



Predicting dispersal-limitation in plants: Optimizing planting decisions for isolated wetland restoration in agricultural landscapes



Jessica L. O'Connell^{a,*}, Lacreia A. Johnson^{b,1}, Benjamin J. Beas^{a,2}, Loren M. Smith^a, Scott T. McMurry^a, David A. Haukos^{b,3}

^a Department of Zoology, Oklahoma State University, Stillwater, OK 74078, USA

^b Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409, USA

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ABSTRACT

Isolated wetlands are often degraded by agriculture, increasing sediment accretion and altering plant composition. Two common opposing wetland restoration practices are self-design vs. intensive revegetation. Self-design restores hydrogeomorphology without inoculating wetland taxa into restoration sites. Self-design may not meet restoration targets if dispersal-limited plants do not colonize restoration sites. Alternatively, intensive revegetation (hydrogeomorphic restoration combined with revegetation) is costly and time consuming. We investigated plant dispersal-limitation in 309 isolated wetlands among two agricultural landscapes in the U.S. Great Plains (the western High Plains (WHP) and the Rainwater Basin (RWB)) and three land-uses (reference, croplands, and previous croplands) to predict optimal restoration practices. We present analytical tools predicting whether self-design or intensive revegetation will be more successful elsewhere. In the WHP and RWB, perennial wetland cover was 61% and 31% greater in reference than in other land-uses. Distance to the nearest reference wetland explained perennial wetland richness in both regions, and area of reference wetlands within 15 km also was important in the WHP. Annual wetland species were over-represented in previous cropland wetlands and were less influenced by landscape isolation. We analytically identified dispersal-limited and cosmopolitan species in reference wetlands, with distance to reference wetlands and area of surrounding reference wetlands important in determining composition. Further, dispersal-limited plants in reference wetlands had greater cover in clustered than isolated wetlands in previous croplands. Plant community patterns in reference conditions may predict composition in restored wetlands. This aids selection of self-design or revegetation restoration approaches for individual plant species in isolated wetlands.

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1. Introduction

Loss of wetlands is pervasive in the United States (Dahl, 2000) and worldwide (Finlayson et al., 1999). Many remaining wetlands have been impacted by conversion of watersheds from native to agricultural conditions (Brinson and Malvárez, 2002). This is particularly true of isolated depressional wetlands globally (Brinson and Malvárez, 2002). We define isolated wetlands as those in indi-

vidualized catchments, often containing groundwater connections, but lacking surface water connections to other aquatic areas under normal conditions. Isolated wetlands are estimated to account for 20% of the numerical total of wetlands in the United States (Tiner et al., 2002), though comparable estimates elsewhere are lacking. Isolated wetlands are especially vulnerable to agricultural conversion because they occur in flat, fertile landscapes, encouraging wetland drainage and infilling (Smith et al., 2008). Further, isolated wetlands frequently dry seasonally and are readily cultivated when dry. In this paper, we describe common opposing practices to restore vegetation communities in isolated wetlands and generate analytical models for predicting optimum restoration methods.

Isolated wetlands are important because of services they provide generally common to wetlands, including carbon storage capacity, flood water mitigation, habitat for wetland biota, and water purification (Tiner, 2003; Smith et al., 2008). Further, isolated wetlands maintain stable meta-populations among nearby wetland patches (Hanski, 1998; Tiner, 2003). Isolated wetlands also provide important stopover sites for migrating wildlife.

* Corresponding author. Present address: Department of Environmental Sciences, Policy & Management, UC Berkeley, Berkeley, CA 94720-3114, USA. Tel.: +1 405 744 5555; fax: +1 405 744 7824.

E-mail address: jessica.oconnell@okstate.edu (J.L. O'Connell).

¹ Present address: United States Fish and Wildlife Service, 7660 East Broadway Blvd., Suite 303, Tucson, AZ 85710, USA.

² Present address: Illinois Natural History Survey, University of Illinois, Champaign, IL 61821, USA.

³ Present address: U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, 205 Leasure Hall, Kansas State University, Manhattan, KS, USA.

Two philosophies for wetland restoration currently are practiced. The first is based on self-design (Mitsch et al., 1998). This restoration technique relies on unaugmented colonization by organisms to sites following hydrology and geomorphology restoration. Self-design has also been called the “Field of Dreams” hypothesis: “If you build it, they will come” (Hilderbrand et al., 2005). This hypothesis suggests that after restoring abiotic processes, organisms self-assemble. For example, in agricultural isolated wetlands, restoration by self-design involves plugging ditches or drainage tiles that de-watered wetlands for cultivation. Removal of upland sediments from wetlands and grading to restore microtopography also are common (Galatowitsch and Van der Valk, 1998). Wetland plant communities then are expected to develop from seed banks and dispersal.

However, self-design approaches have been criticized (Streever et al., 2000; Galatowitsch, 2006) because dispersal of some plants may be limited (van Dorp et al., 1996; Galatowitsch, 2006). For example, wetland plants requiring moist habitats may be dispersal-limited because of lower establishment in intervening non-wetland habitat (Tiner, 1991). Further, perennial plants should be more susceptible to landscape isolation than annuals because perennials generally are *k*-selected whereas annuals are *r*-selected (Pianka, 1970). This previous statement theorizes concerning average plant traits, but we present analytical tools for determining traits of individual species. Perennials were called *k*-selected because they are long-lived, slow-growing and competitive in stable environments. Perennials also produce fewer offspring annually (Pianka, 1970; Hautekèete et al., 2001; Bonser and Aarssen, 2006). Annuals conversely, are short-lived, competitive in fluctuating or disturbed conditions, and produce many offspring in one breeding episode. Species rarely are strictly *r*- or *k*-selected, but fall somewhere on the continuum between extremes (Pianka, 1970).

Thus, we expect reduced wetland perennial colonization in disturbed environments such as croplands. Further, perennial seed sources should also be reduced in cropland seed banks because plowing annually removes adults before seed production. We term this model the dispersal-life history wetland plant model. By life history, we mean annual vs. perennial life history strategies. Foundations of this model have been described by others (Godwin, 1923; Zedler, 2000; Ozinga et al., 2005; Galatowitsch, 2006; Poschlod et al., 2007). Our model assumes that the probability of a propagule reaching a given location increases with the number of propagules produced. As a result, lower yearly rates of perennial seed production reduce the probability of perennial dispersal to distant locations, assuming other confounding factors such as seed size, growth form and dispersal mode are equivalent. Thus, the model predicts, that relative to reference wetlands, perennial wetland plants will be underrepresented and wetland annuals over-represented in agricultural wetlands, or wetlands with a past history of disturbance, such as new restoration sites where agriculture previously occurred. Dispersal capabilities of individual species of course may vary. Therefore, in this paper we quantify both general traits and individual species responses.

A wetland restoration approach addressing dispersal-limitation is more time and materials intensive than self-design. The intensive approach involves introducing organisms into restoration sites following restoration of hydrology, usually by seeding or transplanting from nearby reference sites (Streever et al., 2000). Seeding or planting has the advantage of jump-starting plant assembly, potentially reducing establishment of introduced species (Zedler and Kercher, 2005). Further, high initial restoration investments sometimes increased restoration success (Klimkowska et al., 2007). We use “introduced” as defined by the USDA PLANTS database (e.g. plants occurring outside their native range) (USDA and NRCS, 2010). Disadvantages of the intensive approach include ex-

pense, failure of some transplants to establish, and potential failure of restored sites to resemble natural communities (Zedler and Kercher, 2005; Noël et al., 2011). The latter is particularly true if plants are not local genetic varieties or establish disproportionately to native abundance (Zedler and Kercher, 2005).

Intensive revegetation and self-design restoration approaches are currently practiced globally (e.g., Klimkowska et al., 2007; Poschlod et al., 2007; NRCS, 2008). Ideally, we would like to predict effective restoration methods to increase efficiency and the probability of reaching restoration goals. We will explore the applicability of the dispersal-life history wetland plant model to aid restoration of isolated wetlands. We investigated this model in two landscapes where isolated wetlands and agriculture occur in high density. We compare effects of landscape isolation on wetland plant communities within major land-use categories to elucidate general principles. These land-use categories are reference land-use (i.e., that with the least history of anthropogenic disturbance), wetlands within row-crop agricultural lands, and wetlands within croplands that have been taken out of production. This latter land-use lends insight into community assembly after agricultural disturbance has ceased, similar to what might occur in self-design restoration.

We develop analytical approaches that use extant plant communities in reference wetlands to predict the best restoration practice in regions of interest. We test these predictions using plant communities in wetlands in previous croplands. Our approach analyzes the degree to which landscape isolation may limit plant dispersal for individual plant species. Should isolation be strongly influential, we suggest revegetation is more likely to establish that species in restoration communities than self-design. Our approach is useful because it may identify the best restoration strategy for individual species of concern before restoration is initiated.

2. Materials and methods

2.1. Study area

We surveyed plants in isolated wetlands, called playas, within two regions of the U.S. Great Plains: the western High Plains (WHP) and the Rainwater Basin (RWB) (Fig. 1). These regions differ in dominant vegetation, land-use history and climate (Smith, 2003). Playas in both regions have hydric clay Vertisol soils and are freshwater, recharge wetlands. As such, hydrologic inputs to playas are precipitation and overland sheet flow, while outputs are limited to evapotranspiration and groundwater recharge (Smith, 2003). Playas are temporary to seasonal wetlands, remaining wet for weeks to months (Smith, 2003). RWB playas are wetter than WHP playas and typically inundate from 1 to several months (Wilson, 2010). Individual playas inundate unpredictably and remain dry for indeterminate periods (Smith, 2003; Wilson, 2010). When dry, playas contain upland prairie vegetation, but seed banks and immigrating propagules rapidly transform playas into wetland plant communities following inundation. Playas in both regions are dominant surface freshwater features because rivers and lakes are rare (Smith, 2003; Wilson, 2010).

The WHP, a 30 million ha sparsely settled landscape, is a short-grass prairie eco-region encompassing six states. Climate in the WHP is semiarid with precipitation varying from 38 cm to 63 cm along a west–east gradient (Smith, 2003). Playas average 7 ha (S. McMurtry, unpublished data) and are generally round in shape. Up to 60,000 playas occur in the WHP (Playa Lakes Joint Venture, <http://pljv.org/>). We investigated three land-uses in the WHP, native short-grass prairie (covering ~12 million ha of the region), row-crop agriculture (~15 million ha) and croplands taken out of production (~3 million ha) (O'Connell et al., 2012). This latter

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