical model includes three general causes of  
109 succession (site availability, species availability, and species performance), ecological processes  
110 that influence these three general causes and factors that in turn modify ecological processes.  
111 The core point of this model is that the ability of managers to guide plant community change in a  
112 favorable direction hinges on the ability to modify and repair the appropriate ecological  
113 processes that are the drivers of the three general causes of succession (Luken 1990; Whisenant  
114 1999; Sheley et al. 2006). This framework integrates assessment and adaptive management

115 efforts with the successional management model. Therefore, this holistic approach incorporates  
116 a conceptual model linking drivers of plant community change to specific ecological processes,  
117 methods to identify damaged ecological processes that may be responsible for directing  
118 successional patterns in a negative direction, and a formal procedure to quantify the success of  
119 various management strategies and make ongoing adjustments to management as needed.  
120 However, this current framework provides no general principles allowing managers to understand  
121 how various tools will modify ecological processes. Instead managers are left to utilize their  
122 own experience and intuition to identify tools and approaches needed to successfully repair and  
123 modify ecological processes. In order to provide managers with a general restoration framework  
124 that has some ability to predict outcomes across a suite of scenarios but is practical and easy to  
125 implement, principles that link management tools and strategies to ecological processes must be  
126 identified.

127

### 128 **Ecological principles forming the conceptual basis of EBIPM**

129 In this section, we take an initial step to synthesize existing scientific literature and identify  
130 general principles that will allow managers to link tools and strategies to ecological processes that  
131 may need to be repaired relative to the three general drivers of succession (site availability,  
132 species availability and species performance). For each of the three causes of succession, the  
133 general ecological processes that influence the causes are described then principles are outline  
134 that pertain to each particular ecological process. Each ecological principle provides an  
135 ecological objective that management might try to attain to stimulate favorable vegetation  
136 dynamics. There may be more than one principle for any process, and there are likely multiple

137 processes to consider for each of the three causes of succession used in this framework. These  
138 principles detailed below are outlined in Table 1.

139

#### 140 Site Availability

141 A sufficient amount of safe sites must be available to incoming propagules for species  
142 composition to change. A safe site provides the specific set of conditions allowing a seed to  
143 germinate and a seedling to establish and can include factors such as soil water content, air and  
144 soil temperature, light, soil organic matter, soil texture, density, identity and distribution of  
145 neighboring plants (Harper et al. 1965). Traditionally, plant communities have been classified as  
146 being limited by either propagule or safe site availability (Turnbull et al. 2000). Most  
147 communities, however, tend to exhibit some degree of both propagule and safe site limitations  
148 (Clark et al. 2007). The magnitude of the effect of these factors on plant population varies  
149 greatly depending on the plant community. In general, site availability tends to be more limiting  
150 in late successional plant communities and in portions of the community with higher vegetative  
151 cover (Turnbull et al. 2000). An important consideration is that species can differ substantially  
152 in their safe site requirements so any particular safe site might reflect a range in quality for a  
153 suite of coexisting species (Harper et al. 1965). Disturbance is the central ecological processes  
154 affecting site availability and is therefore a double-edge sword. Some form of disturbance is  
155 natural in all systems and is key to maintaining recruitment windows for newly arriving and  
156 established species (Hobbs and Huenneke 1992). On the other hand, disturbance also provides  
157 opportunities for invasive plants to establish. Below, the general concept of disturbance as an  
158 ecological process is outlined, followed by key principles that help identify how disturbance can  
159 be manipulated to favor desired species.

160

161 *Process: Disturbance*

162 Disturbance can be defined as a relatively discrete event in time that alters ecosystem,  
163 community or population structure, changes resource availability or the physical environment  
164 (White and Pickett 1985, Hobbs and Huenneke 1992, Krueger-Mangold et al. 2006). Not all  
165 disturbances are the same but differ in type (e.g. grazing; fire; flood; drought), frequency  
166 (common or episodic), intensity (low or high), and extent (patch or landscape). Disturbance  
167 often kills or damages existing vegetation, decreasing resource uptake by resident vegetation and  
168 opening up gaps for new seedlings to establish. Disturbance also stimulates nutrient cycling  
169 (Smithwick et al. 2005). The decrease in uptake of resources by the resident vegetation  
170 combined with an increase in nutrient cycling, usually results in a pronounced increase in  
171 resource availability following disturbance (Davis et al. 2000). Several principles provide  
172 insight into how disturbance can be managed to favor establishment of desired species and  
173 discourage establishment and population growth of undesired species.

174

175 *Principle: Lower disturbance frequencies will favor establishment of desired species compared*  
176 *to higher disturbance frequencies*

177 Many invasive species are characterized by rapid growth, short generation time and abundant  
178 seed production while most desired species are characterized by slow-growth, long periods  
179 between seed production and they tend to invest a relatively lower proportion of their biomass in  
180 seed production each year (Noble and Slatyer 1980; Rejmanek and Richardson 1996). As a  
181 consequence, frequent disturbance will tend to favor invasive species while less frequent  
182 disturbance regimes will tend to favor desired species.

183

184 *Principle: Lower disturbance intensity will favor establishment of desired species compared to*  
185 *higher disturbance intensity*

186 As disturbance intensity increases, nutrient cycling rates increase and the ability of resident  
187 vegetation to sequester nutrients decreases, increasing nutrient availability (Davis et al. 2000).

188 The rapid growth rate exhibited by most invasive species is favored in nutrient rich environments  
189 (Lambers and Poorter 1992). Therefore, invasion will be directly and positively related to  
190 disturbance intensity. Most desired species have traits that increase longevity of root and shoot  
191 tissue and therefore allow conservation of previously captured resources (Lambers and Poorter  
192 1992). These traits confer a competitive advantage in low nutrient environments (Berendse et al.  
193 1992). As a result, low disturbance intensity will tend to favor desired species to a greater extent  
194 than high disturbance intensity.

195

196 *Principle: Smaller scale disturbances spread through time will be less likely to promote growth*  
197 *of weed populations than simultaneous large scale disturbances*

198 Plants have a fixed amount of resources to allocate to reproduction (Smith and Fretwell 1974).

199 Thus, each plant species is faced with a trade-off between producing a small amount of large  
200 seeds or a large amount of small seeds. Producing large amount of small seeds is assumed to  
201 provide an advantage in terms of colonization while producing a small amount of large seed is  
202 assumed to provide an advantage in terms of ability to establish in harsh microsites where  
203 competition from neighboring vegetation may be high (Tilman 1994). Most invasives share  
204 traits of colonizing species and thus tend to producer many small seeds. This strategy is  
205 expected to be favored in areas with large scale disturbances where population growth is

206 primarily limited by the amount of seed a species can disperse across the landscape (Noble and  
207 Slatyer 1980). Likewise, the colonization strategy of invasive species is usually associated with  
208 rapid germination and little seed dormancy mechanisms, allowing invasive plant seed banks to  
209 quickly and uniformly respond to a disturbance but leaving little seed carryover in the seedbank  
210 (Benefield et al. 2001; Meyer et al. 2007). As a consequence of the greater colonizing ability of  
211 most invasive plants compared to desirable plants, minimizing the scale of disturbance and  
212 spreading planned disturbances through time will be critical in minimizing the spread of weed  
213 populations

214

215 *Principle: The need to use disturbance for creating safe sites is greater in late seral communities*  
216 *with high plant cover compared to early seral communities with low plant cover*

217 The amount of bare soil is positively related to safe site availability (Turnbull et al. 2000). The  
218 amount of bare earth reflects the distribution and size of competing neighbor vegetation and is  
219 therefore a reflection of the intensity of competition a seedling might experience and amount of  
220 resources available at that safe site. However, the amount of bare soil is not necessarily  
221 proportional to safe site availability since microsite characteristics (e.g. soil cracks) unrelated to  
222 gaps created by disturbance strongly influence seedling establishment (Clark et al. 2007).

223 Planned disturbance will be particularly important for creating safe site in late seral communities  
224 in areas in the community with high vegetation cover but a proportional relationship between  
225 bare soil created by the disturbance and safe site availability cannot be expected.

226

227 Species Availability

228 Propagule limitations of desired species usually are present to some degree in all communities  
229 and often are pronounced in degraded and weed infested systems (Navie et al. 2004; Clark et al.  
230 2007). If sufficient propagules of desired species are not present at a site, it will not be possible  
231 to move the structure or composition of a community toward a more desired state. Propagules  
232 can include reproductive (e.g. seed) and vegetative components (e.g. rhizomes). Propagule  
233 limitations can be due to dispersal limitation, the amount of propagules produced (propagule  
234 pressure), or both factors. Limitation by propagule pressure occurs when not enough seeds are  
235 produced to saturate potential recruitment sites even if all seeds produce reach a site. Dispersal  
236 limitations occur when seeds produced do not reach all potential sites, even though enough seeds  
237 are produced to saturate safe site that are available. Because dispersal and propagule pressure  
238 limitations often co-occur, recruitment of desired and undesired species can be viewed as a  
239 probabilistic event (Davis et al. 2000). As a consequence, managing plant community change  
240 requires managing both the frequency of dispersal and propagule pressure of both desired and  
241 undesired species. Below, the general concept of dispersal and propagule pressure as ecological  
242 processes are outlined, followed by key principles that help identify how these processes can be  
243 manipulated to favor desired species.

244

#### 245 Process: Propagule dispersal

246 Dispersal is the movement of propagules away from parent plant or population through time and  
247 space (Harper 1977). Dispersal is the first step determining if new species will be admitted into  
248 a community. Potential mechanisms of dispersing through space include wind, animal and  
249 hydrologic vectors. A range of seed dormancy and other biochemical mechanisms allow some  
250 species to disperse propagules through time (Baskin and Baskin 2001). Most species tend to

251 have dispersal adaptations particularly advantageous for a specific vector (e.g. plumes as  
252 adaptations for wind dispersal) but this does not necessarily preclude dispersal by other vectors.  
253 Several principles provide insight into how dispersal can be managed to favor establishment of  
254 desired species and discourage establishment and population growth of undesired species.

255

256 *Principle: Increasing frequency of dispersal of desired species and decreasing frequency of*  
257 *dispersal of undesired species can allow plant communities to change in a favorable direction*

258 In systems that display some degree of heterogeneity in site availability, successful colonization  
259 of a site by a particular species will involve at least some random elements. Lottery models have  
260 been used to describe some of these effects. In these models, seeds of species that successfully  
261 colonize sites are drawn randomly from a pool of potential species. A particular species has a  
262 greater chance of arriving at a site if it disperses more frequently, even if it is an inferior  
263 competitor (Sale 1977) . As a consequence, managers can facilitate plant community change  
264 toward a desired state by increasing dispersal frequency of desired species and/or decreasing  
265 dispersal frequency of undesired species.

266

267 *Principle: Less competitive desired species can “win” a safe site from more competitive invasive*  
268 *species by arriving at the safe site first*

269 Competitive hierarchies have been widely demonstrated in plant ecology (Tilman and Wedin  
270 1991), directly questioning how subdominant species can establish in areas where competitive  
271 dominants also are dispersing seed. However, even very small differences in the order in which  
272 seeds arrive at a site (e.g. weeks), can influence what species establish and ultimately, the  
273 composition of the community (Egler 1952; Korner et al. 2008). In general, the species that

274 arrives first tends to be most successful (Drake 1991). Because of this “priority effect”, in areas  
275 where a weak competitor arrives first, it can persist even when more competitive species  
276 subsequently establish. As a consequence, small shifts in dispersal timing that favor early  
277 dispersal of desired species and delayed dispersal of undesired species can facilitate plant  
278 community change toward a desired state.

279

280 *Process: Propagule pressure*

281 Propagule pressure can include both reproductive and vegetative components but management  
282 often centers on seed production since this is the main way most species colonize  
283 heterogeneously dispersed gaps in communities. Low propagule production by the resident  
284 community may leave safe sites open to possible invasion by undesired species. Several  
285 principles provide insight into how propagule pressure can be managed to favor establishment of  
286 desired species and discourage establishment and population growth of undesired species.

287

288 *Principle: Increasing propagule pressure of desired species and decreasing propagule pressure*  
289 *of undesired species can allow plant communities to change in a favorable direction*

290 As outlined on dispersal principles, site availability is heterogeneous in most systems, indicating  
291 that while competitive hierarchies may exist among species, colonization of a site by a  
292 particular species will involve at least some random elements. As a result, a particular species  
293 will have a greater chance of colonizing a site if that species produces a greater number of  
294 propagules than other species (Sale 1977). As a consequence, managers can facilitate plant  
295 community change toward a desired state by increasing propagule pressure of desired species  
296 and/or decreasing propagule pressure of undesired species (Von Holle and Simberloff 2005).

297

298 *Principle: Broad control of seed production by invasive plants will be required to realize*

299 *benefits of seeding desired species*

300 As discussed under disturbance principles, plants have a fixed amount of resources to allocate to  
301 reproduction (Smith and Fretwell 1974) forcing plants to choose between producing a small  
302 amount of large seeds or a large amount of small seeds. Producing large amount of small seeds  
303 is assumed to provide an advantage in terms of colonization while producing a small amount of  
304 large seed is assumed to provide an advantage in terms of ability to establish in marginal  
305 microsites where environmental stress or competition from neighboring vegetation may be high  
306 (Tilman 1994; Turnbull et al. 1999). While the per capita ability of seed of desired species to  
307 establish may be higher than undesired species, undesired species often produce much more seed  
308 per plant than desired species. Even moderate difference in seed production can overwhelm the  
309 per capita establishment advantage of desired species, acting as an effective filter limiting  
310 recruitment of desired species (DiVittorio et al. 2007). As a consequence of the greater propagule  
311 pressure exhibited by most invasive plants compared to desirable plants, control of propagule  
312 production by undesired species will need to be higher than predicted just based on undesired  
313 plant density if seed of desired species is going to establish.

314

315 *Principle: Inducing stress or damage to vegetative material may have a larger negative effect on*

316 *seed production by desired plants than invasive plants*

317 All plant species face a trade-off in supplying energy to vegetative or reproductive growth and a  
318 minimum amount of energy reserves needs to be developed to produce viable seed (Bloom et al.  
319 1985). As a consequence, any physical damage or stress to a plant during vegetative growth will

320 force a plant to reallocate energy to repairing vegetative components, reduce energy reserves for  
321 seed production and, ultimately, reduce seed viability and/or total seed production. Therefore,  
322 management strategies can be designed that reduce propagule pressure of undesired species,  
323 even if it is not possible to fully kill the entire population of undesired species. However,  
324 undesired species tend to be more plastic in their allocation to growth and reproduction than  
325 desired species (Caldwell et al. 1981; Rogers and Siemann 2005; Hempy-Mayer and Pyke 2008).  
326 As a consequence, an important constraint is that the same level of stress or physical damage  
327 applied to undesired species likely will have an even greater affect on seed production of desired  
328 species.

329

### 330 Species Performance

331 Species performance is associated with a range of ecological processes that determine how a  
332 species captures and utilizes resources to maintain and increase population size. Species  
333 performance can be modified by resource supply patterns of the ecosystem (resources),  
334 physiological processes that allow a plant to affect and respond to the immediate environment  
335 (ecophysiology), the patterns of birth, mortality and growth of individuals in a population (life  
336 history), how a species responds and maintains fitness under harsh abiotic conditions (stress) and  
337 how individual of a species are influenced by neighbors of different species (interference).

338 While the ecological processes associated with species performance are varied and potential  
339 interactions among processes can be complex, not all processes need to necessarily be modified.

340 By managing a subset of key processes, either by altering environmental conditions to favor

341 performance of a desired species or altering the target pool of the desired species to match

342 environmental conditions, it will be possible to direct weed infested plant communities toward a

343 more desired state. Below, the general concepts of the major ecological processes influencing  
344 species performance are outlined, followed by key principles that help identify how these  
345 processes can be manipulated to favor desired species.

346

347 *Process: Resources availability*

348 Resources refer to any item that a plant needs to procure from the environment that is essential  
349 for survival (Bloom et al. 1985). Not all resources are limiting, however, so manipulation of any  
350 particular resource may not alter species performance. The resources that tend to be the most  
351 limiting are light, water and soil nutrients nitrogen (N) and phosphorous (P) (Lambers et al.  
352 1998). Because plants require relatively high quantities of N to support growth compared to the  
353 amount of N supplied by most ecosystems, N limitations are fairly ubiquitous in natural systems  
354 (Vitousek and Howarth 1991). While most ecosystems experience some N limitations, water or  
355 light limitations also occur depending on regional climate and weather as well as canopy  
356 structure of the plant community. Several principles provide insight into how resource  
357 availability can be managed to favor establishment of desired species and discourage  
358 establishment and population growth of undesired species.

359

360 *Principle: Managing environments for low resource availability will favor resource conservation*  
361 *over resource capture by plants, favoring desired species over invasive species*

362 Research on plant ecological strategies based on leaf and root tissue economics have  
363 demonstrated a universal trade-off between construction of tough, long-lived tissue capable of  
364 yielding a long return on tissue but at a low rate, or construction of thin, short-lived tissue  
365 capable of yielding short returns on tissue but at a high rate (Diaz et al. 2004; Wright et al. 2004).

366 Empirical studies and models suggest construction of short-lived tissue with a high rate of return  
367 is beneficial in resource-rich environments while construction of long-lived tissue with a slow  
368 rate of return is beneficial in resource poor environments (Berendse and Aerts 1987; Berendse et  
369 al. 1992; Berendse 1994; Fraser and Grime 1999). Not surprisingly, many invasive species are  
370 characterized by construction of short-lived tissue while many natives and desirable species are  
371 characterized by construction of long-lived tissue (Grotkopp and Rejmanek 2007; James and  
372 Drenovsky 2007; Leishman et al. 2007). Managing environments for low resource availability,  
373 therefore, should favor performance of desired species over invasive species.

374

375 *Principle: Initial establishment of desired species needs to be successfully managed to realize*  
376 *any benefit of resource management*

377 The benefits of resource conservation in low resource environments are manifested through time  
378 by mechanisms such as nutrient resorption and recycling (Chapin 1980). During the  
379 establishment phase both invasive and desirable plants need to capture the bulk of their resources  
380 from the immediate environment. Since these species groups have comparable resource  
381 requirements during the establishment phase, low resource availability is not expected to  
382 differentially affect species performance of these two groups (Van der Werf et al. 1993; Ryser  
383 and Lambers 1995; James 2008). Therefore, if factors such as high propagule pressure or rapid  
384 growth of invasive plants are not managed and prevent desired species from establishing, no  
385 amount of resource management will improve the performance of desired species (DiVittorio et  
386 al. 2007).

387

388 *Principle: Within a given community, managers can minimize resource availability primarily by*  
389 *maximizing biomass and secondarily by managing for variation in traits such as phenology and*  
390 *root distribution of dominant species.*

391 Research examining the effects of species or functional group diversity on resource availability  
392 largely has overlooked the importance of how natural variation in species abundance influences  
393 resource capture by a particular species or group of species (Zavaleta and Hulvey 2006). Theory  
394 and empirical work indicate an overriding importance of biomass in determining how much  
395 resource a species sequesters (Aarssen 1997; Grime 1998). More abundant species sequester  
396 more resources. While considering the primary importance of abundance, plant communities  
397 that have co-dominant species that differ in phenology and root distribution or other traits that  
398 influence the pattern of resource capture can sequester more resources than monoculture  
399 communities (Hooper and Vitousek 1997; Fargione and Tilman 2005). This suggests managers  
400 can minimize resource available by first managing for biomass and then subsequently, variation  
401 in traits among potential dominant species.

402

403 *Principle: Managers can minimize the amount of resources directly available to an invader by*  
404 *establishing desired species that are functionally similar to an invader.*

405 The potential for different species to influence ecological processes and properties in a similar  
406 manner due to similar morphological and physiological characteristics long has been recognized  
407 (Botkin 1975). From this researchers have arranged species into functional groups (e.g. shrubs,  
408 grasses, forbs) and have recognized that functional group composition (i.e. what particular  
409 groups are present) and functional identity of the invader are major determinates of invasion and  
410 invasion resistance (Symstad 2000; Turnbull et al. 2005). Desired and invasive species within

411 the same functional group tend to have similar patterns of resource capture and use. As a  
412 consequence, desired species functionally similar to potential invaders will have a  
413 disproportionately greater negative effect on resources available to the invader than would be  
414 predicted by their biomass alone (Pokorny et al. 2005).

415

416 *Process: Ecophysiology*

417 Ecophysiology generally encompasses any physiological or morphological mechanism allowing  
418 a plant to affect and respond to the immediate environment (Lambers et al. 1998) and therefore  
419 involves a wide range of processes and attributes. Initially, there was much hope that these traits  
420 could be used to identify traits of invaders so that potential new invasions could be predicted  
421 (Noble and Slatyer 1980; Rejmanek and Richardson 1996). Unfortunately, identifying universal  
422 traits was elusive and limited the ability to develop predictions beyond certain families or life  
423 forms (Mack et al. 2000). Nevertheless, a few underlying traits and associated principles have  
424 emerged that can help identify how systems can be managed to favor desired species over  
425 invasive plants. These principles are outlined below.

426

427 *Principle: Managing environments to favor resource conservation over resource capture will*  
428 *favor desired species over invasive species*

429 As outlined in the Resource principles section one of the unifying traits that distinguishes many  
430 invasive species from their native counterparts is centered on how they allocate biomass to  
431 develop root and shoot systems. Natives tend to invest in energetically expensive, heavily  
432 protected tissue while invasives tend to invest in cheaper, poorly protected tissue (Diaz et al.  
433 2004; Wright et al. 2004). These alternative strategies result in a suite of ecophysiological

434 differences among these groups which, in turn, allows these species groups to be favored in  
435 different environments. For example, by constructing cheap, poorly-protected tissue, invasives  
436 can create much more root surface and leaf area per unit biomass allocated to roots and leaves.  
437 A high specific leaf area (SLA) and high specific root length (SRL) allow these species to  
438 rapidly compound the rate of return on root and leaf tissue investment (Lambers and Poorter  
439 1992). Higher photosynthetic capacity and lower respiration rates are associated with a high  
440 SLA and higher root nutrient uptake rates per biomass of roots are associated with a higher SRL  
441 (Leishman et al. 2007). Construction of thin, poorly defended root and leaf tissue, however,  
442 comes at a cost. A high SLA and SRL is associated with less lignified tissue and tissue with  
443 thinner cell walls (Harris and Wilson 1970; Van Arendonk et al. 1997). This makes high SRL  
444 and SLA tissue susceptible to environmental stress (e.g. wind, drought) and more susceptible to  
445 damage by generalist herbivores (Coley et al. 1985; Lambers et al. 1998). Combined these  
446 factors interact to greatly reduce the longevity of these tissues. In resource poor environments,  
447 conservation of previously captured resources, and maintenance of previously constructed tissue  
448 may be more important than capturing new resources and developing new tissue. Consequently,  
449 the high SLA and SRL and associated traits that characterize some of the core ecophysiological  
450 advantages invasives have in high resource environments should be disadvantageous in low  
451 resource environments.

452

453 *Principle: A sufficient amount of abiotic or biotic stress will need to be applied at appropriate*  
454 *times to inhibit performance of invasive species in low nutrient environments.*

455 As outlined above, nutrient conservation should be as important as nutrient capture in low  
456 nutrient environments. While a trade-off between SLA and tissue longevity has been described

457 along with the implications this has for resource conservation, resource conservation also can be  
458 achieved by using resources efficiently. Producing thinner leaves (higher SLA) means invasives  
459 can allocate less N to each unit of leaf area to maintain similar levels of photosynthesis,  
460 compared to species with lower SLA (Osone et al. 2008). This may allow invasives to achieve  
461 greater N use efficiency than natives and maintain greater growth than natives in low N soils  
462 (Funk and Vitousek 2007; James 2008). As outlined above, a high SLA comes at a cost in terms  
463 of tolerance to abiotic and biotic stress. To ensure low nutrient environments disproportionately  
464 affect invasives more than desired species these stresses will need to occur at a magnitude and  
465 time that will ensure that invasive species incur a cost associated with having high SLA.

466

467 *Principle: Broad control of invasive species germination during the first growing season will be*  
468 *required when seeding desired species in areas with moderate to high seed banks of invasive*  
469 *species*

470 Many invasive species have faster germination rates than native species (reviewed in Krueger-  
471 Mangold et al. 2006). Earlier growth establishes important initial size differences between  
472 seedlings of invasive and desired species. Because competition for soil resources is generally  
473 size symmetric (Bartelheimer et al. 2008), with bigger plants getting more resources, slight  
474 differences in germination timing can result in large differences in competitive ability even if the  
475 amount of resources sequestered per unit biomass is the same between species (Korner et al.  
476 2008). Therefore, management of these differences in germination timing is a key first step  
477 when trying to reassemble a desired plant community from seed.

478

479 *Principle: Using desired species that have similar resource capture and utilization strategies as*  
480 *invaders can increase chances of successfully establishing a desired plant community*

481 In the previous sections, the advantage invaders have in ecophysiological traits such as SLA and  
482 germination rate have been highlighted. There also is substantial variation in these traits within  
483 the pool of desired species that might be use to restore a site (Monaco et al. 2003; James and  
484 Drenovsky 2007; Drenovsky et al. 2008). In areas where initial control of invasive propagules is  
485 difficult and conditions are expected to continue to favor ecophysiological traits of invaders,  
486 restoration will be more successful if variation in specific ecophysiological traits such as  
487 germination timing and SLA are used as the basis to design species mixtures.

488

489 *Process: Life History*

490 Life history describes patterns of birth, mortality and growth of individuals in a population as it  
491 passes from seed to adulthood and plants have evolved a range of life history strategies through  
492 time. As outlined under site availability, plants allocate a limited amount of resources to  
493 reproduction so plants are faced with an inevitable trade-off between producing many small  
494 seeds or fewer, larger seeds. In most cases a trade-off between seed size and establishment  
495 success in unfavorable environments can be demonstrated (Harper 1970; Rejmanek and  
496 Richardson 1996; Turnbull et al. 1999). Natural selection in a particular habitat favors the life  
497 history strategy that optimizes the number and size of seeds produced. There are two broad  
498 approaches to describing variation in life history: categorical approaches (e.g. r and K-selection  
499 or ecological strategies (MacArthur and Wilson 1967; Grime 1977) that classify life history  
500 based on selection forces, and demographic approaches that consider plant life span and size in  
501 which a plant reproduces (e.g. annual, biennial, perennial). These two approaches have different

502 advantages and disadvantageous but nevertheless both allow some general principles to emerge  
503 about how life-history can be used to help direct plant communities toward more desired states.

504

505 *Principle: Less frequent and less intense disturbances will favor establishment and population*  
506 *growth of desired species*

507 Population growth rates are mainly determined by the chance of an individual surviving to  
508 reproductive age times their reproductive output if they do survive (Gurevitch et al. 2002). A  
509 common trait of many invasive plant species is a short juvenile period and in perennial plants, a  
510 short period between large seed crops (Rejmanek and Richardson 1996). These traits reflect an  
511 ‘r-strategy’ or ruderal strategy under the categorical approach to life history, and allow rapid  
512 population growth (MacArthur and Wilson 1967; Grime 1977). This life history strategy should  
513 be most beneficial when survival of adult plants is much lower than survival of juvenile plants  
514 (Charnov and Schaffer 1973). Conversely, when survival of adult plants is much higher than  
515 survival of juvenile plants, life history traits of most invaders are not favored. Disturbance  
516 frequency and intensity are major factor influencing plant survival. Less frequent and less  
517 intense disturbances will tend to favor the life history characteristics of desired species.

518

519 *Principle: Establishing desired communities with species having a diverse life-history can*  
520 *increase stability*

521 As outlined above, different life history traits are favored in different environments and under  
522 different disturbance regimes. Ecosystem stability involves both the ability of a community to  
523 resist change following a disturbance and the ability of the community to recover following  
524 disturbance (Grime 1987; Chesson and Huntly 1997). Because disturbance frequency and

525 intensity is difficult to predict and manage, maintaining at least some level of a seed bank of  
526 desired species with a range of life history should provide a greater level of stability than a less  
527 diverse seed bank

528

529 Process: Stress

530 Stress can be generally defined as any condition that limits plant growth (Grime 1977). Because  
531 conditions rarely are completely optimal for growth in natural systems, stress levels tend to range  
532 along a continuum from mild to severe. While not all forms of stress are induced by disturbance,  
533 most forms of disturbance induce some degree of stress with the magnitude depending on  
534 disturbance type, intensity, and frequency as well as the stress tolerance of the particular plant  
535 species. Therefore, while disturbance may be used as a process to alter site availability,  
536 disturbance also can be applied in various ways to induce stress on undesired species. As  
537 outlined earlier, plants need to balance resources to support tissue maintenance, new growth and  
538 resources need to support reproduction (Bloom et al. 1985). Any physical or physiological  
539 damage to a plant during vegetative growth ultimately means less energy is available to support  
540 new growth as well as reproduction. Therefore, if a few key principles are considered, stress can  
541 be used as an ecological process to influence species performance.

542

543 *Principle: Moderate, prolonged stress will favor desired species over invasive species compared*  
544 *to short-duration, intense stress*

545 Stress tolerance at the community and species levels includes resistance, the ability of a  
546 community or species to avoid changes in production or population size when exposed to stress,  
547 and resilience, the ability of a community or species to recover back to initial levels following

548 stress (Leps et al. 1982). The ability of a species or plant community to resist stress is negatively  
549 correlated with intrinsic growth rate (Macgillivray et al. 1995) . In addition, there also is a  
550 negative correlation between resistance and resilience (Leps et al. 1982). Most invasive species  
551 have a high intrinsic growth rate and greater physiological plasticity than desired species  
552 (Niinemets et al. 2003; Grotkopp and Rejmanek 2007; James and Drenovsky 2007). As a  
553 consequence, it is expected that this species group will have higher resilience and be favored  
554 under short but intense stress regimes. On the other hand, moderate, prolonged stress should  
555 favor the greater stress resistance of desired species.

556

557 *Principle: Desired species with high tissue density will be more resistant to stress than species*  
558 *with lower tissue density*

559 As outlined in previously, tissue density (reflected in specific leaf area (SLA) and specific root  
560 length, (SRL) has surfaced as a primary axis that differentiates plant ecological strategies,  
561 including stress resistance (Craine et al. 2001; Wright et al. 2004; Leishman et al. 2007). In  
562 general, species with lower SLA and SRL will produce long-lived, tough tissue, more capable of  
563 sustaining function under stresses such as drought, freezing, wind abrasion, herbivory and low  
564 nutrient availability (Lambers and Poorter 1992; Craine et al. 2001). Therefore, rankings of  
565 species response to a range of stress types should remain similar based on their tissue density,  
566 with high tissue density species being the most resistant to stress.

567

568 *Process: Interference(any other pertinent info?)*

569 Interference refers to the reduction of fitness of neighboring plants from various mechanisms  
570 including competition, allelopathy, resource availability, and other trophic interactions (Pickett et

571 al. 1987). Interference is the broadest and likely most difficult of the processes to quantify and  
572 the processes where principles appear to be the least developed. Nevertheless some core patterns  
573 have emerged allowing us to identify a few key principles.

574

575 *Principle: If priority effects are managed, desired species will have a proportionately greater*  
576 *competitive effect on invasives and a greater ability to respond to competitive pressure of*  
577 *invasives compared to high resource environments*

578 Competitive ability involves both the ability to negatively influence neighbors (competitive  
579 effect) and the ability to tolerate neighbors (competitive response) (Goldberg 1990). As outlined  
580 under process associated with resource availability and ecophysiology, many native species have  
581 a number of traits that allow efficient conservation of captured resources while many invasives  
582 have a number of traits that allow rapid capture of resources (Chapin 1980; Leishman et al.  
583 2007). The value of these traits and the degree to which they contribute to competitive effect and  
584 response of a species should be a function of the resource environment, with low resource  
585 environments giving a proportional advantage to native species and high resource environments  
586 giving a proportional advantage to invasive species. As outlined earlier, however, early  
587 germination and rapid growth of invasives can inhibit establishment of natives even in low  
588 resource environments. As a consequence, these priority effects will have to be overcome in  
589 order to allow natives to realize a competitive advantage in resource-poor systems.

590

591 *Principle: Desired species or functional groups with patterns of resource capture similar to the*  
592 *invader will have a greater competitive effect per unit biomass compared to species with less*  
593 *similar patterns of resource capture*

594 Resource sequestration by a species is broadly related to species abundance, per unit rate of  
595 resource uptake and loss, and duration of resource uptake (Grime 1998). Differences in rooting  
596 depth and phenology as well as root and leaf physiology and morphology are important drivers  
597 of species specific uptake patterns. Species more similar in these traits will have more  
598 comparable patterns of resource capture than species less similar in these traits. While  
599 competition for below ground resources is expected to be size symmetric with larger plants  
600 expected to acquire proportionately more resources than smaller plants, native species with  
601 resource capture traits functionally similar to invaders will have a greater negative effect on  
602 resource capture by invaders compared to native species with less similar traits (Dukes 2002;  
603 Pokorny et al. 2005).

604

## 605 **Conclusion**

606 The need to extract general ecological principles and use them to formulate frameworks that  
607 allow practitioners to predict outcomes of alternative management strategies and guide  
608 restoration efforts has been widely acknowledged (Cairns 1993; Hobbs and Norton 1996;  
609 Clewell and Rieger 1997). While there have been recent valuable efforts to develop unifying  
610 frameworks that predict patterns of biological invasion as well as efforts to integrate various  
611 conceptual models of ecosystem degradation and repair (King and Hobbs 2006; Barney and  
612 Whitlow 2008; Catford et al. 2009), a complete, ecologically-based, decision-making process for  
613 land managers has not emerged. In this paper, we have demonstrated how ecological principles  
614 can be incorporated into a holistic EBIPM framework that includes necessary steps to assess  
615 management needs, formulate management strategies, identify appropriate management tools  
616 and options as well as quantify and adjust management outcomes for invasive plants. While this

617 effort largely focuses on merging succession and invasion ecology, fields that share many  
618 similarities but have been minimally integrated (Catford et al. 2009), this process based  
619 framework can serve as a useful template to identify and develop further principles associated  
620 with plant community change and repair. This initial effort recognizes that identification of  
621 ecological principles and the conditions in which they hold are still being developed and it is  
622 expected that this general framework will be expanded, modified and improved. Nevertheless,  
623 this initial effort shows the critical need for basic and applied ecology to jointly work on  
624 development of general principles that will allow restoration and other land management  
625 activities to move away from recurring agronomic inputs designed on a site by site basis and  
626 toward sustainable, ecologically-based strategies that can be easily applied to a range of  
627 restoration scenarios.

628

629

630

631

632

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