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Baer, Sara G.; Engle, David M.; Knops, Johannes M. N.; Langeland, Kenneth A.; Maxwell, Bruce D.; Menalled, Fabian D.; and Symstad, Amy J., "Vulnerability of Rehabilitated Agricultural Production Systems to Invasion by Nontarget Plant Species" (2008). *Faculty Publications in the Biological Sciences.* Paper 132.
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Environmental Management
DOI 10.1007/s00267-008-9167-6

Vulnerability of Rehabilitated Agricultural Production Systems to Invasion by Nontarget Plant Species

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Received: 17 October 2007 / Accepted: 26 May 2008
Springer Science+Business Media, LLC 2008

Abstract Vast areas of arable land have been retired from crop production and "rehabilitated" to improved system states through landowner incentive programs in the United States (e.g., Conservation and Wetland Reserve Programs), as well as Europe (i.e., Agri-Environment Schemes). Our review of studies conducted on invasion of rehabilitated agricultural production systems by nontarget species elucidates several factors that may increase the vulnerability of these systems to invasion. These systems often exist in highly fragmented and agriculturally dominated landscapes, where propagule sources of target species for colonization may be limited, and are established under conditions where legacies of past disturbance persist and prevent target species from persisting. Furthermore, rehabilitation approaches often do not include or successfully attain all target species or historical ecological processes (e.g., hydrology, grazing, and/or fire cycles) key to resisting invasion. Uncertainty surrounds ways in which nontarget species may compromise long term goals of improving biodiversity and ecosystem services through rehabilitation efforts on former agricultural production lands. This review demonstrates that more studies are needed on the extent and ecological impacts of nontarget species as related to the goals of rehabilitation efforts to secure current and future environmental benefits arising from this widespread conservation practice.

Keywords Agri-environment schemes · Conservation programs · CRP · Invasive species · Restoration

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Introduction

Retiring arable lands from production and promoting perennial, native, and/or more diverse plant communities has become a widespread conservation practice to improve environmental quality (e.g., reduce soil erosion, increase water infiltration, reduce run-off of nutrients to surface water, improve soil quality, increase cover for wildlife, etc.) in agricultural landscapes of the United States (e.g., US Department of Agriculture [USDA] Conservation Reserve Program) and Europe (i.e., Agri-Environment Schemes [AES]). These lands, which we refer to as rehabilitated production systems (RPS), include arable systems that have been removed from agricultural production and "improved" through some conservation practice. These systems may differ from restorations, as Bradshaw (1996) explicitly defined rehabilitation as human facilitated

recovery of some aspects of ecosystem structure (e.g., species diversity and complexity) and function (e.g., productivity, nutrient cycling), but not fully representative of the original system prior to human disturbance. Although rehabilitation goals of former agricultural production systems vary widely and practices invoked to achieve conservation goals can be antagonistic (Marrs and others 2007), both USDA programs and Agri-Environment Schemes generally aim to improve one or more aspects of ecosystem structure (e.g., plant diversity and/or dominant life forms) and/or function (e.g., soil stabilization, nutrient mitigation) (Dunn and others 1993; Anonymous 1994; Gibson 2009).

Thorough reviews of invasive species in natural systems (Mack and others 2000; Pimentel and others 2000; Pimentel 2002; Lodge and others 2006) demonstrate that invasions can change community, trophic, and/or physical structure, which in turn can result in cascading alterations to ecosystem functions (e.g., nutrient cycling and productivity [Vitousek and Walker 1989]) and landscape dynamics (e.g., fire and hydrologic regimes [D'Antonio and Vitousek 1992]). Although quantitative data are scarce, landowners and officials that monitor and administer programs for rehabilitating formerly cultivated lands recognize that many of these rehabilitations become colonized by nontarget species of concern (See Fig. 1). We define nontarget species as native and/or exotic species of concern, some of which are invasive, that can compromise the trajectory of community recovery and rehabilitation goals (D'Antonio and Meyerson 2002; Suding and others 2004). Despite the absence of literature on the extent to which RPS are colonized by nontarget species, numerous studies on the variety of factors influencing and ecological consequences of colonization and persistence of nontarget species in RPS (Table 1), coupled with recurring recommendations to control nontarget species in RPS (D'Antonio and Meyerson 2002; Forshay and Morzaria-Luna 2005; Antonsen and Olsson 2005; Fischer and others 2006) underscores the wide-spread and international nature of this phenomenon. Here, we identify multiple factors that might increase the vulnerability of RPS to invasion by nontarget species of concern. Through this synthesis on the vulnerability RPS to invasion by nontarget species of concern, we aim to increase recognition of this problem and promote further investigation of impacts of these species on RPS to secure long-term ecological benefits of conservation practices that aim to improve environmental quality.

Fig. 1 A United States Geological Survey researcher surveying breeding birds in a CRP field planted to *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass) and invaded by *Melilotus officinalis* (L.) Lam. (yellow sweetclover) in Sheridan County, Montana (photo by Lawrence D. Ig1)

Susceptibility to Invasion

Landscape-, disturbance-, plant community-, and process-related factors affect the vulnerability of rehabilitated agricultural production systems to invasion by nontarget species (Table 1). These rehabilitated systems often exist as isolated habitats within a matrix of highly modified and managed agricultural landscapes. Surrounding agricultural systems can harbor many nontarget species that can spread to colonize noncropping systems (Johnson and others 2006; Seabloom and others 2006; Smith and others 2006), and increased connectivity of improved or natural areas within these landscapes has been shown to slow the spread of nontarget species (Alard and others 1994; Donald and Evans 2006). For example, colonization and persistence of invasive shrub species have been correlated with historical agricultural land use (Johnson and others 2006; DeGasperies and Motzkin 2007). Furthermore, Clements and others (2004) documented significant within- and among-population genetic variability in traits related to invasiveness of agricultural weeds and proposed that the potential for rapid evolution of invasive traits exists in agriculturally dominated landscapes.

Alterations (i.e., cultivation of soil, replacement of natural plant communities with monocultures of crops, water diversions, herbicide carryover, etc.) to the environment where RPS commonly occur can present a legacy of disturbance outside the natural range of variation to which native historical species are adapted (Table 1). These altered environmental conditions may be less suited to support historical or target communities (Graham and Hutchings 1988; Bakker and others 1991; Galatowitsch and van der Valk 1996). As a result, RPS may not include all of the species, processes, or spatial scales that may be key to resisting invasion (Naeem and others 2000; Sheley and Krueger-Mangold 2003).

Disturbance can further promote invasion by generating space and resources for new species to capitalize (Elton

Table 1 Synthesis of factors related to increased vulnerability of rehabilitated production systems to invasion by nontarget species of concern

Vulnerability factor	Aspect of vulnerability factor	Evidence from rehabilitated production systems	Reference(s)
Landscape	Fragmentation	Increased landscape connectivity slows spread of invasive species.	Donald and Evans (2006)
		Maintenance of improved grasslands in intensive agriculture landscape requires connectivity with species rich grasslands.	Alard and others (1994)
	Historical land-use	Occurrence, abundance and spread of invasive shrub related to historical agricultural land-use.	DeGasperies and Motzkin (2007)
		The most influential factor affecting the colonization and spread of invasive shrubs was proximity to historical and present agricultural fields in the landscape.	Johnson and others (2006)
Disturbance legacies	Propagule limitations	Seed banks of fewer target species, lower density of target species, and/or abundance of nontarget species limit rehabilitation of arable lands.	Graham and Hutchings (1988), Bakker and others (1991), Galatowitsch and van der Valk (1996)
	Altered Hydrology	Altered water regimes can result in unexpected (nontarget) community establishment during restoration, resistant to change.	Klotzil and Grootans (2001)
		Broad scale hydrologic constraints limit success of rehabilitation target structure and function of bottomland forests.	King and Keeland (1999)
	High nutrient availability	Non target species of concern more prevalent in rehabilitated systems where nutrient availability is high resulting from past agricultural disturbance, reducing soil fertility increases target species and/or target plant diversity by limiting establishment of nontarget species.	Green and Galatowitsch 2001, Baer and others (2002), Gough and Marrs (1990), Marrs (1993), Blumenthal and others (2003), Walker and others (2004), Vinton and Goergen (2006)
Community structure	Low diversity	Rehabilitated/restored systems contain lower diversity than native remnant systems.	Galatowitsch and van der Valk (1996), Lesica and DeLuca (1996), Christian and Wilson (1999), Wilson and Partel 2003, Baer and others (2005), Martin and others (2005)
	Exotic/nontarget species	Higher exotic species diversity in rehabilitated grasslands relative to remnants.	McLachlan and Knispel (2005)
	Resistance to improved structure	Formerly cultivated systems planted to invasive exotic species resistant to efforts to improve native species diversity.	Christian and Wilson (1999), Gendron and Wilson (2007)
Altered processes	Nutrient availability and cycling	Establishment of nonnative grasses alters nutrient transformations, availability, and/or storages of organic matter and nutrients.	Christian and Wilson (1999), Vinton and Goergen (2006)
	Management	Attaining target community structure of species-poor grassland established following long-term cultivation is improved with active management that mirrors historical ecosystem drivers.	Antonsen and Olsson (2005), Walker and others (2004), Pywell and others (2007), Chapman and others (2004b)

1958), and RPS commonly possess biotic, physical, hydrologic, and nutrient perturbations that may persist long after rehabilitation. For example, grasslands converted from row-crop agriculture contain minimal legacy of the historic plant community, as well as severely altered soil structure and nutrient status following long-term cultivation (Low 1972; Baer and others 2002; McLauchlan 2006). Moreover, hydrology of agricultural landscapes may be permanently altered due to altered drainage, increased sedimentation and erosion, and decreased infiltration and decreased plant water uptake by annual crops. These changes can constrain rehabilitation of community structure and function (King and Keeland 1999; Klotzil and Grootans 2001). Finally, altered resource availability from surrounding land management, such as excess nutrients and/or water, may produce more subtle forms of disturbance that can constrain community assembly, structure, and function (Davis and others 2000; Stohlgren and others

2003; Zedler and Kercher 2004; Vinton and Goergen 2006). In rehabilitated agricultural systems, excess nutrients have been invoked as an important mechanism promoting nontarget species persistence (Green and Galatowitsch 2001; Gough and Marrs 1990; Marrs 1993) and reducing nutrient availability has been shown to increase target and reduce nontarget and invasive species in RPS (Baer and others 2002; Blumenthal and others 2004; Walker and others 2004; Vinton and Goergen 2006).

The legacy of disturbance in RPS (e.g., altered soil structure, high available nutrients, permanently modified hydrologic regimes, etc.) may leave vacant or create novel niches for nontarget species to fill in a community. Colonization by native species is likely to be hindered by their low abundance and subsequent dispersal in agricultural landscapes, whereas weedy nontarget species are likely to be abundant and/or widely distributed. Deliberate attempts to restore high plant diversity in rehabilitated grasslands are commonly fraught with difficulty (Kindscher and Tieszen 1998; Baer and others 2005; Polley and others 2005). Furthermore, if incentive programs to improve environmental quality are short in duration (e.g., <10 years) then there may not be sufficient time for native community development in some systems comprised of slow growing species (e.g., trees). Rehabilitations are also generally not provided with the full historical complement of species, but rather a few dominant species. If target species establish slowly, then nontarget and invasive species may have a generous window of opportunity to establish and persist. Finally, lack of disturbances (e.g., fire, grazing, and/or hydrologic fluctuations) that historically were critical to promoting cover, dominance, and diversity of native species also may facilitate invasion in RPS (Naeem and others 2000; Pokorny and others 2005, D'Antonio and Chambers 2006).

Several aspects of community structure in RPS may also facilitate invasion and persistence of nontarget species (Table 1). First, rehabilitated agricultural systems often contain lower diversity than historical communities in the US, where agriculture and management for resource use has not persisted as long as in European countries (Gibson 2009). Rehabilitated grasslands in North America contain lower plant diversity (Christian and Wilson 1999; Baer and others 2005; Martin and others 2005; Polley and others 2005) and more nontarget exotic species (McLachlan and Knispel 2005) than grasslands that have never been cultivated in the same regions. Furthermore, rehabilitated systems planted to exotic species are highly resistant to efforts to introduce native species in the US (Bakker and others 2003; Christian and Wilson 1999; Wilson and Partel 2003; Gendron and Wilson 2007), as well as Europe (Crawley and others 1999).

Natural plant communities are often structured by ecological drivers, e.g., fire and grazing, and the absence of these drivers in some RPS may compromise the persistence of target plant communities historically maintained through these processes. Managing RPS for communities that resist invasion represents one of the most important tools in preventing invasion by nontarget species (D'Antonio and Chambers 2006), and in most regions these drivers are imposed through active management. In some instances, treating RPS as "set aside" systems, as opposed to an alternative type of "working land" may compromise the attainment and persistence of target communities. For example, attaining target community structure of species-poor grasslands from long-term intensive agricultural practice in Europe is improved with active management (Antonsen and Olsson 2005; Walker and others 2004; Pywell and others 2007).

Encroachment of woody species can be detrimental to wildlife conservation goals of rehabilitated grasslands (Chapman and others 2004a). Prescribed fire is an effective tool in preventing and managing these nontarget species invasions (Bernardo and others 1988; Ortman and others 1998). Selective grazing has long been recognized as a cost-effective, ecologically compatible tool to manage certain nontarget plants, including woody species (Vallentine 1990). Recent evidence suggests that prescribed grazing, especially when combined with prescribed burning in a spatially dynamic approach called patch burning, can reduce nontarget species while improving overall grassland function and suitability for native wildlife habitat (Fuhlendorf and Engle 2001, 2004; Cummings and others 2007). Mowing and haying are common management practices in rehabilitated grasslands and, when timed and applied properly, can eliminate or reduce woody encroachment (DiTommaso 2000). Unlike grazing, mowing is species-nonselective, and if used improperly, can promote plant invasion (DiTommaso 2000). Also, mowing and haying generally fail to functionally substitute for grazing in nutrient cycling (McNaughton 1984; Ruess and McNaughton 1987, Anderson and others 2006) that might play a pivotal role in ecosystem resistance to invasion (Davis and others 1998; Knops and Tilman 2000; Baer and others 2003).

Using cultural practices that act as ecological drivers is limited to appropriate sites, and less is known about the interaction between invasive and native species in response to these practices (CAST 2003; Langeland and Stocker 1997). For example, fire and grazing may be successful management practices if nontarget species do not share a common evolutionary history with these ecological processes or if species are functionally different from the native constituents (MacDougall and Turkington 2005; D'Antonio and Chambers 2006). Alternatively, invaders that are functionally similar to native species (e.g., phenology and photosynthetic pathways) may respond similarly to management practices as native species, representing a real dilemma for managers (Reed and others 2005).

Uncertainties Regarding Nontarget Species and Rehabilitation Goals

If nontarget species colonizing rehabilitated agricultural systems are also invasive, then the goals of rehabilitation efforts may be compromised. Goals regarding restoration of ecosystem services such as sequestering carbon (Lal 2004), improving soil and water quality (Davie and Lant 1994; Baer and others 2002), and increasing connectivity and quality of wildlife habitat (Reynolds and others 2001) may be particularly vulnerable because species differentially affect inputs, storage, and fluxes of nutrients in ecosystems. For example, invasion of grasslands by woody species alters carbon allocation to greater aboveground storage (Norris and others 2001). Invasive species may also alter multiple aspects of carbon cycling through differences in aboveground net primary productivity and root distribution (Wilsey and Polley 2006). Furthermore, modifications to nutrient pools and fluxes by invading species can promote the persistence of these species through feedback mechanisms (Ehrenfeld 2003; Vinton and Goergen 2006), particularly if invading species are capable of nitrogen fixation (Vitousek and others 1987; Rice and others 2004; Baer and others 2006).

If nontarget species in RPS are invasive, these species may also compromise goals of improving plant diversity. Lessons from ecological invasions demonstrate that invaded plant communities often exhibit lower species diversity than uninvaded communities (Levine and others 2003). Although it is often unclear whether an invasive species causes declines in diversity, invades as a result of low diversity, or capitalizes on conditions that negatively impact other species (MacDougall and Turkington 2005), removal of an invasive species usually results in an increase in native species abundance and/or diversity (e.g., Farnsworth and Meyerson 1999; Hulme and Bremner 2006). Exceptions to this response occur when the invasive species leaves a legacy of physical, chemical, or biological alterations to the environment. For example, crested wheatgrass (*Agropyron cristatum* L.) changes the soil microbial community such that it is more favorable for growth of other invasive species than for native species (Jordan and others 2008).

Not all rehabilitations aim to improve biodiversity. For example, the primary goal of the USDA Conservation Reserve Program was to reduce soil loss from highly eroded cultivated lands (Baker 2000), as reflected by the widespread plantings of exotic species, many of which are invasive (Lesica and DeLuca 1996; White and Dewald 1996; Harmoney and others 2004). Several southern Great Plains states in the US were seeded to vast areas of Old World bluestem (*Bothriochloa ischaemum* [L.] Keng) varieties cultivated to compete vigorously with native species (Dabo and others 1988; Belesky and Fedders 1995; Harmoney and Hickman 2004). Furthermore, species poor grasslands dominated by exotic species in the US are highly resistant to changes in composition (Bakker and others 2003; Wilson and Partel 2003; Gendron and Wilson 2007). Initiating restorations with native species can constrain invasion (Bakker and Wilson 2004) and increasing use of native species and options to select higher diversity seed mixes in US landowner incentive programs represents a progressive change in program directives with potential benefits to biological diversity.

Summary and Conclusions

As the global environment becomes increasingly converted and managed for human resource use, we will gradually depend more on rehabilitations of production lands for conservation of resources, biodiversity, and ecosystem functions. Biological invasions are now considered a major global change phenomenon (Vitousek and others 1996). Increased concern about threats invasive species pose to biodiversity, productivity, ecosystem services, human welfare, and the economy in *nonproduction* systems has recently provoked recommendations to improve prevention, adopt scientific-based risk assessment, increase surveillance and information sharing, provide support for early control, protect uninvaded systems, and coordinate policy (Lodge and others 2006). We demonstrate that RPS are also highly vulnerable to invasion due to landscape factors, legacies of disturbance, novel plant communities, and the absence of ecological drivers that historically maintained target communities. However, there are few examples and subsequently great uncertainty surrounding whether nontarget species of concern compromise the long term goals of rehabilitation efforts towards improving biodiversity and/or ecosystem services in former agricultural production systems.

Acknowledgments This synthesis is a product from the Invasive Plant Species and the 2007 Farm Bill Workshop (March 20–21, 2007) that was organized and supported by the Center for Invasive Plant Management, Bozeman, Montana. We are grateful for the time and effort contributed by M. Johnson and J. Clark towards organizing the agenda, discussion, and outcome of this workshop. Lawrence D. Igl, T. Shaffer, Ryan P. Klopf, Virginia H. Dale, Gregory Houseman, and three anonymous reviewers provided constructive comments towards this manuscript.

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