Harvesting native seed to supply landscape-scale restoration: evaluating risks and sustainable practices

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Justin Carl Meissen

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Dr. Susan M. Galatowitsch, Dr. Meredith W. Cornett

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ABSTRACT

Seed supply limits large-scale restorations, which often rely on seed collection from remnant ecosystems. Overharvesting seed may deplete populations, exacerbate seed limitation, and jeopardize ecosystem integrity, but these risks have not been formally studied. Many life history traits are linked to species' reliance on seed reproduction, and so may provide a useful framework to address seed harvest risks.

I evaluated whether life history traits predict susceptibility to overharvest by comparing tallgrass prairies in Minnesota (USA) harvested at varying frequencies (every year, once per 3-5 years, unharvested). I identified species less likely to occur on frequently harvested sites then tested whether lifespan, clonality and seed production predicted harvest sensitivity. Short-lived, non-clonal species were sensitive to seed harvest while long-lived clonal species were not, suggesting that life history traits provide a means to predict seed harvest risk.

To verify the predictive utility of life history traits and determine extinction risks from seed harvest over long restoration timeframes (25 years), I used matrix models of clonal *Solidago canadensis* and *Anemone canadensis* and non-clonal *Rudbeckia hirta*, *Packera aureus*, *Zizia aurea*, and *Liatris ligulistylis* to simulate seed harvest and extinction risk. I simulated 5 scenarios: no harvest; annual harvest at 50%/75% intensity; and triennial harvest at 50%/75% intensity. Non-clonal species were insensitive to triennial and 50% harvest, but susceptible to extinction risks of up to 92% with annual 75% harvest. Clonal species were insensitive to all harvest scenarios. To maintain populations of non-clonal species in the long-term, high intensity annual harvest should be avoided.

To demonstrate the risk of overharvest in short-lived, non-clonal species and determine sustainable harvest regimes, I conducted a field experiment varying seed harvest intensity (0, 50%, or 100% seed removed) and management (burned or unburned) for *R. hirta* populations. I compared seedling recruitment and seed production among treatments, and found that seed production nearly doubled with burning. Moderate intensity harvest with burning allowed high levels of seedling recruitment, but high harvest intensity prevented recruitment, as predicted for a short-lived, non-clonal species. A regime combining moderate intensity harvest with fire management provides seeds while also conserving at-risk seed donor sources.

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GENERAL INTRODUCTION

Ecological restoration has become an essential tool to ameliorate intensifying anthropogenic impacts in ecosystems worldwide. There is now an established understanding that the scope and extent of ecological restoration must increase rapidly if the aims of global biodiversity conservation are to be met (Merritt & Dixon 2011; Suding 2011; Aronson & Alexander 2013). In landscapes that have been largely converted to intensive anthropogenic land use, the importance of expansive restoration is particularly pressing. Remnant ecosystems in such landscapes are small and isolated, and natural dispersal to the surrounding landscape and among remnants is insufficient to support either long-term biodiversity conservation or natural regeneration in degraded ecosystems (Fischer & Stöcklin 1997; Thomson et al. 2009). Thus, the active revegetation of entire landscapes has become a central goal of global efforts to conserve biodiversity (Brudvig 2011; Broadhurst et al. 2015).

One of the greatest barriers to restoring landscapes is securing a steady and sufficient supply of appropriate native seed. Using seed rather than installing plants to restore native vegetation is highly desirable, as seeding allows large areas to be much more efficiently planted with genetically diverse propagules (Galatowitsch 2012). Large quantities of seed are typically needed to restore biodiverse ecosystems— for example, seeding rates of 2.8 to 5.4 million seeds/ ha are common in tallgrass prairies (Packard & Mutel 2005, NRCS 2005). With restorations commonly reaching thousands of hectares or more in size, a single large-scale project can require billions of seeds. However, commercial seed sources are rarely able to supply genetically appropriate seed in sufficient quantities to restore biodiverse landscapes (Broadhurst et al. 2008; Borders et al. 2011). Because demand for native seed so far exceeds supply, some have asserted that landscape restoration projects are facing a "crisis of scale," where seed limitation prevents the achievement of restoration goals (Merritt & Dixon 2011).

Commonly, restoration practitioners rely on harvesting seed from remnant ecosystems to overcome seed limitations. By using mechanized seed harvest techniques such as combine harvesters, brush harvesters, or seed haying, large quantities of seed can be procured quickly and efficiently (Olson 1984; Scotton et al. 2009). Wild harvesting

also gives practitioners options for selecting the most appropriate genetically adapted seed sources, since donor seeds can be harvested from remnants that experience ecological conditions similar to the restoration area (Havens et al. 2015). Experience gained in restoring tallgrass prairies shows that extensive mechanized seed harvest can overcome the seed supply barrier to landscape restoration. By harvesting seed from nearby remnant prairies, The Nature Conservancy's 9000-ha Glacial Ridge Project was able to restore up to 6 ha of prairie from seed harvested from 1 ha of remnant donor prairie (Gerla et al. 2012).

Though wild seed harvest promotes restoration seed supply, it also poses risks to seed donor sites. When seeds are collected, the regenerative potential of plant populations is reduced. If seed collection is very intense or frequent, populations may no longer be able to grow, which may lead to decline and eventual species loss from remnants (Menges et al. 2004; Broadhurst et al. 2008). The loss of species from seed donor sites may compromise the resilience of the very remnants that landscape restoration was intended to enhance. For instance, Zavaleta & Hulvey (2004) found that even losses of rare species could lead to a profound loss of ecological functionality. Depleting seed donor populations also presents a risk to the outcomes of landscape restoration itself. By diminishing already scarce sources of native seed through overharvest, the capacity to carry out landscape-scale restoration may become even more seed limited.

The purpose of this dissertation is to assess the risks of seed harvest in tallgrass prairies and outline practical harvest guidelines that mitigate the risks. Currently, little information exists on the nature and magnitude of the risk that wild harvest presents to donor populations (Smith et al. 2007). Existing harvest guidelines (Mortlock 2000a; Packard & Mutel 2005) have not been verified by empirical or theoretical research (but see Menges et al. 2004). A promising approach to investigate the risks of seed harvest and improve harvest guidelines is to use life history traits as a means to predict the response of species to seed harvest. Because seed harvest limits reproduction from seed, species with life history traits that are linked to a reliance on seed for population persistence are likely to be sensitive to seed harvest. Conversely, species with life history traits linked to vegetative reproduction and survival are less likely to be affected by

harvest. One of the key strengths of using a life history-based approach to assess seed harvest risk is practicality— it is generalizable to all species regardless of taxonomic classification. Trait data are often readily available in existing databases or quickly measured in the field (Cornelissen et al. 2003; Lavorel et al. 2007; Kattge et al. 2011).

In the first chapter of this dissertation, I investigate how prairie remnants respond to seed harvest, and whether life history traits predict the susceptibility of species to seed harvest. I conducted an exploratory study of 17 prairies harvested for seed frequently (annually/biennially), infrequently (2-3 times), or not at all. I used multivariate techniques and ANOVA contrasts to identify species less likely to occur on frequently harvested sites, and I used logistic regression to test whether lifespan, clonality and seed production predict seed harvest susceptibility. Identifying harvest-sensitive species and understanding the ability of life history traits to predict seed harvest sensitivity establishes a useful framework that can be used to develop seed harvest best practices. This framework will allow conservation practitioners to incorporate readily available life history trait information into harvest guidelines that minimize the risks of overharvest.

In chapter two, I explore the role of life-history in determining the long-term risks of prairie seed harvest. I assessed the risk of population extinction for 2 clonal and 4 non-clonal prairie species using stage-based matrix models. I simulated 5 seed harvest scenarios: no harvest, annual harvest at low/high intensity (50% and 75% seeds removed), and triennial harvest at low/high intensity. For each scenario, I compared differences among species in the finite rate of increase and projected extinction risk over 25 years. The findings from this study outline general seed harvest guidelines for prairies based on easy to measure life history characteristics. These guidelines provide harvesting strategies to mitigate the long-term risks of seed harvest. Implementing these strategies will enable conservation practitioners, who usually lack extensive demographic field data, to make better decisions about how much and how often seed may be harvested without adverse impacts on donor populations.

In the final chapter, I examine how seed demand for landscape-scale restoration can be met sustainably for harvest sensitive species. In a field experiment, I manipulated management type (burned or unburned) and seed harvest intensity (0, 50%, or 100% seed

removed) to evaluate important factors for seedling recruitment rates or seed production. I measured changes in seedling recruitment and seed production among treatments and used mixed-effects models and *post-hoc* tests to discern the effects of harvest intensity and fire. The results from this chapter highlight actions land managers can take to maximize the benefits and minimize the risks of harvesting seed to supply landscape-scale restoration. With the implementation of sustainable seed harvesting and management strategies, landscape-scale restorations will benefit from a reliable and steady seed supply while the integrity of remnant ecosystems is conserved.

Dissertation Format

The first chapter of this dissertation has been peer-reviewed and published in the journal *Restoration Ecology.* Chapters two and three will be submitted to peer-reviewed journals for publication. A general conclusion, bibliography, figures, and tables follow the main body of the dissertation. I wrote the entirety of this dissertation and I created all tables, figures, and photographs. I also carried out all data collection, data analysis, and data interpretation on which this dissertation is based. My advisors and thesis committee assisted me in developing the scope and design of each study described in this dissertation, and provided me guidance in data analysis and results interpretation. My advisors Dr. Meredith Cornett and Dr. Susan Galatowitsch will be listed as co-authors on all three publications based on this dissertation.

Risks of overharvesting seed from native tallgrass prairies

Abstract

Seed supply often limits the size and scope of restoration projects that require active revegetation. To meet demand from more and larger tallgrass prairie restoration projects in the Great Plains, USA, seed is wild-harvested—collected from remnant habitats— using agricultural combine harvesters. I investigated the potential impacts of wild-harvest by comparing prairie remnants of northwestern Minnesota that varied in their histories of harvest frequency but were otherwise similar. I asked: 1) Do wild-harvested prairies differ in species composition from unharvested prairies? 2) If so, can life history traits be used to predict the response of prairie communities to wild-harvest? I conducted a retrospective study of 17 prairies harvested for seed frequently (annually/biennially), infrequently (2-3 times), or not at all. I sampled vegetation at 45 points within each site, recording all species present within $0.25m^2$ quadrats. To address the first question, I used non-metric multidimensional scaling and Mantel tests, followed by ANOVA contrasts to identify any species less likely to occur on frequently harvested sites ("harvest-negative"). For the second question, I used logistic regression to test whether lifespan, clonality and seed production predicted harvest-negative species. Plant community composition in frequently harvested prairies differed from that of infrequently or unharvested prairies. Fourteen species, generally short-lived and non-clonal, were classified as harvest-negative. My results suggest that frequent wild-harvest disrupts reproduction of species relying on seed, and that life history traits may provide a basis for predicting a species' response to wild-harvest.

Introduction

Ecological restoration has emerged as a promising solution to repair the function and resiliency of degraded lands (Suding 2011), and there is a growing awareness that ecological restoration efforts should greatly increase in scale to achieve conservation aims (Brudvig 2011). However, a lack of native vegetation can be a barrier to restoring landscapes, especially in fragmented regions where few patches of intact vegetation remain in a matrix of degraded vegetation. Because propagule sources in these relict landscapes are usually isolated, rates of natural dispersal to degraded patches are very low for many species, making passive revegetation approaches too inefficient to be reliable (Thomson et al. 2009). Seeding is the preferred active revegetation technique used to restore native vegetation in many ecosystems since transporting and storing seed is inexpensive, efficient, and expenses associated with rearing stock in greenhouses or nurseries can be avoided (Galatowitsch 2012). Seeds of many terrestrial species also store well over long periods of time, allowing flexibility in restoration project timelines. Most importantly, seeds can be quickly and effectively sowed across large areas. Because demand regularly exceeds limited native seed supply, seed availability is one of the top constraints for restoration projects (Rowe 2010). Seeding rates among different ecosystems range from 13,000 to 40,000 seeds/ha in temperate forest to 2.8 to 5.4 million seeds/ha in tallgrass prairies (Packard & Mutel 2005). Large-scale prairie restoration projects, which currently can include thousands of hectares, require billions of seeds. Some assert that a "crisis of scale" exists in the use of native seeds for restoration around the world (Merritt & Dixon 2011), and suggest there is a seed-limited capacity to carry out a growing number of projects. In extreme cases, projects have been abandoned altogether due to lack of appropriate seed (Wilkinson 2001).

To overcome seed availability limitations, native seed supplies can be obtained either through production farming or wild-harvest. Regional native seed production industries exist in some locales, which can meet some of the demand (Peppin et al. 2010). In a production farm, wild seed is planted into single-species fields, which serve as a seed source for restoration projects. These operations require considerable resources and time; many species require four years or longer before producing seed (Bender et al. 2000),

creating a substantial lag time for restoration action. In contrast, wild seed can be sowed immediately after harvest. Wild-harvest also circumvents risks associated with production farming, in particular artificial selection of genotypes adapted to production conditions (Schoen & Brown 2001; Dolan et al. 2008) and consequent loss of genetic diversity (Vander Mijnsbrugge et al. 2010).

Despite the benefits to restoration, wild-harvest may pose risks to harvested native plant communities. By removing seed, the reproductive capacity of plant populations is reduced, lowering the chance for seed to reach the soil and recruit new seedlings. If repeated over many years, seed removal may result in population declines (Peres et al. 2003; Kolb et al. 2007). Using population viability analyses for a variety of perennial plants, Menges and others (2004) demonstrated two relevant modeled responses to seed harvest: 1) "insensitive" responses, in which populations tolerate harvest at high frequency and intensity and 2) "sensitive" responses, in which populations tolerate only low harvest levels. They reported that many of the "sensitive" species were non-clonal herbs. In contrast, many of the "insensitive" species were long-lived or highly fecund woody plants. Other studies corroborate the "sensitive"/ "insensitive" construct that clonality and lifespan affect the degree to which seed input drives a species' ability to sustain its population over time (Silvertown et al. 1993; Schulze et al. 2012). Information on life history traits, such as clonality, lifespan, and fecundity, may be useful in predicting the likelihood of population declines from wild-harvest. Assessing the relative sensitivity of plant species to wild-harvest has the potential to inform harvest in ways that optimize the benefits of seed collection while minimizing risk to source populations. To determine whether wild-harvest alters prairie plant community composition and to examine the potential of life history traits to predict a species' response to seed removal, I conducted a retrospective, exploratory study of tallgrass prairies which varied in wild-harvest frequency.

Methods

Study area and site selection

This study was conducted in the wet-mesic tallgrass prairies of northwestern Minnesota (between lat 48°99'N and 46°94'N, long 95°91'W and 96°63'W). Tallgrass prairie restoration efforts have been ongoing in the region for decades with several large projects completed (e.g. The Nature Conservancy's 9000 ha Glacial Ridge Project), creating an ongoing demand for native seeds (Gerla et al. 2012). Seed supplies in this region are obtained chiefly by using modified agricultural combine harvesters to remove wild seed from remnant prairies, making this a good model system to study the impacts of wild-harvest. Standard practice in northwestern Minnesota involves wild-harvest in the fall following prescribed spring burns that boost seed production, as is typical in northern Great Plains grasslands (Anderson & Bailey 1980; Glenn-Lewin et al. 1990). Harvest frequency of the region's prairie remnants varies from once per year to once every five years.

Ownership, native plant composition, and ease of access are the key factors influencing harvest frequency of remnant prairies. Within the study area, frequent harvest (once per year) only occurs on privately owned prairies, while infrequent harvest (once per 3-5 years) takes place on both publicly and privately owned prairies. Because presence of weed seed or low diversity in seed lots often results in rejection by buyers, wild-harvest is generally limited to relatively diverse and weed-free prairies. All unharvested prairies within the study area are publicly owned and are similar in soils and hydrologic conditions to other harvested prairies. These prairies remain unharvested only due to their inaccessibility to agricultural combine harvesters (i.e. they are far from roads or surrounded by swampy or shrubby terrain).

To locate sites for this comparative study, I interviewed land managers throughout northwestern Minnesota, developed a pool of candidate sites, and compiled information on all wild-harvested prairies in the region (*n*=47). I created a spatial database of all remnant prairies and recorded soil characteristics, land management history (e.g., prescribed fire and grazing), location, and frequency of wild-harvest for each. To minimize variation unrelated to wild-harvest I selected remnant prairies with similar soil

characteristics and land use history (*n*=17) (Table 1.1, Table 1.2). I blocked by geographic position to account for systematic variance due to the 225 km latitudinal gradient along which sites occurred (Fig. 1.1). Each block contained two sites with each of three levels of wild-harvest frequency except one which only contained one frequently harvested site. In all, I chose 17 sites to compare.

Field data collection

I collected all field data from late June to early August 2012. I first delineated randomly generated two-hectare sampling area polygons within sites using open source software QGIS (Quantum GIS Development Team 2012). I created sample area polygons that excluded patches of woodland, then randomly generated forty-five sampling points within each (765 points total). In the field, I used a handheld GPS unit to locate sampling points at each site. At each point I verified published soil information (Natural Resources Conservation Service (NRCS) 2010) with cores taken to a depth of 30 cm. I sampled vegetation within a 0.25m^2 square quadrat at each point. All species present, including seedlings and vegetative plants, were identified and recorded. To aid in accurate identification of seedlings, I conducted a seedbank emergence assay prior to the field season, using soil from a remnant prairie within the study region. Nearly all individuals could be readily identified to species through vegetative characters, although seedlings of some could only be identified to genus (e.g. *Carex*, *Aster*). Due to extensive hybridization between *Helianthus* species in northwestern Minnesota, I grouped these to the genus level. I collected specimens for plants that could not be confidently identified in the field; these were vouchered at the University of Minnesota. Nomenclature follows the Great Plains Flora Association (1986).

Life history traits

I used published literature and publicly available databases to compile information on life history trait attributes hypothesized to influence a plant's response to wild-harvest: clonality, fecundity, and lifespan (Table 1.3). The timing of seed production was also considered as a trait in my analysis, but is not discussed further because it did

not contribute to my observed wild-harvest response. I gathered trait information for 59 common species, i.e., those that occurred in at least 4 of 17 sites and had overall mean frequency of ≥ 5% among all sampled sites. I classified clonality according to the presence/absence of vegetative reproductive structures (e.g. stolons, rhizomes). Fecundity was estimated using species' average individual seed mass, which correlates negatively with the overall number of seeds produced per plant during reproduction (Westoby et al. 2002). For lifespan, I grouped species into 4 ordinal classes following Bender et al. (2000). Lifespan classes considered whether each species is a graminoid (Poales), a species' age of maturity, and whether a species can reproduce clonally. Graminoids are longer lived compared to forbs, and lifespan increases as age of reproductive maturity increases. For species with the same age of maturity, clonal vs. non-clonal species are longer lived. I validated the accuracy of the lifespan classification system using field observations reported in Lauenroth and Adler (2008). The classification system correctly predicted the true lifespan class 72% of the time, and misclassified only one species to a non-adjacent class (e.g. 5-10 yrs classified as >15 yrs).

Data analysis

To explore possible relationships between community composition and wild-harvest frequency, I compared the species composition of sites using non-metric multidimensional scaling (NMDS) including the common 59 species defined above. I conducted NMDS ordination using Bray-Curtis dissimilarity with the function *metaMDS* of the *vegan* package for R (Oksanen et al. 2012). I determined whether observed differences in community composition among sites were associated with wild-harvest frequency or other environmental factors (soil drainage, soil particle type, and latitude) by performing Mantel tests. Mantel tests strictly assess the association between distance matrices and thus rely on few assumptions, which is a key strength in an observational study such as this one. I used separate tests for each environmental variable to identify which ones were most associated with community differences. A dissimilarity matrix for plant species composition was calculated using Bray-Curtis dissimilarity, and dissimilarity matrices for environmental variables (wild seed harvest frequency, latitude,

soil drainage and particle type) were calculated using Euclidean distances. For wild seed harvest frequency, I used the continuous measure of "times harvested since 2000" when calculating a distance matrix. For each test, I used 2000 permutations using the *vegan* package for R (Oksanen et al. 2012). I also conducted distance-based redundancy analysis (dbRDA) to test for association between plant community and environmental variables, although results from this analysis were so similar to those of the Mantel tests I did not report the dbRDA results. In addition to NMDS ordination, I also compared mean species richness per m^2 among unharvested, infrequently harvested, and frequently harvested prairies using Student's t-tests.

To identify species less abundant in frequently harvested sites (i.e., "harvest-negative species"), I compared species-specific differences in abundance (proportion of quadrats occupied by a species at each site) using analysis of variance (ANOVA), based on 59 two-factor fixed effects models (one per species) with harvest frequency category and geographic block as additive factors. Contrasts were calculated to compare frequently harvested and unharvested sites, as well as infrequently harvested and unharvested sites. To test for significance of lesser abundance in harvested sites, I used a *p*-value threshold of 0.10 to ensure fewer type-II errors (false negatives). To ensure I identified all species potentially sensitive to seed harvest, I used a high alpha value to generate a conservative (from a biological and management perspective) list of harvest-negative species. I used logistic regression to test whether lifespan, clonality, and fecundity predict whether a species is more likely to be less abundant in frequently harvested sites compared to controls. I first modeled each effect separately using GLM in R (R Development Core Team 2012) to identify significant terms. I then added significant terms together to test a larger model and the smaller one-factor models to identify the best model. I used the best model to compute the predicted probability that a species would be harvest- negative at each level of a life history trait while holding the others constant. I treated lifespan data as categorical, clonality data as binary, and seed weight data as continuous. Seed weight was log-transformed to better fit a normal distribution. Goodness of fit for each model was tested using likelihood-ratio tests with a chi-square distribution and a test threshold *p* < 0.10.

Results

Plant community composition

The composition of frequently harvested prairies is distinct from infrequently harvested and unharvested prairies (Fig. 1.2, Fig. 1.3, Fig. 1.4). Species typical of frequently harvested sites include *Eleocharis compressa*, *Agrostis gigantea*, and *Viola pedatifida* (i.e., those with the most positive NMDS1 loadings). Species typical of infrequently and unharvested sites include *Helianthus* spp., *Thalictrum dasycarpum*, and *Zizia aurea* (i.e., those with the most negative NMDS1 loadings). Species more frequent in the most northern sites have positive NMDS2 loadings (e.g. *Spartina pectinata*) while southern species tend to have negative NMDS2 loadings (e.g. *Sorghastrum nutans*). Species richness is also distinctly lower in frequently harvested prairies compared to infrequently harvested ($t = 3.21$, $p < 0.05$) and unharvested prairies ($t = 3.75$, $p < 0.01$), though there was no difference in richness between infrequently harvested and unharvested prairies.

Of variables considered, wild-harvest frequency is most strongly associated with observed differences in species composition (Mantel $r = 0.56$, $p < 0.002$). Apart from wild-harvest frequency, latitude is the only other factor associated with differences in community composition. In my study, community composition did not vary by soil texture (Mantel $r = -0.14$, $p > 0.05$), soil drainage (Mantel $r = -0.17$, $p > 0.05$), or soil taxonomy (Mantel $r = 0.27$, $p > 0.05$), which suggests my site selection process succeeded in isolating wild-harvest frequency as the key variable being observed. Although latitude is associated with species composition (Mantel $r = 0.35$, $p < 0.003$), I accounted for it by blocking on geographic position in my fixed effects models.

Fourteen of the 59 species included in my analyses are "harvest-negative," that is, they are 10% to 53% less abundant on frequently harvested sites compared to unharvested sites (Table 1.4, Fig. 1.4). Four of these species (*Fragaria virginiana*, *Galium boreale*, *Thalictrum dasycarpum*, *Zizia aurea*) are on average 46 ± 2.27 % less abundant in frequently harvested sites ($p < 0.05$). Of the fourteen harvest-negative species, three (*Liatris ligulistylis*, *Muhlenbergia richardsonis*, *Senecio pauperculus*) are less abundant (from 11-28%) in infrequently harvested sites as well ($p < 0.05$). Most

species (41 of 59) occurred with similar abundance regardless of harvest frequency. I also identified four "harvest-positive" species (*Agrostis gigantea, Eleocharis compressa, Panicum virgatum, Viola pedatifida*) that are marginally more abundant (from 13-38%) at frequently harvested sites compared with unharvested sites ($p < 0.10$).

Life history traits

Lifespan and clonality are predictors of harvest sensitivity. In particular, short-lived species (~1 to 5 years) are marginally less likely to occur in frequently harvested sites ($X^2 = 7.4$, $df = 3$, $p < 0.06$). Further, short-lived species have a 75% chance of being harvest-negative, in contrast with long-lived species (~>15 years), which have only a 10% chance of being harvest-negative. Species with intermediate life spans of ~5 to 10 years and ~10 to 15 years have a 21% and 28% chance of being harvest-negative, respectively. Clonality also predicts lower likelihood of occurrence in frequently harvested sites ($X^2 = 4.7$, $df = 1$, $p < 0.03$). Non-clonal species are 40% likely to show a harvest-negative response, compared with a 13% chance for clonal species. Clonality and lifespan together predict whether a species was less abundant in frequently harvested sites ($X^2 = 9.7$, $df = 4$, $p < 0.05$), but not any better than the two factors singly. I also found that neither the lifespan model nor the clonality model was better than the other. This shows that clonality and lifespan are both important by themselves in predicting harvest-negative species. Fecundity was not useful for predicting whether a species was harvest-negative.

Discussion

My results indicate that frequent wild-harvest alters plant species composition of remnant tallgrass prairies. Because I accounted for other factors that contribute to observed variation in plant communities such as differences in soil, topography, hydrology, and past land use (White & Glenn-Lewin 1984), it is very unlikely that differences in community composition were the result of factors other than wild-harvest. It is notable that I detected such large and consistent differences among the prairies studied, as the variability in prairie plant communities can render subtle differences

undetectable (Russell & Roy 2008). These results suggest that wild-harvest is a driver of change on par with other management practices like grazing, haying, fertilizing, and burning (Collins 1998; Dornbush 2004) which requires risks be evaluated during harvest planning.

The lesser abundance of 14 species accounts in large part for the distinctive composition of frequently harvested sites when compared to controls. Menges and others (2004) identified two types of "sensitive" species responses that might drive community shifts as a result of seed harvesting: a "sensitive type I" or a "sensitive type II" response. "Sensitive type I" species have high initial extinction risk, often caused by already decreasing population growth rates. For these species, removal of even small amounts of seed exacerbates the decline and heightens the risk of local extinction. "Sensitive type II" species have an initially low extinction risk that is elevated only when subjected to frequent seed removal. The lesser abundance of species subjected only to high harvest levels may indicate that "sensitive type II" species rely on seed for population persistence, but produce more seed than necessary in most years. Only when the majority of seed is frequently removed does seed harvest contribute to population declines. It is likely that most species I observed as less abundant had a "sensitive type II" rather than "sensitive type I" response. If all 14 harvest-negative species were "sensitive type I", they would have been less likely to occur in infrequently harvested prairies as well as in frequently harvested prairies, a result I did not find. Only *Senecio pauperculus*, *Liatris ligulistylis*, and *Muhlenbergia richardsonis* were less abundant in both types of harvested sites, suggesting these species may exhibit a "sensitive type I" response. In the case of *S. pauperculus*, the very low rate of occurrence may suggest that it was not present in harvested sites to begin with, though the similarity in ecological conditions among all sites suggests that it likely was present at some point. It is also unknown why *Fragaria virginiana* showed a sensitive response, as it was likely too short for its seeds to be harvested with combines. It is possible that the stoloniferous nature of this species made it susceptible to early season fires associated with seed harvesting, and that surface fire caused population declines by inhibiting its means of vegetative reproduction.

The majority of tallgrass prairie plant species (41 of 59) appear to be "insensitive" to wild seed harvest. My results show that these 41 species occur just as often in frequently harvested prairies as they do in unharvested prairies. For example, the dominant species of northern tallgrass prairies — *Andropogon gerardii*, *Sorghastrum nutans*, *Calamagrostis stricta*, *Sporobolus heterolepis*, *Aster* spp. *(A. ericoides*, *A. laevis*, *A. lanceolatus*) and most *Solidago* spp. (*S. canadensis*, *S. ridellii*, *S. rigida*)— did not change in abundance. Thus, even in frequently harvested prairies, the dominant community composition remains relatively intact. That most tallgrass prairie species would be insensitive to seed harvest is not surprising, given evidence that most reproduction in tallgrass prairies is vegetative (Dalgleish & Hartnett 2006). However, the lesser abundance of harvest-negative species represents a loss of functional diversity, namely a considerable reduction of short-lived forbs. Grasslands lacking in native short-lived species (which tend to be good colonizers) may be less resilient and more susceptible to invasion by undesirable non-native species after extreme events like droughts (Weaver & Mueller 1942). In northwestern Minnesota, climate change is projected to lead to more frequent, increasingly severe droughts, which may place frequently harvested prairies at higher risk of undesirable long-term community changes.

Although the lesser abundance of harvest-negative species explains most of the compositional differences among sites with different wild-harvesting histories, higher abundance of a few species also contributed to dissimilarities. *Agrostis gigantea, Eleocharis compressa, Panicum virgatum, and Viola pedatifida* were all more common in frequently harvested sites, suggesting they somehow benefit from frequent wild-harvest. These species may benefit from the clearing of canopy vegetation when combine harvesters mow standing vegetation during harvest, which is similar in practice to haying. Haying has been documented to increase available light at the ground level (Collins 1998) which may provide an advantage to seedlings and cool season plants. *A. gigantea*, *E. compressa*, and *V. pedatifida* grow early in the season, but it is unclear why other similar cool season plant species were not more abundant as well, and why *P. virgatum,* a warm season grass, was more abundant. At the very least, these species do not exhibit a sensitive response to wild-harvest, or in the case of *V. pedatifida,* may have escaped wild-

harvest altogether due to its short stature. The height of remaining vegetation after harvest is 30-50 cm, whereas the flowering height of *V. pedatifida* reaches only 15 cm. The elevated abundance of *A. gigantea*, an introduced weedy grass, may appear to indicate that increased movement of machinery through prairies during seed harvest encourages weed species introductions. However, not only did I fail to find elevated abundance of other weed species in wild-harvested prairies, but I also found that richness of introduced species was comparable among prairies of all harvest frequency categories. Thus, the response of *A. gigantea* appears to be anomalous, and that mechanized seed harvest does not increase the abundance of weeds.

Given that spring burns always precede wild-harvest in the fall, my study could not account for fire effects. Therefore, an alternative explanation of my results is that observed community differences were caused by prescribed fire rather than wild-harvest. However, because unharvested control sites were burned at similar intervals as infrequently harvested sites, I should not have found harvest-negative species in infrequently harvested sites if fire were the primary driver of change. In addition, trends I observed, particularly in harvest-negative species, differ from reported fire effects on tallgrass prairie community composition. For example, Anderson and Bailey (1980) found that with annual burning in Alberta prairies, *Galium boreale* and *Muhlenbergia richardsonis* increased in abundance, whereas in my study they were less abundant in frequently harvested prairies. The Alberta study also detected no changes in abundance of *Thalictrum* spp. in annually burned prairies, but my study found them to be less abundant in frequently harvested (i.e. annually burned) prairies.

My findings suggest that differences in life history underlie a species' response to wild-harvest. Specifically, short-lived species and non-clonal species are likely to be less abundant in frequently wild-harvested prairies, while long-lived species and clonal species are unlikely to change in abundance with frequent wild-harvest. Similar findings have been reported in other studies examining seed removal. Menges and others (2004) noted that species they identified to be sensitive to seed harvest tended to be non-clonal herbs, and that most insensitive species were long-lived shrubs, trees, and iteroparous herbs. Kolb and others (2007) also showed that population growth rates of short-lived

herbs decreased much more than those of longer-lived herbs when subjected to seed removal by insect predation. These results are not surprising; life history theory predicts that short-lived species should be more sensitive to seed harvest because a shorter lifespan confers a higher sensitivity to fluctuations in reproduction (Silvertown et al. 1993). Short-lived species rely more heavily on recruitment from seed, not survival or vegetative growth, for their populations to grow or persist. With consistent pressures on recruitment—like frequent wild-harvest—the primary mode of persistence is thwarted, leading to negative population growth and eventual local extinction. Similarly, non-clonal species may be more sensitive to wild-harvest because they also rely heavily on seed to persist. Most prairie plants, such as the warm season grasses and Asteraceae, are clonal—they rely on vegetative growth to maintain population growth, even for those species that are capable of reproducing by seed (Schulze et al. 2012). Being restricted to reproduce only by seed would confer a disadvantage to non-clonal species under frequent wild-harvest, as these species would have no means of reproduction that is not being impacted. It is surprising that I did not find seed production/seed size to influence whether a species was less abundant in frequently wild-harvested prairies. There is a trade-off between the number of recruitment attempts and the probability of recruitment success (Jakobsson & Eriksson 2000). By extension, one would expect that species producing a small number of large seeds would be more sensitive to seed harvest due to the fact that a higher reproductive investment is being removed from the system. However, low seed production is also linked to longer lifespans (Mazer 1989), which appears to confer insensitivity to seed harvest. It is also possible that wild-harvest does limit recruitment in large-seeded species, but that such effects only manifest over longer periods than I were able to detect (>12 years).

Limiting the frequency of wild harvesting in northern tallgrass prairies may minimize the risk of losing native plant species in remnant prairies. My results suggest that when wild-harvest is limited to once every three years in remnant prairies (infrequent harvest), plant community composition may not be substantially changed. However, some populations with a high initial extinction probability (e.g. small populations or "sensitive type I" species) may be lost even with an infrequent level of wild-harvest.

Managers should take care to avoid wild-harvest in sites where losses of such species would be unacceptable (e.g. sites hosting small populations of rare species). In contrast, when seed is harvested annually (frequent harvest) plant community composition may shift substantially, manifested as decreased frequency of short-lived non-clonal species. However, decreasing the intensity of seed removal during frequent wild-harvest (e.g. strip harvesting) may have the potential to mitigate adverse effects, but further study is needed before recommendations can be made. Managers should also be especially conservative when conducting wild-harvest in plant communities that typically have a high abundance of short-lived, non-clonal species (e.g. sand prairies), as the expected shifts in plant communities would likely be considerably greater than those reported in this study, which were mesic tallgrass prairie communities dominated by long-lived clonal species.

My study shows that life history traits may provide a predictive framework to avoid the adverse effects of wild-harvest. Existing seed harvest guidelines (e.g. Packard & Mutel 2005) could likely be improved by incorporating life history trait information available in large trait databases such as the North American USDA PLANTS Database (United States Department of Agriculture (USDA) 2014). In addition, my assessment of the risks associated with wild-harvest would be strengthened if verified with a field experiment. In particular, long-term field experiments that manipulate seed harvest levels while controlling for life history traits are necessary both to confirm the ability of traits to predict harvest response and to understand the relative importance of lifespan and clonality in determining harvest response. Adverse effects on donor seed sources may be reduced by using life history traits to inform the development of harvest guidelines in the interim.

Assessing long-term risks of prairie seed harvest: what is the role of life-history?

Abstract

To meet demand from more and larger tallgrass prairie restoration projects in the Great Plains, USA, seed is frequently collected *en masse* from remnant native plant populations. Overharvesting seed may lead to population extinctions, but little information is available to inform the magnitude of risk associated with extinctions due to seed harvest. Species life history may provide a theoretically sound and generalizable basis for risk assessment. To assess the risk of population extinction for several common types of grassland plants subjected to seed harvest and explore the role of life history in determining extinction risk, I modeled 2 clonal and 4 non-clonal prairie species using stage-based matrix models. I simulated 5 seed harvest scenarios: no harvest, annual harvest at low/high intensity (50% & 75% seeds removed), and triennial harvest at low/high intensity. I compared differences among species in the finite rate of increase and projected extinction risk over 25 years for each scenario. Simulated populations of non-clonal species were robust to triennial and low intensity seed harvest, but were susceptible to decreases in population growth rates of up to λ -0.5 and elevated extinction risks of up to 95% with high intensity annual seed harvest. The risk of population extinction for non-clonal species was also influenced by population growth rate at the onset of seed harvest. Populations of clonal species were unaffected by seed harvest due to a compensatory effect of vegetative reproduction on population growth rates. Adjusting seed harvest regimes can minimize risk of population extinctions. Since clonal/non-clonal life histories are common in grasslands globally, diverse grasslands should not be annually harvested at high intensity in order to maintain diversity of non-clonal species in remnants.

Introduction

 As the scale and intensity of anthropogenic degradation in natural areas has increased, the imperative of ecological restoration to achieve conservation aims is increasingly urgent (Suding 2011). The Convention on Global Biodiversity and the European Union both identified ecological restoration as a critical tool to cease the decline of biodiversity by returning ecological function and native biotic communities to degraded or destroyed ecosystems (EU 2010; CBD 2010).

 To achieve effective biodiversity conservation, restoration must be commensurate with the scale of degradation. Entire landscapes, many of which have been almost fully converted to intensive anthropogenic land use, must often be restored (Brudvig 2011). In particular, row-crop agriculture has transformed temperate grasslands, with landscapes nearly wholly converted to agriculture in regions such as the North American tallgrass prairies or the South American pampas (Gibson 2009; Overbeck et al. 2013). In highly converted landscapes, remnants of natural vegetation play an essential role in conservation and restoration: they are refuges for relict plant populations that prevent extinctions in the landscape and are the "seeds" from which more extensive restoration can proceed (Turner & Corlett 1996). However, most remnant ecosystems are typically very small and spatially disjunct, limiting their capacity to self-recover from further disturbance. Native plant populations in remnants are thus prone to a higher risk of extinction (Fischer & Stöcklin 1997). Restoration increases the area of habitat, offering the potential to increase population sizes and connectivity between remnants, reducing the probability extinctions.

 Revegetation over large areas is most efficient by planting native seeds. Native seeds can be easily transported, stored, and sown in bulk over large areas, making them the preferred propagule source for revegetation (Galatowitsch 2012). Revegetating a whole landscape requires millions of tons of seed (Gerla et al. 2012). Such large quantities are rarely commercially available, making the lack of native seeds a critical barrier to restoration (Broadhurst et al. 2015). While seed markets have emerged to meet demand in some regions (Peppin et al. 2010), the overall increase in demand for native

seed paired with limited supply has culminated in what some suggest is "a crisis of scale in restoration" (Merritt & Dixon 2011).

Native seed supplies can be procured either through seed farming or wild harvest, each with its own risks and benefits. Seed farming, the process of growing native plants for seed in an agricultural setting, can yield large quantities of seed with minimal impact to wild populations. However, there is risk of germplasm adapting to production conditions (Schoen & Brown 2001) or losing genetic diversity (Vander Mijnsbrugge et al. 2010). Many long-lived plants also take several years to produce seed in production settings (Bender et al. 2000), introducing a lag-time that can disrupt time-bound restoration goals. In contrast, wild harvested seed is immediately available, and for some species and ecosystems, mechanized collection techniques can provide large amounts of native seed that can be sown immediately after collection (Olson 1984). Wild harvested seed also avoids the genetic risks of adaptation to production conditions (though some especially fragmented populations may be susceptible to inbreeding, see Broadhurst et al. 2008). Thus, the benefits of wild seed make it the preferred, if not the only viable, restoration seed source in many regions.

Despite the benefits of using wild harvested seed to meet demand for ecological restoration, overharvest poses a risk to remnant native plant populations acting as seed sources. Seed removal reduces the reproductive capacity of populations. If enough seed is removed over time, populations may decline and eventually go extinct (Louda & Potvin 1995; Peres et al. 2003). Given the importance of these seed donor populations to biodiversity conservation and future restoration efforts, such extinctions are unacceptable. However, most plant species produce a surplus of seeds that are normally lost to competition (Clark et al. 2007), suggesting that harvesting some portion of seed should be compatible with maintaining populations. Sustainable levels of wild-harvest could help maximize restoration benefits at the landscape scale while minimizing the risk of population extinction.

Evidence-based recommendations are currently lacking for seed harvest practices. A few sources offer general guidelines, such as the US Bureau of Land Management's "Seeds of Success" program and Australia's FloraBank revegetation manual, which

suggest harvesting no more than 20% of viable seed from donor sources (Mortlock 2000a; BLM 2015). Similarly, Packard and Mutel (2005) suggest harvesting no more than 10% of seeds from annual species or 50% from "strong perennial" species.

A more rigorous approach to set wild seed harvest guidelines for remnant ecosystems may be population viability analysis (PVA). PVA assesses the likelihood of future population persistence under a set of environmental or demographic trends through a combination of empirical and modelling data (Menges 2000). Because PVA enables evaluation of management options through model projections, high risk scenarios can be identified *a priori*. PVA offers a practical option for assessing extinction risks associated with different rates of seed harvest. For example, Witkowski and others (1994) used PVA to estimate that 20% harvest of *Banksia hookeriana* flowers was sustainable and used this result to develop harvest guidelines for managers (CALM 1998). By subsequently monitoring harvested *B. hookeriana* populations over many years, Lamont and others (2001) confirmed these guidelines allowed for population growth and effectively minimized extinction risk due to seed harvest.

However, obtaining sufficient demographic data to conduct PVAs for individual populations or species can be resource and time intensive. In supplement to PVA, life history traits may provide a basis for risk assessment that is both theoretically based, but also readily generalizable to many species and habitats (Silvertown et al. 1993). My previous work shows that life history is predictive of population responses in tallgrass prairie plants annually harvested for seed. Specifically, non-clonal species are susceptible to decline from high harvest frequency, while clonal species are not (Chapter 1). Other studies also note the potential importance of life history traits in determining response to seed harvest (Silvertown et al. 1993; Menges et al. 2004; Schulze et al. 2012). However, the degree to which life history traits influence seed harvest-induced extinction risk, and their utility to inform seed harvest guidelines has not been examined. In this paper, I present an approach to assessing seed harvest risks by using matrix models to compare population viability under a range of seed harvest scenarios in species with varying life-history traits. My objectives were to 1) assess the long-term risk of population extirpation

for several common types of grassland plants subjected to various seed harvest regimes, and 2) evaluate the role of life history in determining seed harvest response.

Methods

Model species

 I modeled 6 common perennial prairie forbs that represent a range of life history characteristics and seed harvest responses typical of grassland plants that are regularly wild-harvested for seed (Table 2.1). I chose model species that reflected key differences in clonality (four non-clonal species and two clonal study species). Based on my previous work, clonality is the strongest predictor of seed harvest sensitivity (Chapter 1). Moreover, clonality separates species into distinct life history strategies that are affected differently by seed harvest, making this trait especially useful in a comparative context. I also chose model species based on their observed response to seed harvest, in order to further explore how life history traits contribute to that response. In particular, I chose four non-clonal species that are known to be sensitive to seed harvest (i.e. their populations decline with high levels of seed harvest) and two clonal species that are insensitive to seed harvest (Chapter 1). All six study species are currently widespread throughout their range, and all are frequent in mesic tallgrass prairies, particularly those of the Northern Tallgrass Prairie ecoregion (Minnesota Department of Natural Resources 2005; Kartesz 2015). Because the study species are ubiquitous in tallgrass prairies, their seed is in high demand for use in prairie restoration projects, which often leads to high levels of wild-harvest in remnant populations (Gerla et al. 2012). The increased exposure to wild-harvest and the potential for adverse effects (i.e. population reduction and extinction) make the study species especially useful model systems in assessing the risks of wild seed harvest.

Modelling approach

 To assess the risk of population extirpation due to seed harvest in tallgrass prairie plants and investigate the role of life history traits in determining seed harvest responses, I used stage-based matrix models (Lefkovitch 1965) as a basis for simulating population

responses of study species to varying frequency and intensity of seed harvest. I used these population models to simulate seed harvest scenarios varying in frequency and intensity of seed removal by restricting the seed-to-seedling transitions within each model, a method previously used in modelling seed harvest (Menges et al. 2004; Ticktin 2004). I then projected future population abundances based on these seed harvest scenarios and compared the resulting model behavior, extinction risks, and finite rates of growth among each species and life history type.

Matrix construction

I used RAMAS Metapop (Akçakaya 2005) to construct stage-based matrix models for each of the six study species, parameterized by demographic data found in previously published studies (Table 2.2). To build each model, I used life cycle diagrams based on each species' life history or previously published models to identify and define the important stages an individual plant can exist in throughout its lifetime, as well as the possible transitions between stages that individuals can take in a one-year time step (Figure 2.1). I conducted a literature search to estimate transition probabilities between stages in each species model (Figure 2.2).

For species with insufficient demographic data, I approximated vital rates using available data from the most phylogenetically related and functionally similar species (demographic "surrogates"). Because these demographic surrogates were similar both phylogenetically and functionally, I assumed their life cycles and life cycle transitions approximated those of study species. I chose surrogate species from the same genus of the study species that were also native to grasslands. *Zizia aurea* was an exceptional case because *Zizia* is a poorly studied genus of only three species and I did not find sufficient demographic data during my literature search to construct a full matrix. I instead chose a species in the next most closely related Apiaceae genus, *Lomatium*. *L. bradshawii*, a native of Oregon, USA prairies. Like *Z. aurea*, *L. bradshawii* is also a non-clonal, sub-dominant perennial herb found in wet-mesic prairies (Kaye and Kirkland 1994). While not congeners, the similarities in function, ecology, and habitat of these two species make *L. bradshawii* a good demographic surrogate for *Z. aurea*. My models also incorporated

demographic stochasticity and assumed that populations were density independent. Because each of the six study species is generally sub-dominant to more competitive grasses in their native habitat (Rabinowitz et al. 1989), their populations are likely regulated more by inter-specific competition than by intra-specific competition. Thus, rather than incorporating a density dependency function into the models, I set a carrying capacity (K) at 150 individuals to model the upper limit of population sizes theoretically set by competition from more dominant species.

Seed harvest simulations

I simulated five seed harvest scenarios that reflect the full range of frequency and intensity of wild-harvesting practices common in northern tallgrass prairies. Using the "Catastrophe" function in RAMAS Metapop, I simulated seed harvest by reducing the seed reproduction transitions in each model by either 50% or 75% every year or every three years. I chose 50% and 75% reductions because harvesting half of seeds has been suggested as a safe collection limit in restoration guides (Packard & Mutel 2005), and 75% harvest approximates the upper bound of seeds removed with combine seed harvesters (Teiken pers. comm.)(a common method in tallgrass prairies). To characterize the baseline model for each species, I ran an unharvested scenario. The five scenarios I simulated were: 1) no harvest (baseline), 2) 50% triennial harvest, 3) 75% triennial harvest, 4) 50% annual harvest, and 5) 75% annual harvest. Each simulation started with 100 individuals at stable stage distribution and had duration of 25 years; I repeated each simulation 1000 times to assure precision of risk estimates (Akçakaya 2005). I included demographic stochasticity in my model runs with RAMAS, where the number of surviving individuals in each stage after each stage transition was sampled from a binomial distribution and the number of offspring from a Poisson distribution. I chose a simulation length of 25 years to represent the maximum expected duration of large restoration program timeframes and set the initial population size at 100 to represent typical mid-size populations found throughout tallgrass prairie remnants (Hendrix 1992). I reported two output measures from the results of each scenario: 1) the finite rate of increase (λ) for each population and 2) its mean extinction risk (ER) after 25 years ($\pm$95%

CI). λ represents the magnitude of growth or decline for a population, and is a useful metric for comparing effects of management practices among different populations (Crone et al. 2011). For unharvested scenarios, I calculated λ by finding the eigenvalue of the baseline stage matrix. For annual scenarios, I calculated λ by finding the eigenvalue of the stage matrix after reducing fecundity transitions by 0.5 or 0.75 percent (based on the harvest intensity of the scenario). For triennial scenarios, the stage matrix differed in harvest and non-harvest years, so I calculated λ by finding the eigenvalue of the stage matrix at each time step and averaged the values over 25 years. ER is the percentage of times the population is reduced to zero in model simulations (Menges et al. 2004).

Analysis

I examined how measures of mean and minimum population size changed over time to identify scenarios where populations behaved differently from the no harvest baseline and each other. To compare the relative importance of the clonality trait in determining seed harvest response, I calculated the change in λ from baseline ($\Delta \lambda = \lambda_{scenario} - \lambda_{baseline}$) in each harvest scenario, and compared the magnitude of change in reproductive output among clonal and non-clonal species. I identified the maximum annual harvest rates for each species that prevented population decline ($\lambda > 1$) and elevated extinction risk (ER < 0.05) by simulating additional scenarios which incrementally varied harvest intensity at high levels. I also conducted sensitivity analysis on each of my baseline models to estimate their robustness to parameter uncertainty. For each model, I calculated elasticities for each stage transition and identified the most proportionately important transition rate parameter (i.e. highest elasticity) on λ, varied that parameter in increments of 10%, and measured the resulting change in λ given the parameter variation.

Results

Unharvested model results

In all unharvested baseline models, populations grew to carrying capacity (150 individuals) and remained stable throughout the 25 year modelling timeframe. No species were at risk of extinction at the end of 25 years, with the exception of non-clonal *Rudbeckia hirta*, which had a very small (0.01±0.03 95% CI) baseline probability of extinction (Fig. 2.3). All species models had a baseline λ greater than 1, with an average of 1.35. I found that clonal *Anemone canadensis* had the lowest baseline λ with 1.07, while non-clonal *Packera aureus* had the highest λ of 1.67. Variability in λ among species was generally due to a combination of survival and life history strategy. For example *A. canadensis* had high adult survival rates, but low fecundity rates (leading to slow but stable growth) while *P. aureus* had both high overall survival rates and high fecundity rates (leading to fast and stable growth). Average population abundance remained near or at the hypothetical carrying capacity in all species models (Fig. 2.4, 2.5). Generally, the minimum abundance rarely dropped below 25% of the initial population abundance for any unharvested model. *R. hirta* was an exception, and showed a low minimum abundance due to demographic stochasticity. Stable stage distribution in *R. hirta* resulted in the flowering stage having very few individuals when initial population size was 100. As the number of individuals in a stage became small, the probability of all individuals in that stage dying due to chance increased, and thus the probability of a model run resulting in a very low minimum abundance increased as well. Sensitivity analysis showed that models were relatively robust to perturbation— a 10% change in the most important transition parameter resulted in a change in λ no greater than 0.05.

Scenario results

The 50% triennial seed harvest scenario introduced small oscillations in population abundance, but was otherwise very similar to the baseline scenario. All species models continued growing (i.e. λ >1), and extinction risk was zero at the end of 25 years, with the exception of non-clonal *R. hirta*, which had extinction probability of

0.04±0.03 95% CI (Fig. 2.3). Average population abundance tended to oscillate around or just below the hypothetical carrying capacity, with declines following the year of seed harvest and increases in the years between seed harvest (Fig. 2.4, 2.5). These oscillations were strongest in non-clonal *R.hirta*, with periodic changes reaching up to 50 individuals, and weakest in clonal *Solidago canadensis*, with no apparent oscillation. Expected minimum abundance appeared relatively unchanged from the baseline scenario in all models. I found small but distinct differences in clonal vs. non-clonal model behavior, notably the lower degree of oscillation in clonal species. Δ λ was higher in non-clonal species (mean 0.08) compared to clonal species (mean 0.01) (Fig. 2.6).

Most populations remained stable and behaved similarly to the baseline models in the 50% annual harvest scenario, but extinction risk increased for *R. hirta*. All populations grew in this scenario, and extinction risk was zero for all species except non-clonal *R. hirta* which showed an elevated extinction risk of 0.13±0.03 95% CI (Fig. 2.3). While average population abundance was maintained at the hypothetical carrying capacity in most species (Fig. 2.4 & 2.5), the abundance of *R. hirta* never exceeded the initial population size, and ended the simulations with approximately 10% fewer individuals. Expected minimum abundance was not appreciably different from baseline in non-clonal *P. aureus*, *Liatris ligulistylis*, and clonal *S. canadensis*, but was lower in non-clonal *R. hirta*, *Z. aurea*, and clonal *A.canadensis*, particularly in the last 10 years of the scenario. Differences in model behavior between clonal and non-clonal species were not apparent, but Δ λ was notably higher in non-clonal species (mean 0.23) compared to clonal species (mean 0.02) (Fig. 2.6).

The 75% triennial seed harvest scenario resulted in populations that were stable throughout the 25 year simulation, but had strong oscillations in population abundance, especially in non-clonal species. All populations continued to grow under this scenario, and extinction risk remained at zero at the end of 25 years, with the exception of non-clonal *R. hirta*, where I found that the probability of extinction increased from 0.01 to 0.08±0.03 95% CI (Fig. 2.3). Average population abundance oscillated just below the hypothetical carrying capacity, with steep declines following the year of seed harvest and increases in the years between seed harvest (Fig. 2.4, 2.5). These oscillations were

strongest in non-clonal *R. hirta*, with periodic changes reaching up to 100 individuals, and weakest in clonal *S. canadensis*, with no apparent oscillation. Minimum population abundance was no different from the baseline scenario in any model populations. The magnitude of oscillation in non-clonal species was considerably larger compared to clonal species, and $\Delta \lambda$ was seven times higher in non-clonal species (mean 0.14) compared to clonal species (mean 0.02) (Fig. 2.6).

The 75% annual seed harvest scenario resulted in declining non-clonal populations but generally stable clonal populations (Fig. 2.4, 2.5). Extinction risk increased in non-clonal *L. ligulistylis,* which showed a marginal extinction risk of 0.02 ±0.03 95% CI, while *Z. aurea* showed a relatively high extinction risk of 0.33±0.03 95% CI (Fig. 2.3). Non-clonal *R. hirta* was at an extremely high risk of extinction (0.92±0.03 95% CI) in this scenario. Extinction risk did not increase for other species. Average abundance steadily decreased throughout the scenario in non-clonal *L. ligulistylis*, *Z. aurea*, and *R. hirta*, as well as in clonal *A. canadensis*, to varying degrees (reduction by ~50%, ~75%, 100%, and ~30% respectively). Non-clonal *P. aureus* and clonal *S. canadensis* remained near their hypothetical carrying capacity (Fig. 2.4, 2.5). Minimum population abundance showed a similar pattern as average abundance, with considerable decreases in all but non-clonal *P. aureus* and clonal *S. canadensis*. I found that 3 of the 4 non-clonal populations exhibited $\lambda<1$, (*L. ligulistylis* and *Z. aurea* at $\lambda=0.99$ and *R. hirta* at $\lambda=0.88$), but P. aureus grew at $\lambda=1.11$. Clonal *S. canadensis* grew strongly under this scenario ($\lambda=1.28$), while *A. canadensis* was virtually static ($\lambda=1.01$). The apparent decrease in average population in *A. canadensis* despite a positive finite rate of increase was due to demographic stochasticity in my model. By the time stage distribution stabilized after the initial perturbation from seed harvest, some stages had only a few individuals surviving. As the number of individuals becomes small, the likelihood of continued decrease due to chance becomes significant even if vital rates remain constant (Akçakaya 1991). $\Delta \lambda$ in non-clonal species (mean 0.42) was much larger compared to clonal species (mean 0.05) (Fig. 2.6).

Maximum annual harvest rates for non-clonal populations were lower and more variable than for clonal populations (Table 2.2). Maximum harvest rates that prevent

population decline (λ>1) ranged from 63% in non-clonal *R. hirta* to 85% in clonal *A. canadensis*, while *S. canadensis* continued growing (vegetatively) even under 100% harvest. I found that annual harvest rates that keep extinction risk low (0.05) over 25 years were only important for non-clonal species, as extinction risk in neither clonal species was elevated even under 100% harvest. For non-clonal species, low risk maximum harvest rates averaged 66.5% overall, but ranged from 38% in *R. hirta* to 88% in *P. aureus*.

Discussion

      Increasing demands for wild seed to supply restoration underscores the importance of assessing risks of wild harvest to remnant populations of native plants. By using life history to compare population viability under varying harvest scenarios, I developed a new approach to assess the risk of population extinction associated with different seed harvest regimes. I found that sensitivity to seed harvest is heavily influenced by life history and that high-frequency seed harvest posed a risk of extinction to non-clonal plant species. In northern tallgrass prairie remnants where non-clonal species constitute as much as one-third of the total plant community, extinctions caused by excessive seed harvesting could compromise the resilience of these important refugia of biodiversity. I propose that by assessing risk associated with seed harvesting through the use of life history traits, conservation decision-making can be informed by elucidating risk mitigation options. Here I examine in detail the influences of seed harvest practices on a species' risk of extinction and offer general guidelines for low-risk seed harvesting.

Minimizing risks of seed harvest regimes

      High-frequency harvest poses the greatest risk of population extinction. The effects of high-frequency harvest are most pronounced under circumstances when harvest intensity is also high— extinction risk increased by more than ten-fold in non-clonal species when harvested annually as opposed to triennially. By refraining from harvest in some years, populations are able to recover in off-years, prolonging the persistence of populations. The increased extinction risk associated with high-frequency seed harvest

has also been observed in the field. In Chapter 1, I demonstrated that increasing seed harvest frequency from triennial to annual resulted in population declines in non-clonal species. Interestingly, Menges and others (2004) found seed harvest intensity to be more important than harvest frequency. However, this finding was based on highly divergent harvest scenarios, i.e. very low (10%) and very high (100%) harvest frequency and intensity. Very high seed harvest intensity even in a single year can cause populations of some short lived species without a seedbank to decline rapidly, resulting in small populations more susceptible to extinction in subsequent years. In contrast, the present study focused on a more moderate subset of medium (50%) to high (75%) seed harvest intensities that are more common in seed harvest regimes focused on supplying restoration. The more realistic scenarios I examined may not have been extreme enough to elicit the population crashes that could result in seed harvest intensity to be of greater importance.

By limiting the frequency and intensity of seed harvest, managers can reduce the risk of population extinction in prairie plants while still allowing wild harvest. In general, I found that clonal species were robust to all seed harvest scenarios, and that even 75% annual harvest poses minimal risk to clonal plants, especially strongly rhizomatous species. However for non-clonal plants, annual 75% seed harvest should be avoided. These recommendations for clonal and non-clonal species can be applied to selective seed harvest methods (e.g. hand harvesting, small-scale brush/ vacuum harvesting) since harvest intensity can be controlled by either removing a set proportion of seed from each plant (hand harvest) or by removing seed from a set proportion of plants in a population (small-scale brush/ vacuum harvesting). However, recommendations for larger scale methods (e.g. combine harvesting, seed-haying) should be more conservative. Because large-scale methods harvest many species and populations at once (including non-clonal species), harvest rates for these techniques should ensure low risk outcomes for any species potentially being harvested. Thus, annual 75% seed harvest should also be avoided when using large-scale seed harvest methods. While it can be challenging to directly control percentage seed harvested with large scale methods, varying the percent

harvested area of a plant community may afford a degree of control over regulating harvest intensity.

Seed harvest guidelines should be adjusted according to restoration timeframe. For short-term restoration projects requiring large amounts of seed early in the process (e.g. interseeding), a seed harvest intensity of 75% may be warranted but only if further harvest is suspended for at least two years. Such a regime may provide sufficient seed to meet restoration objectives while simultaneously minimizing risks to donor populations. For long-term projects (e.g. landscape restoration), consistent seed supply may be required over time. In these instances, high-frequency/low-intensity seed harvest can provide sustained yield with relatively low extinction risk. For example, a 50% annual harvest regime results in low extinction risks for non-clonal species, and seed supply over ten years is 40% greater than a 75% triennial harvest regime.

Seed harvest recommendations should also take into account population growth prior to seed harvest. Because the recommendations discussed here are based on models of populations growing strongly at the onset of seed harvest ($\lambda > 1.1$), they should only be applied to well-established, healthy populations in the field. Harvesting slowly growing populations ($\lambda \sim 1$) requires a more conservative approach. For example populations at the edge of their range or growing in suboptimal conditions may exhibit minimal growth and need to be harvested at more conservative rates (Sexton et al. 2009; Phillips-Mao et al. 2016). Because reliable information on population dynamics is rarely available, any populations harvested for seed should be monitored and seed harvest regimes altered if population declines are observed.

Role of life history

Results from this study support using species life history, specifically clonality, as a central factor in seed harvest risk assessment for tallgrass prairies. Model simulations indicated that non-clonal tallgrass prairie species are more vulnerable to population extinction from wild seed harvest than clonal species, especially when subjected to high frequency/high intensity harvest. Some authors suggest that because clonal species, particularly warm-season grasses, are prevalent in tallgrass prairies, these communities

are in general not dependent on seed for population persistence (e.g., Benson & Hartnett 2006); it follows that seed harvest should have little impact in these communities. However, non-clonality is an important strategy in northern tallgrass prairies—34% of the most frequent species in wet-mesic northern tallgrass prairies are non-clonal (Chapter 1). Rabinowitz and others (1989) highlighted two key persistence strategies in populations of tallgrass prairie species: 1) predictable seed output (non-clonal species) or 2) sporadic, opportunistic seed output paired with asexual growth (clonal species). Both strategies allow populations to persist, though at different abundances: species with the clonal strategy are relatively dominant while species with the non-clonal strategy are less common.

Non-clonal species are vulnerable to population extinction from seed harvest because they rely on seed for population growth. The restricted means of reproduction in these populations, namely that any seed removal directly lowers the sole means of population growth, is likely driving the elevated extinction risks I observed in my model simulations. The importance of seeds for population growth in non-clonal plants is well-supported by other studies (Waloff & Richards 1977; Kinsman & Platt 1984). For example, in examining the impact of seed predation (analogous to seed harvest by humans) on a short-lived non-clonal thistle, Louda and Plotkin (1995) found that loss of seeds precipitated significant declines in population size, an effect they attributed to a heavy reliance on seeds for persistence.

Clonal life history may confer an intrinsic resilience to seed harvest-induced population extinction. In clonal species, changes in population growth remain small even as harvest frequency and intensity increase. The ability of clonal species to compensate for the loss of growth via sexual reproduction with an additional asexual mode of reproduction confers resistance to seed harvest. Specifically, in the clonal species models, the transition from vegetative or flowering adults to new clone ramets increases overall population growth, and that transition is unaffected by the removal of seeds in the population. However, the degree of resilience to seed harvest is related to the strength of clonal growth in each population. For example, *S. canadensis* adults rapidly proliferate via multiple rhizomes, each of which has a relatively high survival rate and likelihood to

become new vegetative or flowering individuals (Hartnett & Bazzaz 1985a). Such strong vegetative growth effectively confers total immunity of the population to harvest-induced declines. Similarly, *A. canadensis* reproduces by rhizomes, though less vigorously and reliably. For the closely related *A. nemorosa*, Pontoppidan and others (2011) demonstrated that rhizomatous growth is only possible after adult individuals have flowered, and that only two rhizomes with relatively low survival can be produced per individual. This relatively modest capability for asexual growth provides resilience to seed harvest in *A. canadensis*, but it does not grant immunity. For instance, populations under the annual 75% harvest scenario were still growing, but at a very slow rate—increasing harvest intensity by an additional 10% causes *A. canadensis* populations to decline. However, *A.* canadensis is long lived and exhibits high adult survival rates, so while high levels of seed harvest may cause populations to decline, the rate of decline is slow, and extinction risks at the end of 25 years are still very small.

The risk of population extinction for non-clonal species is especially sensitive to intrinsic population growth rates (i.e. the magnitude of growth in an unharvested setting). The importance of intrinsic population growth was most apparent in *P. aureus,* whose populations remained at low risk of extinction even under the highest levels of seed harvest frequency and intensity. Despite a substantial decrease in population growth caused by seed harvest, high intrinsic growth buffered the loss of reproductive potential that leads to population decline and elevated extinction risk. In terms of the magnitude of population growth decline ($\Delta \lambda$), *P. aureus* and *R. hirta* actually responded similarly to high levels of seed harvest but differences in intrinsic growth rates accounted for the extremely high extinction risk in *R. hirta* and no extinction risk in *P. aureus*. That is, a decrease in λ of ~0.5 was enough to cause decline in *R. hirta* populations (resulting $\lambda <$ 1), but not in *P. aureus* (resulting $\lambda > 1$). The importance of intrinsic population growth in determining the fate of a population is also supported by Menges and others (2004), who found in a modeling study that baseline intrinsic growth rates determined by favorable or unfavorable environmental conditions could influence extinction risk from seed harvest even in populations of the same species. Thus, unless non-clonal populations are clearly growing rapidly in an unharvested setting, it should be assumed that high

frequency/intensity seed harvest will elevate extinction risk. In clonal species, however, seed harvest decreases population growth to a much lesser degree due to the ability to reproduce vegetatively, making intrinsic growth less important as a determinant of population response. Even in populations that are barely growing (i.e. λ very close to 1), clonal species should still remain at relatively low risk of extinction from seed harvest (e.g. *A. canadensis*).

Regions with underdeveloped or emerging native seed markets may especially benefit from using a life history based approach to develop low risk seed harvesting strategies. For instance, an understanding of life history can facilitate comparisons between the development of seed farming efforts vs. wild harvesting in ways that allow mitigation of population extinction risks while also providing seed supply. By shifting to seed farming rather than wild harvest for non-clonal species, the risks to remnant wild populations can be avoided altogether. Non-clonal species also tend to be shorter lived and faster to mature (Bender et al. 2000), making them good candidates for efficient seed farming efforts. However, reliance on seed farming introduces the risk that germplasm used for revegetation may adapt genetically to production conditions, leading to maladaptation in restoration conditions (Schoen & Brown 2001). Given the low risks involved in harvesting seed from clonal species, wild harvest may safely supply seed demands for restoration in these species.

The application of seed harvest risk assessment and mitigation can benefit grasslands worldwide. Grasslands are focus points for restoration globally (Conrad & Tischew 2011; Zaloumis & Bond 2011; Overbeck et al. 2013) and require exceptionally large quantities of seed for revegetation (Packard & Mutel 2005). Given that much of the seed used to supply grassland restoration is collected from remnant wild plant populations (Broadhurst et al. 2015) the need to assess and minimize risks associated with seed harvest is a necessity for global biodiversity conservation. For instance, the *campos sulinos* grasslands of southern Brazil and the temperate grasslands of southeastern Australia are species rich, and harbor many endemic or threatened species (Boldrini 2009; Zimmer et al. 2010). The extent of these grasslands has been greatly diminished by intensive agriculture, and as interest in restoring these ecosystems grows

(Overbeck et al. 2013; Marshall et al. 2015), the need to minimize population extinction risks from seed harvest is crucial.

A life history based approach to risk assessment provides a sound framework from which general seed harvest guidelines can be set. Because clonal/non-clonal life histories are common in grasslands worldwide and are easily determined using regional floras (Veldman et al. 2015), my approach is particularly useful for conservation practitioners who must make decisions about seed harvest without extensive demographic field data. By using life history to develop seed harvest guidelines that mitigate the risks of seed harvest, seed demand for landscape restoration can be better met while biodiversity in remnants is conserved.

Meeting seed demand for landscape-scale restoration sustainably: the influence of seed harvest and site management

Abstract

Wild seed from native plants is often collected *en masse* from remnant ecosystems to supply landscape-scale restoration projects projects. Successful large-scale restoration depends not only on sustained yield of native seed but also on the persistence of donor populations. Native plants that reproduce solely by seed are especially sensitive to harvesting practices. I addressed the challenge of procuring sufficient seed from remnant sources to restore landscapes while also maintaining remnant populations of native plants on which successful restoration outcomes depend. I evaluated 1) the sustainability of seed harvest at varying intensities in *Rudbeckia hirta*, a short-lived, non-clonal plant, and 2) assess the contribution of fire in promoting sustainability of seed donor populations. I conducted a field experiment consisting of planted populations of *R. hirta,* where I manipulated management type (burned or unburned) and seed harvest intensity (0, 50%, or 100% seed removed), then measured changes in seedling recruitment and seed production among treatments. To evaluate whether harvest intensity or prescribed fire affect seedling recruitment rates or seed production, I analyzed the data using a mixed-effects ANOVA model with multiple comparison Tukey HSD *post-hoc* tests. Seedling recruitment in *R. hirta* is strongly influenced by both burning and seed harvest. With burning, seedling recruitment is generally high. Moderate intensity seed harvest and burning does not significantly reduce seedling recruitment, but high intensity harvest with burning reduced recruitment by 95% compared to controls. Seed production nearly doubled in burned treatments. In unburned prairie, recruitment is overall extremely low, and seed harvest intensity does not have an observable effect on recruitment. By instituting sustainable seed harvesting and management strategies, restoration practitioners can promote steady seed supply while conserving the integrity of remnant ecosystems. For harvest-sensitive species in prairies, a strategy that incorporates moderate intensity seed harvest with burning is most likely to provide seed for large-scale restoration sustainably.

Introduction

Ecological restoration has become an indispensable tool for biodiversity conservation (Suding 2011), but restoration must rapidly expand in extent and scope to counteract growing anthropogenic threats (Merritt & Dixon 2011; Brudvig 2011). Restoring entire landscapes is a priority in highly fragmented regions (Thompson 2011) where remnants of native vegetation tend to be small, isolated, and have limited capacity for self-recovery and self-sustainability (Fischer & Stöcklin 1997). The lack of native vegetation in fragmented landscapes poses a significant challenge for restoration—the distance between remnants prevents effective natural dispersal and makes passive revegetation unreliable (Thomson et al. 2009). To overcome this challenge, native propagules, primarily seeds, are actively reintroduced throughout the degraded parts of the landscape. The effort and material required in reseeding landscapes is extremely large however, and can require thousands of kilograms of seed from hundreds of different species (Gerla et al. 2012; Broadhurst et al. 2015).

Obtaining sufficient quantities of appropriate native seed is one of the greatest barriers to revegetation (Mortlock 2000b; Broadhurst et al. 2008, 2015; Rowe 2010; Tischew et al. 2011). Commercially available seed rarely offers sufficient variety in native plant species or regional genotypes to restore locally adapted, biodiverse stands of vegetation (Smith et al. 2007). When appropriate commercial seed sources can be found, supplies are typically unavailable in sufficient quantity to meet demand (Peppin et al. 2010; Borders et al. 2011). Further, purchasing seed at volumes necessary to supply large-scale restoration can be cost prohibitive (Rowe 2010). Seed farming, the process of growing native plants for seed in agricultural settings, is an alternative way to procure large quantities of native seeds. However, seed farming is resource intensive, and seeds raised in agricultural settings are at risk of adapting to production conditions (Schoen & Brown 2001) or losing genetic diversity (Vander Mijnsbrugge et al. 2010).

Mechanized wild seed harvest can circumvent the risks of maladaptation to production conditions while still efficiently obtaining large quantities of native seeds. By using combines, seed strippers, or seed haying, seeds can be harvested *en masse* from stands of native remnant vegetation (Olson 1984; Scotton et al. 2009). Because seeds

from multiple populations are harvested at a broad spatial scale, mechanically wild harvested seed may capture high levels of genetic diversity (Hoban & Strand 2015). Wild harvested seed can also quicken the pace of restoration since large amounts of diverse seed mixtures can be sown immediately after harvest (Gerla et al. 2012). In some regions, mechanized wild harvest is combined with management to further increase seed harvest efficiency. In tallgrass prairies for example, spring fires are commonly used to boost flowering during the growing season, which in turn results in higher seed production when prairies are harvested in the fall (Olson 1984; Glenn-Lewin et al. 1990; Gerla et al. 2012; Chapter 1).

Though wild seed harvest may help overcome seed supply constraints, it introduces risks to the remnant vegetation being harvested. Seed removal reduces the reproductive capacity of populations, and if too much seed is removed repeatedly, population declines and local extinctions may occur (Peres et al. 2003; Menges et al. 2004). Local extinctions in remnant ecosystems, even of rare or uncommon species, can result in a loss of resilience that might undermine the underlying ecological objectives motivating landscape restoration (Zavaleta & Hulvey 2004; Hooper et al. 2005). In addition, the loss of seed donor populations through overharvest diminishes restoration seed sources, which could further constrain landscape restoration. However, most plant species produce a surplus of seeds that are normally lost to competition (Clark et al. 2007), suggesting that harvesting some portion of seed should be sustainable (Menges et al. 2004).

Life history theory provides a framework for developing sustainable seed harvest methods that minimize risk of overharvest. In order to prevent species loss given the site-scale seed harvest techniques necessitated by landscape restoration, seed harvest regimes must account for the species most susceptible to overharvest. In an exploratory field survey of harvested and unharvested tallgrass prairies, I showed that short-lived, non-clonal species appeared to be most susceptible to decline from seed harvest (Chapter 1). Subsequent modeling studies confirmed the importance of life history, and showed that highly intense (i.e. number of seeds harvested) harvest elevated extinction risk in non-clonal species (Chapter 2), but that low intensity seed harvest did not. However, the

sustainability of comparable seed harvest regimes in a short-lived, non-clonal species has not been demonstrated experimentally.

Fire management may also play an important role in determining a sustainable seed harvest regime for at-risk species. In tallgrass prairies for example, burning may promote population growth in short-lived non-clonal species by improving the ability to regenerate from seed. By 1) increasing seed production (Glenn-Lewin et al. 1990, Johnson et al. 1987, Davis et al. 1987) and 2) by increasing available microsites for seedling establishment (Dix 1960; Endels et al. 2007), fire may bolster the ability of at-risk species to persist while being harvested for seed. Given that strong population growth can decrease extinction risk in seed harvested populations (Menges et al. 2004; Chapter 2), burning may increase the sustainability of seed harvesting.

Detailed study of seed harvest response under different management regimes has the potential to inform conservation strategies and harvest guidelines that optimize the benefits of seed collection while minimizing risk to source populations. To assess the effects of seed harvest intensity and the interactive influence of management on at-risk species, I conducted a field experiment in a remnant tallgrass prairie. In this study, I aimed to 1) evaluate the sustainability of seed harvest at varying intensities in a short-lived, non-clonal plant, and 2) assess the contribution of fire in promoting sustainability of seed donor populations. By identifying sustainable seed harvesting and management strategies, conservation practitioners will be better able to make decisions that ensure reliable and steady seed supply for restoration while conserving the integrity of remnant ecosystems and seed sources.

Methods

Study site and study species

The study area is located within Spring Prairie Preserve, a tallgrass prairie remnant of the Eastern Great Plains in Clay County, Minnesota, US (46°92' N, 96°47' W). Spring Prairie is characterized by exceptionally flat topography and homogenous wet-mesic prairie vegetation typical of the Northern Tallgrass Prairie grassland group (NVCS 2016). The Nature Conservancy owns and manages the site. Management at the

study area historically consisted of cattle grazing, though in 2013 I fenced off the study area (83m x 76m) to exclude grazing. Soils underlying the study area are somewhat poorly drained fine sandy loams (Natural Resources Conservation Service (NRCS) 2010). Mean annual temperature in the region is 5.1°C, and mean annual precipitation is 530mm (NOAA 2010).

I used *Rudbeckia hirta* L. as the study species in my experiment because it exemplifies the short-lived, non-clonal life history predicted to be most susceptible to seed harvest. In addition, it matures rapidly, making it useful as an experimental model. *Rudbeckia hirta* is a perennial herb common in open or early-successional habitats throughout most of North America (USDA 2014). In tallgrass prairies, *R. hirta* is typically found in low abundance (Johnson & Anderson 1986), but it plays an important role as a nectar source for several endangered butterfly species (Grundel et al. 2000; Selby 2005). The life cycle of *R. hirta* typifies many early-successional species— it matures rapidly, flowers in the first or second year, then dies within the following 1-2 years (Nuzzo 1976). *Rudbeckia hirta* possesses no structures that allow vegetative spread (Great Plains Flora Association 1986), so reproduction is entirely dependent on prolific seed production (Stevens 1932). Both observational and modelling studies predict that *R. hirta* is susceptible to seed harvest-induced population declines (Chapter 1; Chapter 2).

Experimental design

To investigate the effects of seed harvest intensity and site management on a short-lived, non-clonal species, I conducted a split-plot experiment from 2013-2015 comprised of transplanted *R. hirta* populations. I manipulated site management, i.e. fire management, in 6 whole-plots (sized 13x15m) and seed harvest intensity in 3 sub-plots (sized 1x1m) containing populations of *R. hirta* (3 replicates). To minimize impacts from trampling, I included 3m buffers between whole-plots and 1.4m buffers between sub-plots. I varied fire management at 2 levels: no burning and annual burning; and varied seed harvest intensity at 3 levels: 0% seed removal (unharvested control), 50% seed removal (low intensity), and 100% seed removal (high intensity).

I planted seedlings of *R. hirta* into the experiment area at the beginning of the growing season in 2013. I grew plants from wild collected seed in the University of Minnesota greenhouse beginning in January 2013, and transplanted them into experimental population plots in May 2013. For each population, I planted 9 juvenile plants in a 3x3 grid, spaced 30 cm apart in the center of the $1m^2$ sub-plots (Fig. 3.1). Planting standardized populations of *R. hirta* into established prairie allowed me to track them in detail from known starting parameters while still observing them under conditions (e.g. interspecific competition, ambient predation, climate) encountered by their counterparts in other harvested native remnants. While *R. hirta* occurs at Spring Prairie Preserve, I found no existing populations in the experiment area, making the presence of confounding effects due to pre-existing individuals or seeds in the soil highly unlikely.

Throughout 2013, 2014, and 2015, I applied prescribed fire and seed harvest treatments to experimental populations, mirroring the timing of common seed harvest and land management methods (Fig. 3.2). Before the growing season began in 2014 and 2015 (April or May, depending on weather conditions), I conducted prescribed burns at the whole-plot level with assistance from The Nature Conservancy's fire crews. I did not burn in 2013 because a fire immediately after planting would have likely killed establishing populations. I applied seed harvest treatments during the first week of August in 2013 and 2014 when *R. hirta* typically finishes flowering. I used a hand-held brush harvester to remove seeds from approximately half of the flowering stems in population plots to harvest 50% of seeds (low intensity treatment). To harvest 100% of seeds (high intensity treatment), I mowed population plots to approximately 10cm above soil and raked out the cut plant material into buffers, taking care to remove any flowering or seeding stems. To ensure uniformity in treatment application, I brush harvested and mowed plot vegetation even if no plants were flowering (Fig. 3.2).

I measured seedling recruitment rates among seed harvest and fire management treatments in 2014 and 2015 once plants were flowering and seedling recruitment was initiated. Seedling recruitment varied substantially depending on the previous year's seed production, so I estimated a standardized rate of seedling recruitment in each population

by dividing the 2015 seedling count by the estimate of 2014 seed production. I counted all seedlings (defined as plants with cotelydons) of *R. hirta* in each $1x1m^2$ population plot during the fourth week of July in 2015. To estimate 2014 seed production, I multiplied the average number of seeds per flowering head by the number of flowering heads in each population plot, which I counted immediately before harvesting. In 2 randomly selected destructive sampling population plots (~18 plants), I counted seeds from all flowering heads and used those values to estimate average seeds per flowering head. I excluded destructive sampling plots in my analysis. Immediately after burning, I also measured litter cover in population plots using visual estimates to verify the effect of fire management on safe-site availability. In July 2013 I recorded the average height of existing vegetation in population plots to assess the importance of vegetation context on seedling recruitment. Existing vegetation had no effect on recruitment and thus I do not discuss further.

Data analysis

To evaluate whether seedling recruitment in *R. hirta* is influenced by seed harvest intensity, fire management, or an interaction, I used analysis of variance (ANOVA) and *post-hoc* comparisons within treatment groups. I conducted ANOVA in R (R Development Core Team 2012) to test for main effects and interactions. Using a mixed effects model, I modeled harvest intensity, fire management, and interactions as fixed effects and whole-plot as a random effect. In *post-hoc* analysis, I used Tukey HSD tests to compare differences in seedling recruitment ($p < 0.05$) among seed harvest intensity treatments at each level of fire management. I also used a mixed-effects ANOVA model to test whether seed production or litter cover differed among treatments. Because the number of observations differed among treatments, I used Satterwaithe's method to calculate degrees of freedom for statistical tests. To meet parametric assumptions for testing, I square-root-transformed seedling recruitment and seed production values. Further, I tested a model using ANOVA that included seed harvest frequency as an additional fixed effect, but I found that model was not significantly better than the

simpler intensity-only model. Thus, I combined the harvest frequency and intensity treatment groups together in my analysis.

Results

Seedling recruitment in *R. hirta* is strongly influenced by both burning and seed harvest. ANOVA showed an interactive effect of fire x harvest intensity ($F_{2,18} = 8.83$, $p < 0.01$) which indicates that the effects of seed harvest depend on fire management. I also found significant main effects for fire ($F_{1,18} = 36.95$, $p < 0.001$) and harvest intensity ($F_{1,18} = 36.95$, $p < 0.001$).

In burned treatments, seed production was higher and litter cover was lower compared to unburned controls. Seed production varied among treatments, but on average, burning increased seed production from 4879 ± 1198 seeds/m^2 to 10362 ± 2688 seeds/m^2 (Fig. 3.3). ANOVA showed that seed production was predicted by burning ($F_{1,19} = 5.18$, $p < 0.05$) but not by interaction or seed harvest. Litter was sparse in burned treatments (28 ± 4.90 % cover) but very extensive in unburned treatments (97 ± 1.63 % cover) (Fig. 3.4). I found that litter cover was also predicted by burning ($F_{1,19} = 95.85$, $p < 0.0001$) but not by seed harvest or interaction effects.

Seedling recruitment is much higher in burned populations than in unburned populations. Burning nearly doubled recruitment rates—they were 96.4% greater in unharvested treatments (Tukey HSD, $t = 5.10$, $p < 0.001$) and 87.5% greater in low intensity seed harvest treatments (Tukey HSD, $t = 4.73$, $p < 0.001$) compared to their unburned counterparts. Seedling recruitment rates in unburned populations were near zero among all treatment levels (Fig. 3.5), averaging 0.095 ± 0.033 %. Although seedling recruitment was extremely low, a few seedlings were present in most unburned populations (mean 3.71 ± 1.37). Seedling recruitment did not differ in burned and unburned plots subjected to high intensity seed harvest.

Seed harvest substantially reduces seedling recruitment in *R. hirta* with burning. In burned controls, seedling recruitment was high (mean: 1.67 ± 0.180%) and seedlings were abundant (mean: 370.5 ± 88.5 seedlings/m^2). As seed harvest intensity increased,

recruitment decreased proportionately (Fig. 3.5). In low intensity harvest treatments (50% seed removal), mean seedling recruitment was 48.0% lower than in unharvested controls, but this difference was not statistically significant. However, seedlings were common in low intensity harvest treatments, averaging 128.5 ± 82.5 seedlings/m^2. In high harvest intensity treatments (100% seeds removed), seedlings were rare (mean: 4.25 ± 1.25 seedlings/m^2) and recruitment was 94.2% lower than in controls (Tukey HSD, $t = 5.81$, $p < 0.001$). I also found that seedling recruitment was lower in high intensity harvest treatments compared to low intensity harvest treatments (Tukey HSD, $t = 4.29$, $p < 0.01$).

Discussion

Landscape-scale restoration in fragmented regions depends on a steady and extensive supply of native seed from remnant ecosystems. At the same time, donor populations must persist in order to maintain the resiliency of remnant ecosystems which are integral to restored landscapes. To fully utilize seed donor populations of an at-risk species sustainably, my results show that increasing seed production to maintain restoration seed availability can be achieved with active fire management. I also showed that promoting the conservation of seed donor populations requires conditions conducive to regeneration and seedling establishment, which can be created by burning. I found that the combination low intensity seed harvest and burning is likely sustainable, and may result in net benefits for both restoration seed supply and biodiversity conservation. However, deviation from this harvest and management regime results in suboptimal outcomes. Here I discuss in detail how seed harvest and site management influence sustainability of seed resources in an at-risk species, and how remnant prairies can be best managed to conserve donor populations and promote seed supply for landscape restoration.

Incorporating burning into prairie seed harvest regimes benefits landscape-scale restoration both by increasing seed production and by ensuring the sustained provision of seed sources. My results showed that on average, seed production more than doubled with burning. For seed limited landscape restoration projects, additional seed supplies can be harvested with increased seed production, allowing more land to be restored per year

(Mortlock 2000b; Gerla et al. 2012). As such, incorporating burning into prairie seed harvest regimes may allow landscape restoration projects to proceed more quickly, reducing operational costs that also tend to limit the size and scope of restoration (Rowe 2010). Additionally, a two-fold increase in seed production allows even low intensity harvest to provide large amounts of seed—I found that 50% harvest with burning actually yields a quantity of seed roughly equal to 100% harvest without burning. Ultimately, my findings suggest that by greatly increasing seed production, burning circumvents the normal tradeoff between increasing the quantity of seed harvested and the integrity of seed donor populations (Menges et al. 2004; Chapter 2)—resulting in a conservation and restoration "win-win" scenario. Fire also creates the conditions necessary for seedling regeneration. I found that burning increased litter-free area by 70%, and that there was a correspondingly high amount of seedling recruitment in burned populations. This result suggests that seeds were better able to reach suitable microsites and establish as seedlings when burned. By ensuring a reliable pathway for seeds to recruit as seedlings, burning increases the likelihood that seeds become reproductive adults (Russell et al. 2010), which are essential for a sustained seed source for landscape restoration.

Low intensity seed harvest allows high levels of seedling recruitment, and likely poses little risk to harvested populations. I found that when harvesting at low intensity, the absolute number of seedlings that established was very high. Over 100 seedlings/m^2 established under the low intensity harvest regime, which is a higher density than other studies of *R. hirta* seedling recruitment have reported (Rabinowitz & Rapp 1985; Williams et al. 2007). The high densities of seedlings I observed under low intensity harvest would be at least sufficient for population replacement, even assuming low rates of seedling survival previously observed for prairie seedlings (14%) (Rabinowitz & Rapp 1985). Such high levels of recruitment even with low intensity seed harvest were likely due to the improved regeneration conditions created by burning. Fire increased both the number of seeds available and the availability of microsites for successful germination and establishment, which in effect led to more new seedling recruits. My experimental results validate projections of modeled populations. Using matrix models to simulate seed harvest, I similarly showed that low intensity (50%) seed harvest was a relatively low risk

harvest strategy, where harvesting at low intensity annually resulted in a 13% extinction risk over 25 years (Chapter 2). By increasing the time between harvests to 2 years, extinction risk dropped to 3%, suggesting that risks associated with low intensity harvest could be further mitigated by decreasing harvest frequency.

High intensity seed harvest prevents regeneration from seed, and is not sustainable for populations of short-lived non-clonal plants. I found that harvesting 100% of seeds reduced seedling recruitment by 95% and effectively precluded any regeneration; only a few seedlings were able to establish. Short-lived non-clonal plants tend to be better seed colonizers than other species that may be more competitive (i.e. long-lived or clonal species), and rely on this advantage to maintain their populations in regularly disturbed ecosystems like tallgrass prairies and other managed grasslands (Coulson et al. 2001; Pywell et al. 2003; Willand et al. 2013). As my results show, harvesting seed from a short-lived, non-clonal species at high intensity diminishes seed colonization ability, and thus thwarts the primary persistence strategy. Without a reliable way to colonize new microsites, short-lived non-clonal species may quickly decline to extirpation (Dickson & Busby 2009). Modeling studies also show that high intensity seed harvest can lead to population extinction. By using seed harvest simulations, I showed that harvesting 75% of seeds from *R. hirta* virtually guaranteed population extinction within 25 years (Chapter 2). Other models show that harvesting seed from several sensitive species at rates comparable to those in the present study resulted in no less than 80% probability of extinction, even when harvesting less frequently (every other year) (Menges et al. 2004). Because my experimental populations lacked an established seedbank, it is possible that more mature populations with a well-developed seedbank could persist for a time even under high intensity seed harvest regimes. While soil seedbanks can be an important source of new seedlings in *R. hirta* and other short-lived non-clonal species, recruitment from the seedbank tends to be low even under ideal conditions (~26 seedlings/m^2 for *R. hirta*) (Johnson & Anderson 1986), suggesting it is unlikely that the seedbank alone could support continued population growth under a high intensity seed harvest regime.

Coupling fire management with low intensity seed harvest may provide the optimal harvest and management regime that allows utilization of seed from wild donor populations while minimizing risk. Under the improved regeneration conditions created by burning, harvesting half of seeds still allows the remainder of unharvested seeds to recruit as seedlings at higher than normal densities. Previous study further suggests that a moderate harvest and burning regime can both supply seeds for landscape restoration and conserve seed donor populations. In a tallgrass prairie landscape restoration in northwestern Minnesota, adequate seed supplies were sustained throughout the project by harvesting and burning prairie remnants at 3-year intervals at approximately 60% harvest intensity (Teiken, pers. comm.; Gerla et al. 2012). After the project ended, the composition of burned and harvested prairies was no different than unharvested prairies, even among at-risk short-lived non-clonal species (Chapter 1).

A low intensity (50%) seed harvest regime can be achieved by applying either selective (e.g. hand harvesting, small-scale brush/ vacuum harvesting) or broad-scale mechanized (e.g. combine harvesting, seed-haying) harvesting techniques. Regardless of the harvesting method, my results demonstrate the importance of leaving 50% of harvestable seeds on-site. Where broad-scale mechanized harvest is employed, I recommend a harvesting pattern of alternating harvested and unharvested strips throughout seed donor sites. Leaving unharvested strips throughout a seed donor site ensures that remaining seeds can disperse into harvested areas and sustain regeneration in species relying on seed for population persistence.

Deviating from a low intensity harvest and burn regime results in either low seed supply or high risk of population depletion. Burning without harvesting is the best harvest and management regime for conserving populations of short-lived non-clonal species, given that seedling recruitment from burning is exceptionally high and all seeds have a chance to disperse. However, a no-harvest strategy does not increase seed supply for furthering landscape restoration, and should be reserved for managing prairies where seed production is not a desired outcome—for example those with populations of rare or threatened species where the risks of harm outweigh potential seed supply benefits. In contrast, high intensity seed harvest with burning provides the greatest seed supply, but

also carries a very high risk of depleting donor populations. While this harvest and management regime may provide the most seed for restoration in the short term, it should be avoided. The depletion of seed donor populations not only may erode resilience in prairie remnants, but the loss of seed sources may erode the capacity to continue landscape restoration in the long term. Both high and low intensity harvest without burning pose equal risks to donor population persistence, but still provide benefits to restoration seed supply. Without the conditions for regeneration provided by burning, populations are unable to recruit new seedlings, regardless of seed harvest. Clearly these management regimes should be avoided, though my findings suggest that unless burning can be incorporated into site management, high intensity seed harvest would do no additional harm to already imperiled seed donor populations. In these harvest and management regimes, harvested seeds likely have a greater chance to establish and persist *ex-situ* in newly sown restoration sites. Interestingly, the most conservative no-harvest, no-burn regime is the worst combination I evaluated. Not only are risks to seed donor populations high from a lack of burning-induced regeneration, but there is also no increase in seed supply for landscape restoration. With neither burning nor seed harvest, populations have little chance of persisting *in-situ*, and no chance at persisting *ex-situ* in restoration sites.

My study provides the first experimental demonstration that moderate seed harvest with fire management may be a sustainable strategy to supply seed for landscape restoration in tallgrass prairies. However, I also showed that overharvest and lack of management may jeopardize seed supply and the integrity of prairie remnants. By incorporating my findings into conservation and restoration decision-making, land managers will be better able to utilize remnant prairies as both biodiversity refugia and as a seed source for landscape restoration. My findings could be built upon with further studies that examine whether other grassland management techniques (e.g. mowing, haying, grazing) can sustain seed resources to the same extent as burning, and whether seed harvest regimes should be more or less restrictive under different types of management. Because the beneficial effect of fire is not universal in grasslands worldwide (Milberg et al. 2014), identifying the most sustainable seed harvest and

management regime should be a top priority if grassland landscapes are to be restored globally. Given that life history was also an important influence on seed harvest response in my study species, more comparisons of short-lived vs long-lived and clonal vs. non-clonal species are needed to confirm life history as a sound and generalizable framework for predicting seed harvest response.

GENERAL CONCLUSION

Life history traits provide a useful framework for predicting seed harvest sensitivity. When comparing differences in species composition among native tallgrass prairies with varying seed harvest histories, life history traits predicted which species were at risk of decline with high frequency seed harvest, and which species were not (Chapter 1). Specifically, short-lived, non-clonal species are sensitive to seed harvest, while long-lived, clonal species are insensitive. Simulations of seed harvest scenarios based on matrix models verified the utility of life history traits to predict seed harvest sensitivity (Chapter 2). These simulations showed that clonal plants like *Solidago canadensis* and *Anemone canadensis* can maintain their populations even with high levels of harvest, while non-clonal plants such as *Rudbeckia hirta*, *Zizia aurea*, and *Liatris ligulistylis* are at risk of extinction under high levels of seed harvest.

Model projections also showed that annual seed harvest tended to increase the risk of population extinction over 25 years in harvest-sensitive species, and that annual harvesting at high intensity virtually assured extinction for the most sensitive species (Chapter 2). By reducing harvest frequency to once every three years, even 75% harvest intensity generally allows for long term population persistence (Chapter 2), a finding consistent with observations that triennially harvested prairies maintained abundances of harvest sensitive species similar to unharvested prairies (Chapter 1). Reducing harvest intensity to 50% also largely ensures the long-term persistence of harvest sensitive species, though to a lesser degree than reducing frequency (Chapter 2).

These insights on the importance of life history traits to predict seed harvest response means conservation practitioners should use this information to avoid the risk of depleting donor seed sources. For example, life history traits could be used to develop monitoring protocols that focus on harvest-sensitive species. If these protocols are deployed at the onset of wild harvesting, practitioners have the opportunity to adjust harvesting levels in response to changes in donor population abundance. To fully test the causality of traits as a determinant of harvest response, a long-term field experiment was initiated. In this experiment, both frequency (annual, triennial) and intensity (50%, 100%) of seed harvest were manipulated for populations of six species with a combination of

lifespan and clonality traits, including short-lived, non-clonal (e.g. *R. hirta*), short-lived, clonal (e.g. *Astragalus canadensis*), long-lived, non-clonal (e.g. *L. ligulistylis*), and long-lived, clonal (e.g. *Asclepias syriaca*) species. With multiple controlled comparisons of seed harvest response for specific life history traits, this experiment will be able to firmly establish the predictive ability of traits. I reported the initial results from this experiment in Chapter 3, showing that a species predicted to be especially harvest sensitive based on life history traits (*R. hirta*) was confirmed to be sensitive to seed harvest. I demonstrated that high intensity seed harvest caused seedling recruitment to be prevented in this species, establishing the mechanism by which seed harvest could cause population extinctions.

In order to support large-scale restoration, a steady and extensive supply of native seed from remnant ecosystems must be sustained over long restoration timeframes. Findings from my field experiment provide insight into how seed harvest can be made more productive and sustainable. Specifically, seed production was greatly increased by coupling seed harvest with fire management, and promoted the ability of seeds remaining after moderate harvest to establish as seedlings (Chapter 3). With large increases in seed production, even low intensity harvest yields a sizable quantity of seed. For example, I showed that 50% harvest with burning yields a quantity of seed roughly equal to 100% harvest without burning (Chapter 3). In effect, incorporating fire management with seed harvest allows conservation practitioners to capitalize on a conservation and restoration "win-win" scenario where more harvestable seed can be supplied for large-scale restoration while population growth in seed donor populations is maintained. Using management to boost seed production has potentially large implications for increasing restoration capacity worldwide, particularly in areas of growing restoration interest without native seed markets or seed farming infrastructure. Further study is needed to investigate whether other management techniques (e.g. mowing, haying, grazing) common in other ecosystems can promote the sustainability of seed resources to the same extent as burning does in tallgrass prairies.

Taken together, my findings provide an empirical and theoretical basis for improving seed harvest guidelines. When using large-scale mechanical harvest methods,

guidelines must be set to accommodate the most susceptible species, i.e. short-lived, non-clonal species, in order to avoid depleting seed donor sources (Chapter 1). Still, existing guidelines that range from 10% harvest every 10 years (Menges et al. 2004) to 20% harvest every year are likely overly conservative (Packard & Mutel 2005) and may limit the ability for wild native seed to help supply large-scale restoration. In tallgrass prairies specifically, incorporating 50% seed harvest after burning at three year intervals should provide a low risk strategy that still supplies sufficient seed to meet demands from large-scale restoration. In practice, this harvest regime may be achieved by using combine harvesters to harvest alternating strips throughout burn units, leaving an amount of unharvested vegetation equivalent to the area of harvested vegetation. This approach will promote dispersal of remaining seeds throughout harvested portions of donor sites. I showed that for a sensitive short-lived, non-clonal species, high seedling recruitment still occurs when harvesting 50% of seeds, at least in the short term (Chapter 3). Further, model projections suggest that 50% harvest intensity avoids significant extinction risks in the long-term, especially if harvesting at 3 year intervals (Chapter 2). In addition, retrospective comparisons of combine harvested prairies showed that harvesting and burning every 3 years retains the abundance of harvest-sensitive species equal to that in unharvested prairies (Chapter 1). Ultimately, by incorporating these guidelines into conservation and restoration plans, practitioners will be better able to utilize remnant prairies in a way that both benefits biodiversity conservation and furthers the objectives of large-scale restorations.

TABLES

Table 1.1. Environmental variables controlled for during site selection. Variables are defined as ecological attributes that account for variation in plant communities at sites. Selectivity requirements are specific attributes of each variable used to constrain variation. To ensure that sites being compared in this study were ecologically similar, only sites that met selectivity requirements were used in this study (17 of 49 possible sites).

Variable	Selectivity requirement
Soil drainage[a]	Moderately well drained to very poorly drained
Soil particle size[a]	Coarse-loamy to fine-silty to sandy over loamy
Soil taxonomy[a]	Endoaquolls, Calciaquolls and Endoaquents
Land use history[b]	No previous sustained grazing, fertilization or tillage

[a]-Determined for each site using the Natural Resources Conservation Service Soil Survey Geographic Database (2010); follows soils nomenclature from USDA.

[b]- Determined by land-manager interviews and Minnesota County Biological Survey (2000) spatial data.

Table 1.2. Prescribed burn history of sites compared in this study. From 2000-2011, sites in the frequently harvested category were harvested for seed 6-11 times, sites in the infrequently harvested category were harvested for seed 2-3 times, and unharvested sites were never harvested for seed. The number of sites in each category is denoted by *n*. Number of times sites were burned was determined by land-manager interviews.

Harvest frequency categories	*n*	*Average times burned from 2000-2011 ± standard error*
Unharvested	6	2.50 ± 1.64
Infrequently harvested	6	4.17 ± 1.94
Frequently harvested	5	9.40 ± 3.05

Table 1.3. Attributes, measures, and data sources of three life history traits tested in determining plant species response to seed harvest. Traits were selected based on their likelihood of determining species reliance on seeds for population persistence. Attributes are the measurable components that represent each trait. Measures denote the data type used to quantify each attribute (binomial, continuous, or ordinal).

Trait	Attribute	Measure	Source
Clonality	Vegetative reproductive structures	Binomial (Present/absent)	Great Plains Flora Association (1986)
Fecundity	Average individual seed mass	Continuous (mg)	Royal Botanic Gardens Kew (2012), Prairie Moon Nursery (2012)
Lifespan	Lifespan class	Ordinal (1-5 yrs, 5-10 yrs, 10-15 yrs, >15 yrs)	Bender et al. (2000)

Table 1.4. Summary of species occurrence (proportion of plots occupied) in prairies wild-harvested for seed frequently (5-11 times), infrequently (2-3 times) or not harvested. For each species, occurrence in frequently and infrequently harvested prairies is compared to unharvested control sites at $p < 0.10$ where "+" indicates that a species is more abundant relative to controls, "-" indicates a species is less abundant relative to controls, and "ns" indicates species abundance is not significantly different. An asterisk (*) denotes that a response was also significant at $p < 0.05$.

| Species | Comparison to unharvested sites | | Average proportion of plots occupied ± standard error | | |
	Frequent harvest	Infrequent harvest	Unharvested	Infrequently harvested	Frequently harvested
Senecio pauperculus	-*	-*	0.16 ± 0.09	0 ± 0	0 ± 0
Liatris ligulistylis	-*	-*	0.24 ± 0.06	0.13 ± 0.06	0.06 ± 0.04
Muhlenbergia richardsonis	-*	-*	0.58 ± 0.1	0.30 ± 0.11	0.24 ± 0.09
Bromus kalmii	-*	ns	0.12 ± 0.04	0.05 ± 0.03	0.01 ± 0.01
Solidago nemoralis	-*	ns	0.14 ± 0.04	0.09 ± 0.05	0.03 ± 0.02
Comandra umbellata	-	ns	0.24 ± 0.09	0.17 ± 0.06	0.06 ± 0.04
Pycnanthemum virginianum	-*	ns	0.31 ± 0.12	0.19 ± 0.09	0.05 ± 0.04
Rudbeckia hirta	-	ns	0.26 ± 0.02	0.30 ± 0.07	0.16 ± 0.04
Senecio pseudaureus	-*	ns	0.54 ± 0.08	0.38 ± 0.11	0.17 ± 0.09
Fragaria virginiana	-*	ns	0.56 ± 0.09	0.40 ± 0.12	0.11 ± 0.04
Helianthus spp.[a]	-*	ns	0.65 ± 0.09	0.50 ± 0.11	0.30 ± 0.06

Zizia aurea	-*	ns	0.77 ± 0.08	0.60 ± 0.13	0.36 ± 0.15
Thalictrum dasycarpum	-*	ns	0.60 ± 0.12	0.62 ± 0.08	0.08 ± 0.03
Galium boreale	-*	ns	0.79 ± 0.06	0.81 ± 0.05	0.33 ± 0.10
Panicum virgatum	+*	ns	0.05 ± 0.03	0.04 ± 0.02	0.17 ± 0.07
Viola pedatifida	+*	ns	0.01 ± 0.01	0.06 ± 0.04	0.14 ± 0.03
Eleocharis compressa	+*	ns	0.01 ± 0.01	0.07 ± 0.02	0.32 ± 0.06
*Agrostis gigantea	+	ns	0.15 ± 0.07	0.27 ± 0.12	0.53 ± 0.15

*-Introduced species.

[a]-Includes the hybrids of *Helianthus giganteus*, *H. maximiliani*, and *H. pauciflorus.*

Table 2.1. Study species, life history, and literature sources supporting model construction.

Species	Life history	Demographic surrogate	Source
Rudbeckia hirta	Non-clonal		Stevens 1932; Halinar 1981; Christiansen 1994; Clark & Wilson 2003; Williams et al. 2007
Packera aureus	Non-clonal	*Senecio integrifolius*	Widén 1987
Zizia aurea	Non-clonal	*Lomatium bradshawii*	Stevens 1957; Sorensen & Holden 1974; Caswell & Kaye 2001; Williams et al. 2007
Liatris ligulistylis	Non-clonal	*Liatris scarriosa*	Ellis et al. 2012
Anemone canadensis	Clonal	*Anemone nemorosa*	Stevens 1932; Shirreffs 1981; Wittig 2008; Pontoppidan et al. 2011
Solidago canadensis	Clonal		Werner & Platt 1976; Hartnett & Bazzaz 1985a, 1985b; Meyer & Schmid 1999a, 1999b

Table 2.2. Maximum annual seed harvest rates preventing population declines ($\lambda < 1$) or elevated extinction risk (ER=0.05) over 25 years in a population with 100 individuals.

Species	Life history	Annual harvest rate (%) resulting in $\lambda= 1$	Annual harvesting rate (%) resulting in extinction risk= 0.05 over 25 yr (n=100)
Rudbeckia hirta	Non-clonal	63	38
Packera aureus	Non-clonal	84	88
Zizia aurea	Non-clonal	74	63
Liatris ligulistylis	Non-clonal	74	77
Anemone canadensis	Clonal	85	100[b]
Solidago canadensis	Clonal	100[a]	100[b]

[a]-No rate of harvest resulted in $\lambda= 1$

[b]- 100% harvest did not elevate extinction risk to 0.05 in these species

Figure 1.1. Locations of 17 study sites in northwestern Minnesota. Regional blocks are shown as labeled ellipses.
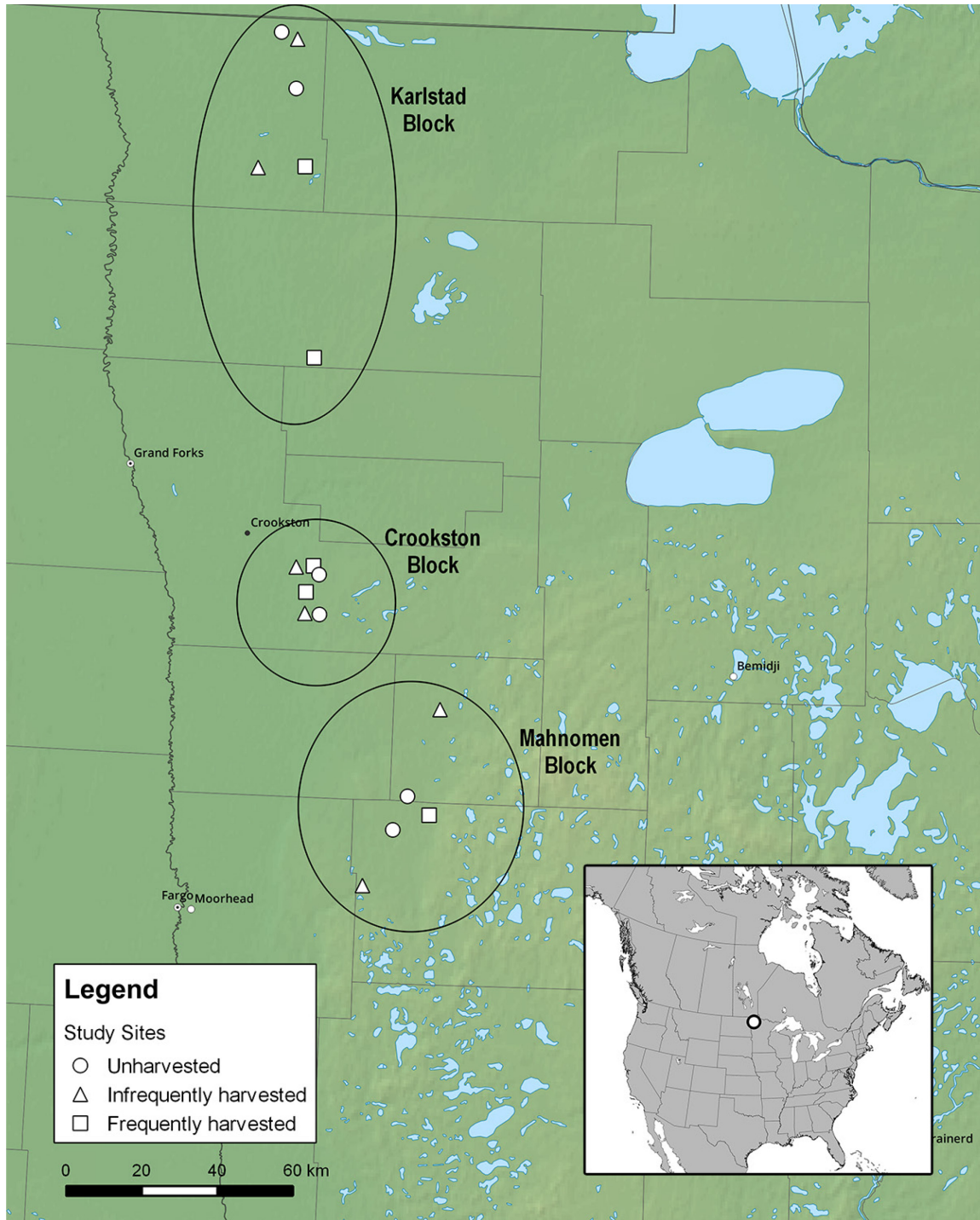
Figure 1.2. Two dimensional NMDS ordination of species found in prairies wild-harvested for seed 0 times (unharvested), 2-3 times (infrequently harvested), or 6-11 times (frequently harvested). Two convergent solutions were found after 8 tries, stress: 0.1299. Scores were half-change scaled, centered, and PC rotated. Species found to be harvest-negative and harvest-positive in frequently harvested prairies based on ANOVA contrasts are colored black and red respectively. Agrgig= *Agrostis gigantea*, Brokal= *Bromus kalmii*, Comumb= *Comandra umbellata*, Elecom= *Eleocharis compressa*, Fravir= *Fragaria virginiana*, Galbor=*Galium boreale*, Helspp= *Helianthus* spp. Lialig= *Liatris ligulistylis*, Muhric= *Muhlenbergia richardsonis*, Panvir= *Panicum virgatum*, Pycvir= *Pycnanthemum virginianum*, Rudhir= *Rudbeckia hirta*, Senpau= *Senecio pauperculus*, Senpse= *Senecio pseudaureus*, Solnem= *Solidago nemoralis*, Thadas= *Thalictrum dasycarpum*, Vioped= *Viola pedatifida*, Zizaur= *Zizia aurea*.
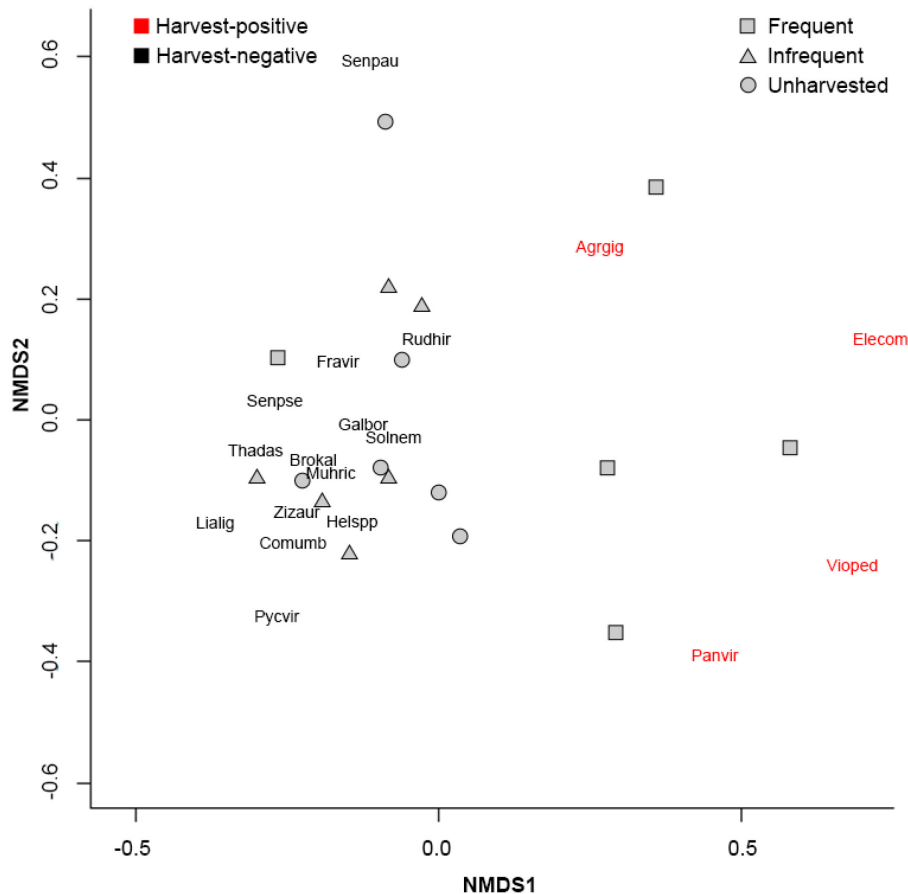
Figure 1.3. Mean species richness (± standard error) per m^2 in unharvested, infrequently harvested and frequently harvested prairies. Significant differences in species richness between harvest categories ($p < 0.05$) are distinguished by different letters (i.e. "a" is different from "b").
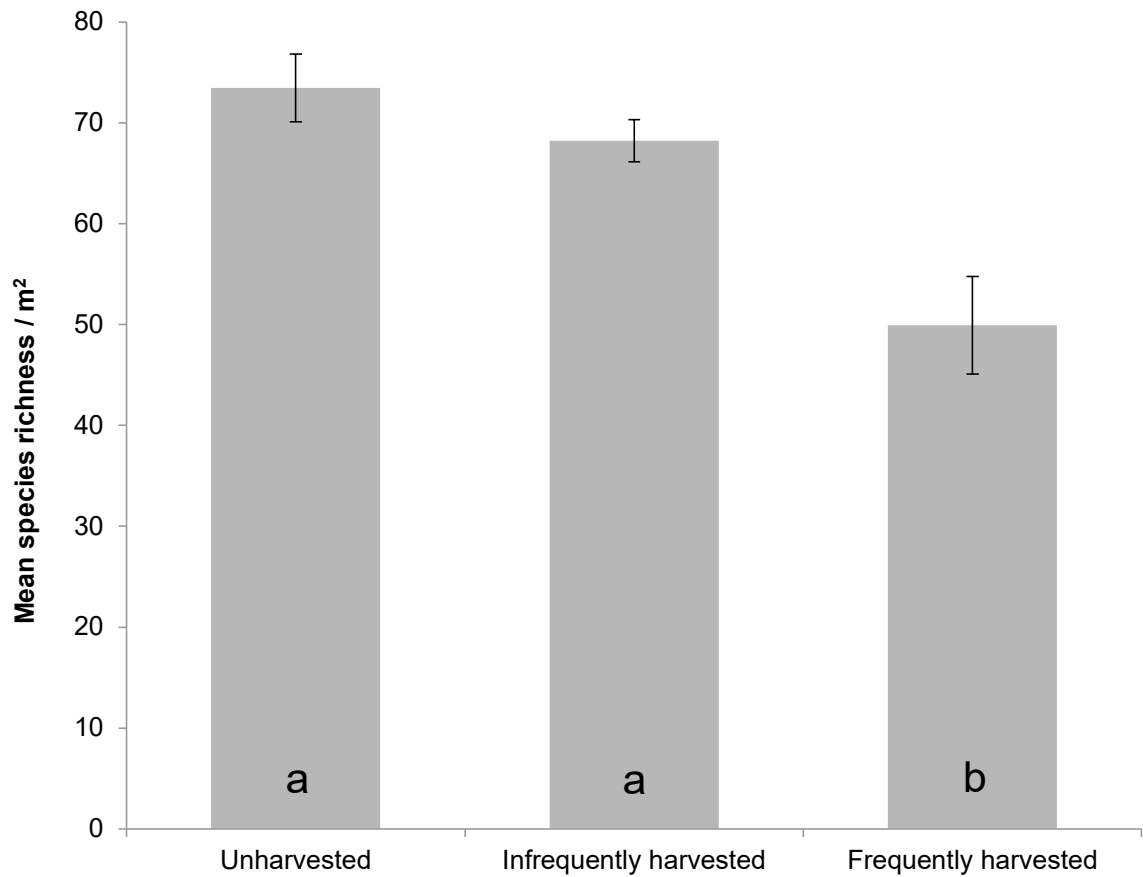
Figure 1.4. Examples of tallgrass prairies harvested for seed over 11 years, with study sites on left (site scale) and their plant community detail (plot scale) on right. From top to bottom, a) unharvested, b) infrequently harvested (3 times), c) frequently harvested (11 times). Notice that all examples appear similar at the site scale but at the plot scale frequently harvested examples are distinct (fewer species visible) compared to infrequently or unharvested examples.
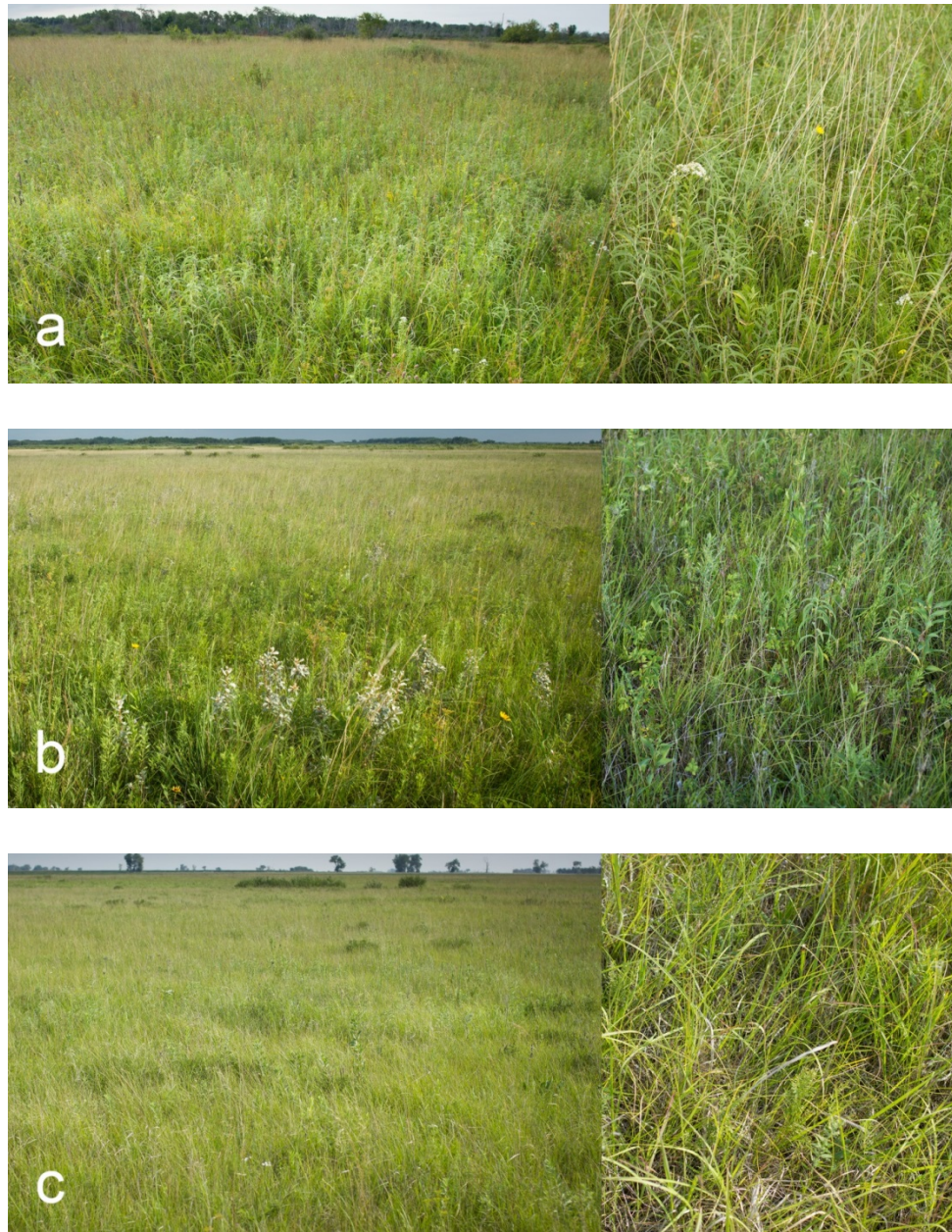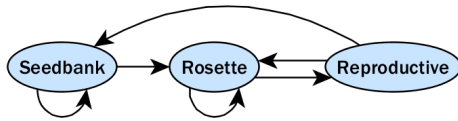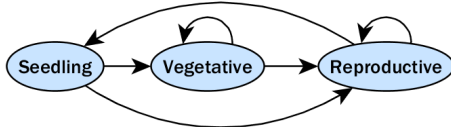
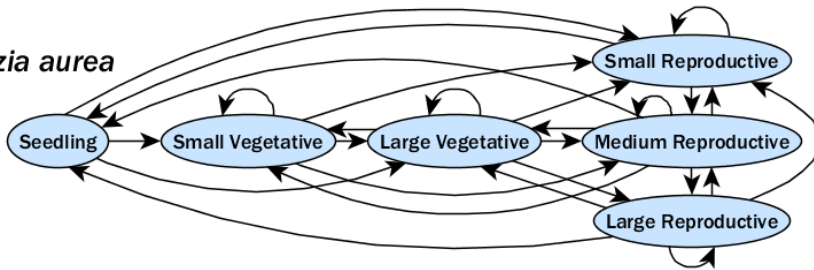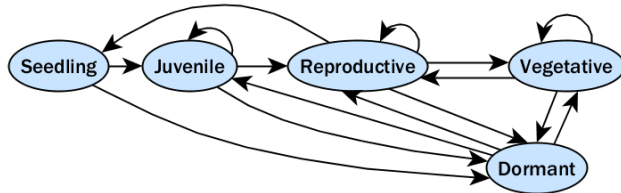Figure 2.1. Study species life cycle diagrams.

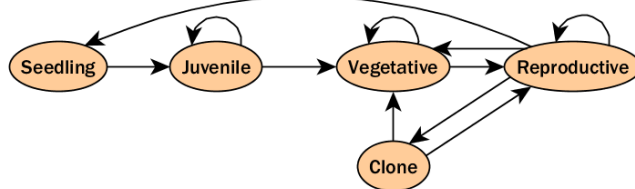*Rudbeckia hirta*

Packera aureus

Zizia aurea

Liatris ligulistylis

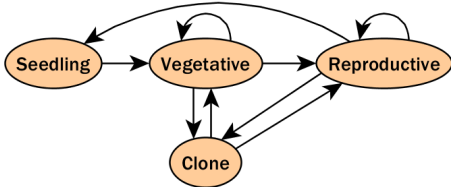*Anemone canadensis*

Solidago canadensis

Figure 2.2. Stage-based transition probabilities used to populate baseline model parameters for simulating seed harvest. Stages and transition probability estimates between stages were inferred from previous demographic studies (see Table 2.1).

Rudbeckia hirta

	Seedbank	Rosette	Reproductive
Seedbank	0.049	0.000	79.458
Rosette	0.031	0.330	2.965
Reproductive	0.000	0.330	0.200

Packera aureus

	Juvenile	Vegetative	Reproductive
Juvenile	0.000	0.000	63.120
Vegetative	0.525	0.572	0.637
Reproductive	0.005	0.071	0.006

Zizia aurea

	Seedling	Small Vegetative	Large Vegetative	Small Flowering	Med Flowering	Large Flowering
Seedling	0.000	0.000	0.000	1.603	17.641	8.5289512
Small Vegetative	0.272	0.308	0.105	0.048	0.026	0.0625
Large Vegetative	0.089	0.171	0.328	0.187	0.114	0.08125
Small Flowering	0.014	0.042	0.197	0.324	0.302	0.0735
Med Flowering	0.000	0.022	0.094	0.274	0.371	0.3295
Large Flowering	0.000	0.003	0.002	0.019	0.055	0.363

Liatris ligulistylis

	Seedling	Juvenile	Flowering	Vegetative	Dormant
Seedling	0.000	0.000	12.107	0.000	0.000
Juvenile	0.570	0.652	0.000	0.000	0.473
Flowering	0.042	0.083	0.261	0.218	0.025
Vegetative	0.000	0.000	0.386	0.178	0.018
Dormant	0.056	0.054	0.063	0.010	0.151

Solidago canadensis

	Seed Juvenile	Clone Juvenile	Vegetative	Reproductive
Seed Juvenile	0.000	0.000	0.000	0.508
Clone Juvenile	0.000	0.000	0.860	0.860
Vegetative	0.387	0.308	0.423	0.423
Reproductive	0.063	0.318	0.437	0.437

Anemone canadensis

	Seedling	Seed Juvenile	Clone Juvenile	Vegetative	Reproductive
Seedling	0.000	0.000	0.000	0.000	1.099
Seed Juvenile	0.612	0.420	0.000	0.000	0.000
Clone Juvenile	0.000	0.000	0.000	0.000	0.200
Vegetative	0.000	0.280	0.495	0.630	0.387
Reproductive	0.000	0.000	0.405	0.270	0.513

Figure 2.3. Extinction risk (± 95% confidence interval) for model species populations under 5 seed harvest scenarios. RH=*Rudbeckia hirta*, PA=*Packera aureus*, ZA= *Zizia aurea*, LL= *Liatris ligulistylis*, AC= *Anemone canadensis*, SC= *Solidago canadensis*. Non-clonal species are denoted by solid shapes while clonal species are denoted by line shapes.
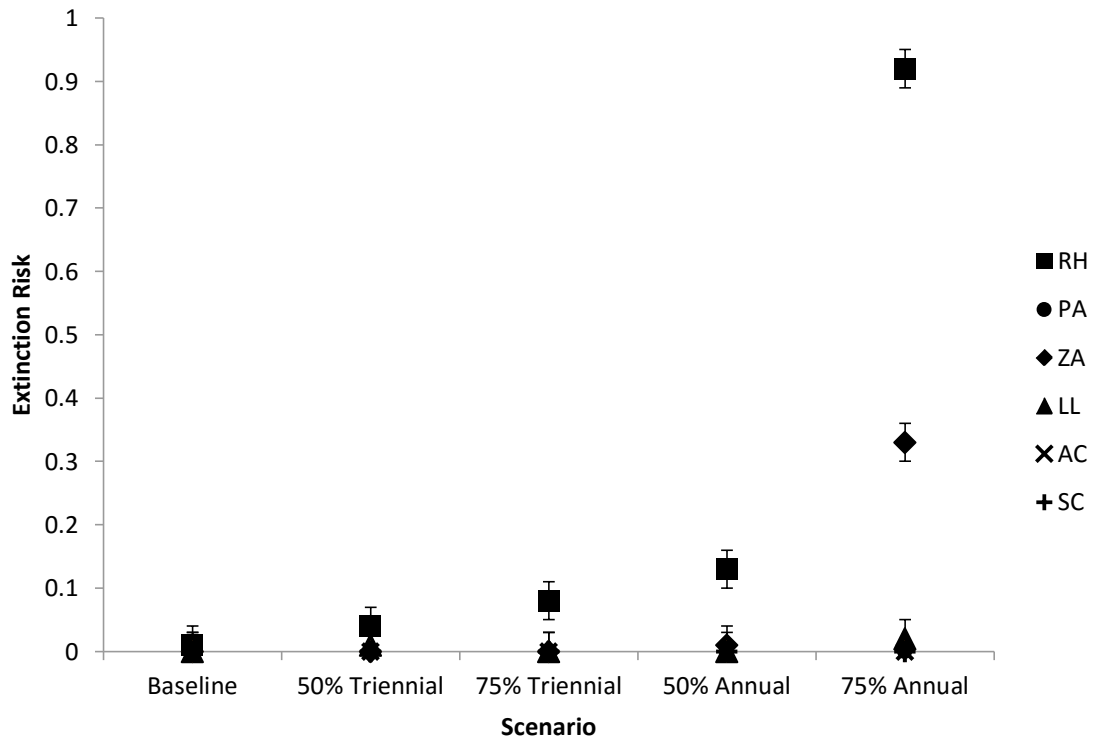
Figure 2.4. Seed harvest scenario output for non-clonal species (1,000 simulation runs each). Solid lines represent average population abundance, shading represents ± 1 SD, and squares represent maximum and minimum population abundance at each time step.
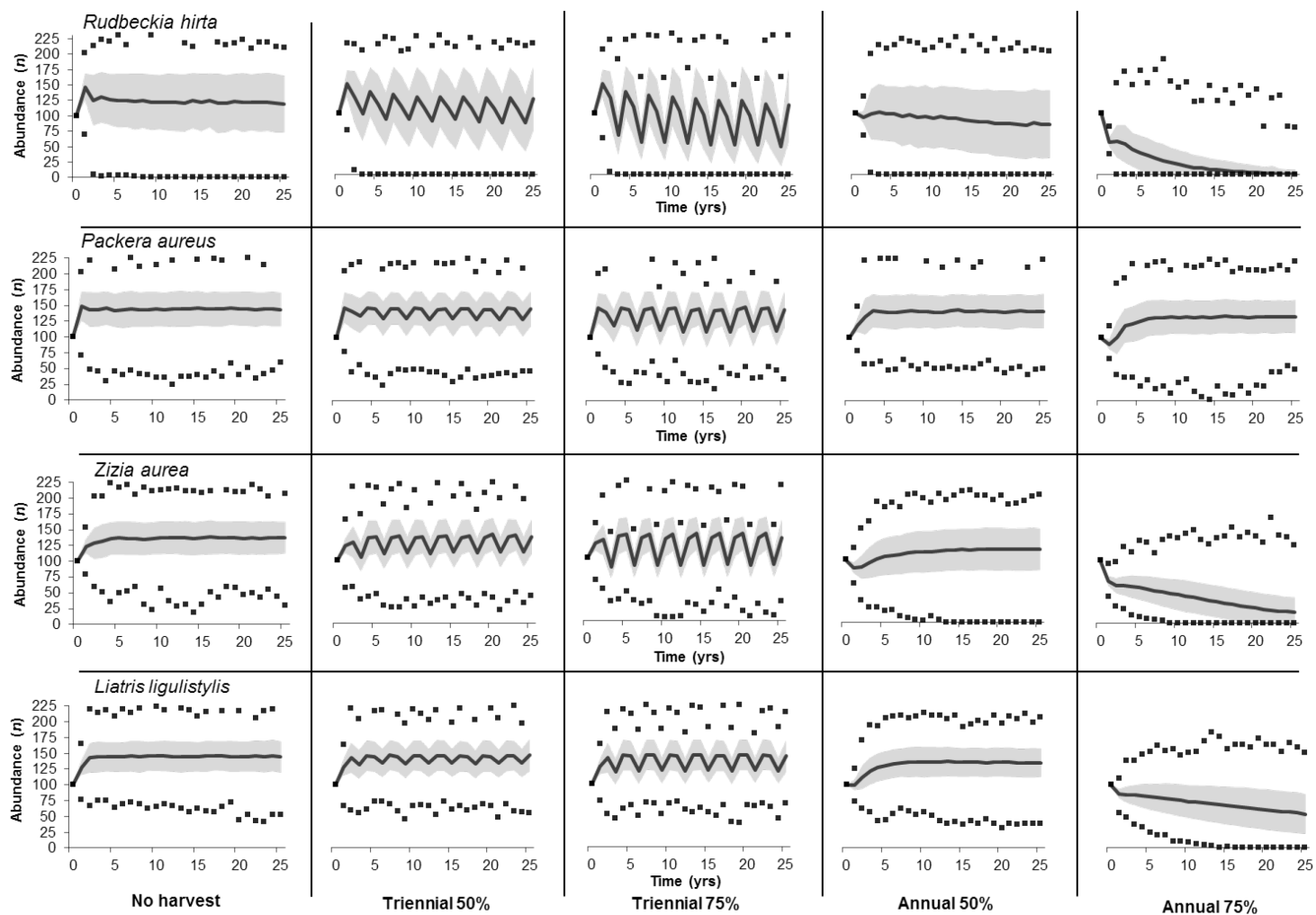
Figure 2.5. Seed harvest scenario output for clonal species (1,000 simulation runs each). Solid lines represent average population abundance, shading represents ± 1 standard deviation, and squares represent maximum and minimum population abundance at each time step.
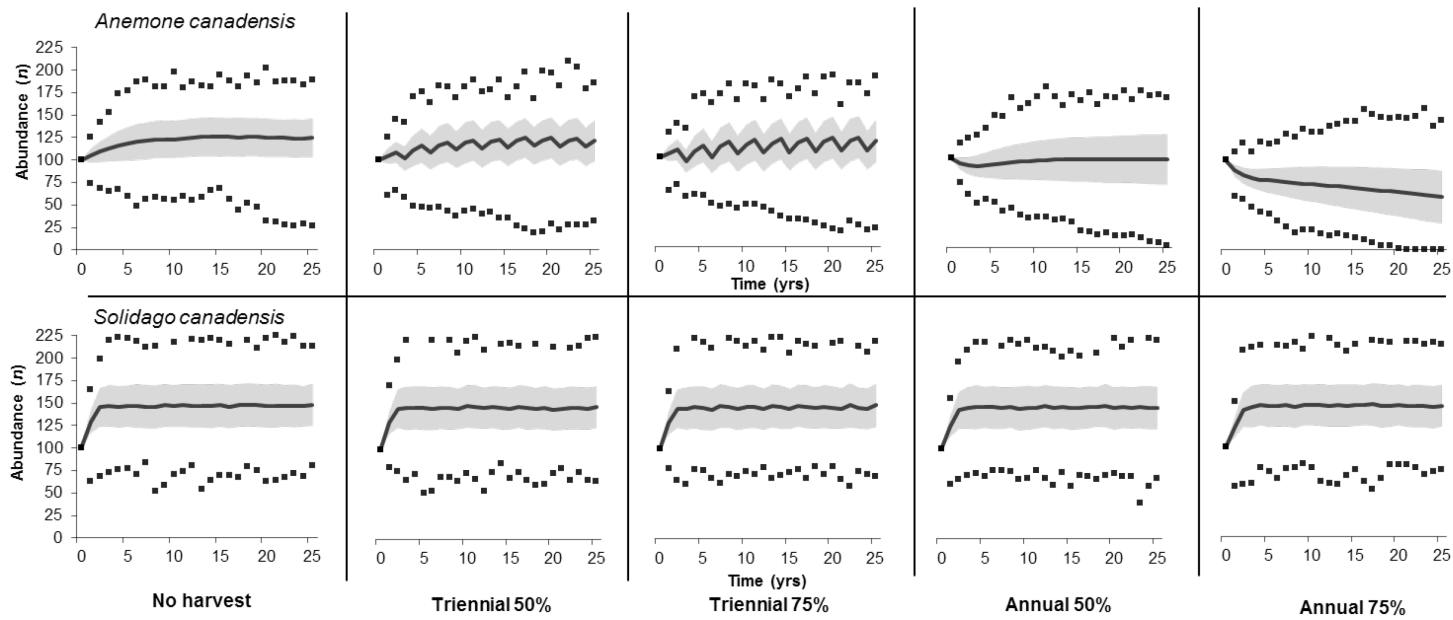
Figure 2.6. Negative change in finite rate of growth (λ) for model species populations under 5 seed harvest scenarios. RH=*Rudbeckia hirta*, PA=*Packera aureus*, ZA= *Zizia aurea*, LL= *Liatris ligulistylis*, AC= *Anemone canadensis*, SC= *Solidago canadensis*. Non-clonal species are denoted by solid shapes while clonal species are denoted by line shapes.
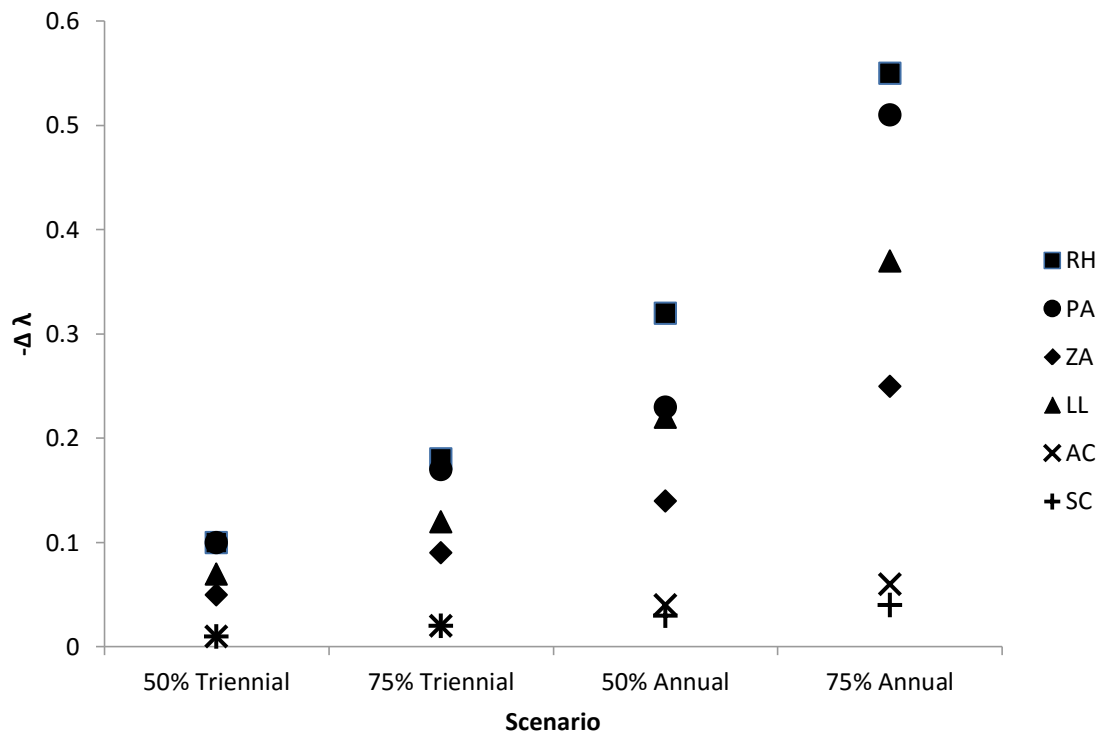
Figure 3.1. Population plot of *Rudbeckia hirta* as seen in 2015. Populations initially consisted of 9 individual plants spaced 30cm apart, and grew or shrank depending on the magnitude of mortality and reproduction. The population pictured consists of 2 flowering individuals and 7 vegetative individuals.

Figure 3.2. Fire management (unburned/annually burned) and seed harvest intensity treatments (unharvested/50%/100% seed removal). Whole-plots are burned (a) using the strip-heading fire technique common in tallgrass prairie management. 100% seed removal is achieved using a sickle blade mower (b) and raking out cut vegetation. Sickle-blade mowers cut vegetation near ground level, allowing cut seed-heads to drop gently without excessive seed scattering. 50% seed removal is conducted with a hand-held brush harvester (c) that allows individual seed-head clusters to be removed with precision.

Figure 3.3. Mean *R. hirta* seed production (± 95% confidence interval) in burned (a) and unburned (b) populations that were unharvested, harvested at low intensity and harvested at high intensity.

Figure 3.4. Mean litter cover of $1m^2$ population plots ($\pm$ 95% confidence interval) in burned (a) and unburned (b) populations that were unharvested, harvested at low intensity and harvested at high intensity.

Figure 3.5. Mean *R. hirta* seedling recruitment rates (± 95% confidence interval) in burned (a) and unburned (b) populations that were unharvested, harvested at low inte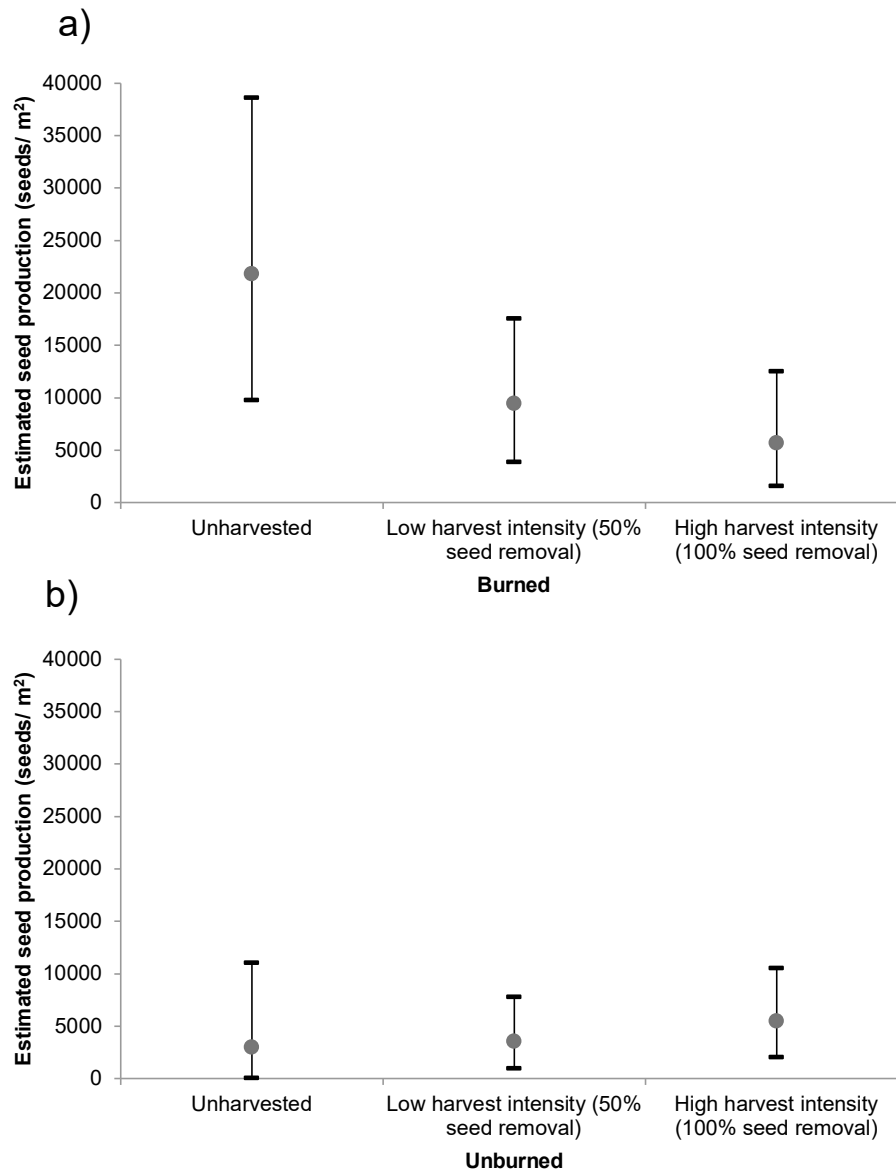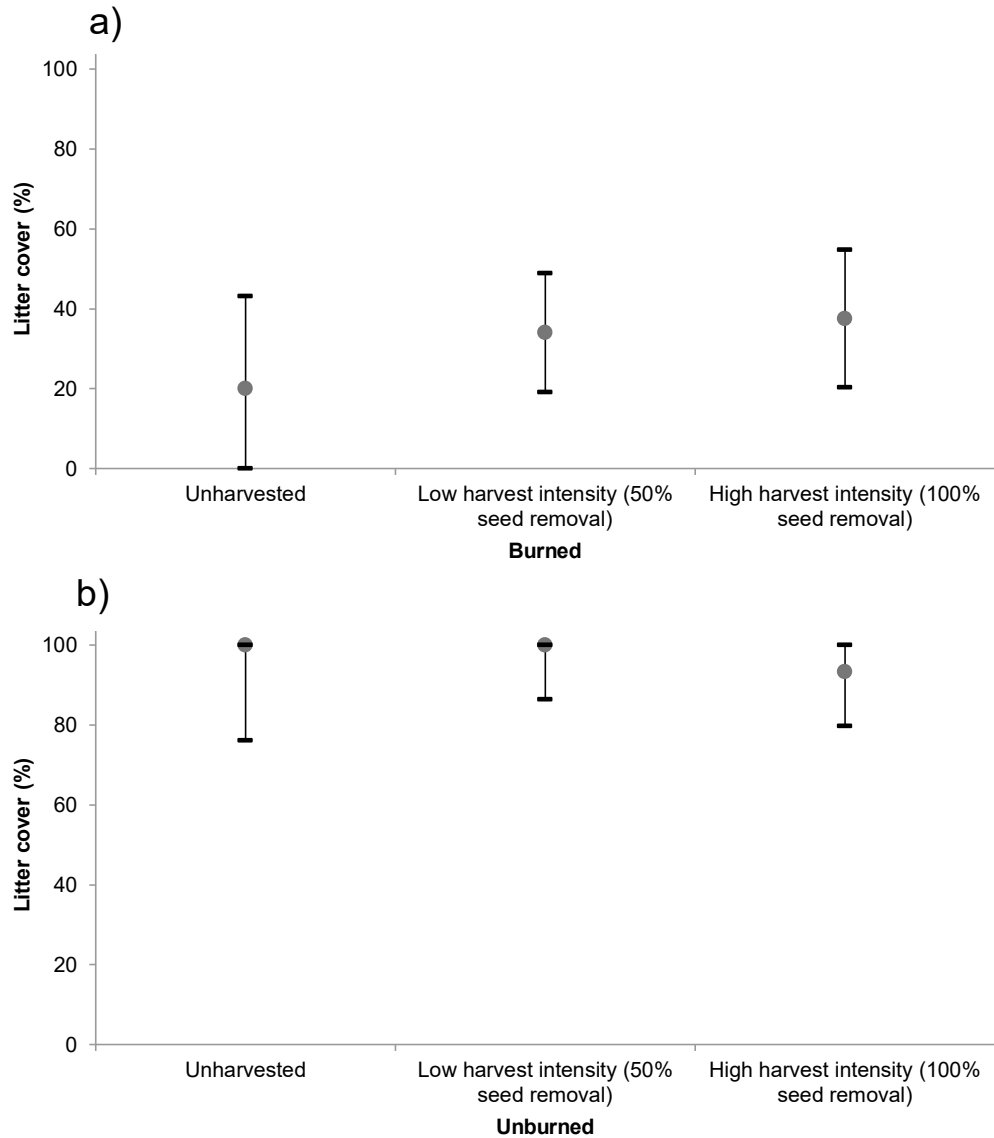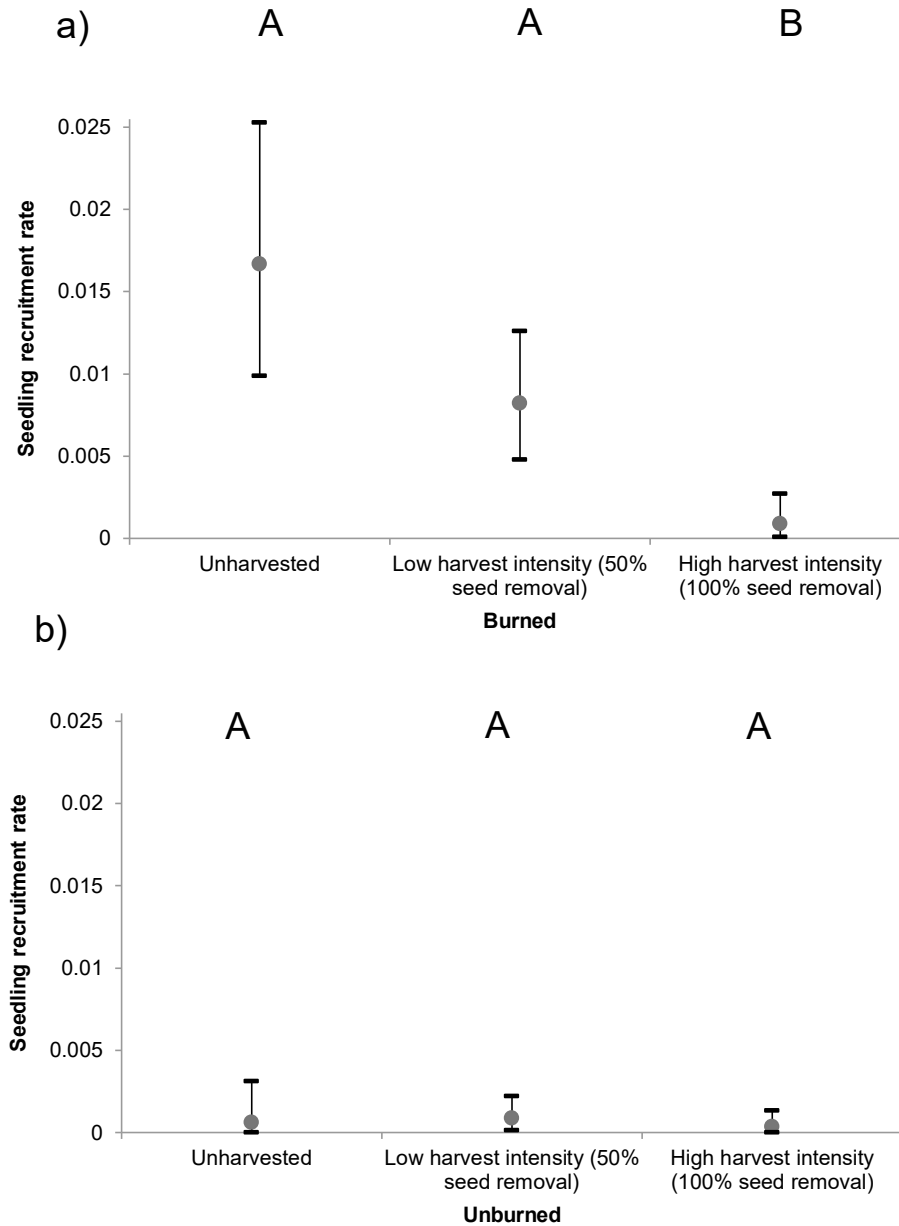nsity and harvested at high intensity. Significant differences in recruitment between harvest intensity treatments (Tukey HSD tests, $p < 0.05$) are distinguished by different letters (i.e. "A" is different from "B").

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