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Fragmentation Effects On Fitness In Five Common Prairie Species

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FRAGMENTATION EFFECTS ON FITNESS IN FIVE COMMON PRAIRIE SPECIES

BY

Lydia Miramontes Loyd

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

Master of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

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Abstract

Midwest tallgrass prairies have suffered extensive habitat loss and as a result persist as isolated and highly fragmented remnants. In such small, isolated remnants, genetic drift and inbreeding depression can lead to a loss of genetic variation over time. Reduced genetic variation is often associated with reduced levels of growth, survival, and reproduction as well as increased susceptibility to stress. This study examined fitness traits of five common prairie species to determine whether plants in small fragmented remnants had reduced fitness as compared to those in a larger remnant. Five prairie species were chosen for this study based on their common occurrence across tallgrass prairies: lead plant, *Amorpha canescens*; purple prairie clover, *Dalea purpurea*; rattlesnake master, *Eryngium yuccifolium*; wild quinine, *Parthenium integrifolium*; and Virginia mountain mint, *Pycnanthemum virginianum*. I collected seeds and reproductive tissue from isolated prairie remnants and compared seed weight, total reproductive output and germination rates. Seedlings were also grown in a greenhouse for 30 days to determine seedling vigor including seedling biomass, height or leaf length, and leaf area. In five out of six fitness measures, at least one plant species from a small fragment had reduced fitness when compared to the larger fragment. *Dalea purpurea, P. integrifolium*, and *P. virginianum*, all had lower percentage of seeds germinate in the smaller fragments as compared to the large. *Eryngium yuccifolium* seedlings had shorter leaf lengths and less total leaf area in one of the smaller prairie remnants as compared to the larger remnant. These results suggest that even common species have suffered the effects associated with habitat fragmentation potentially driven by loss of genetic variation. This has implications for land and resource managers as they must take steps to insure the health of common as well as rare species in small isolated remnants around the world.

Dedication

I would like to dedicate this thesis to my husband Mike Loyd
for his willingness, patience, and prodding as we moved from state to state so I could
pursue my education and career.

I would also like to dedicate this to my grandparents who bestowed on me a genetic
predisposition towards a fascination with plants
and my parents who instilled in me a curiosity and love of nature.

Acknowledgements

The author began her Master of Science in Biological Sciences at Eastern Illinois University in 2003 under the guidance of Dr. Scott Meiners. It has taken the author several years to complete this document and many individuals have given support. Several of these people were instrumental in helping the author with her research project. She wishes to acknowledge these individuals: Kathryn Yurkonis, Mercedes Miramontes, and Mike Loyd for assistance pollinating milkweed plants as part of the first research project; Bill Stewart and Elise Tulloss for assistance collecting seed; and students of Scott Meiners fall 2004 General Botany class for help weighing and counting seed.

The author's research project was funded by grants from the Illinois Native Plant Society, Prairie Biotic Research, the Illinois Department of Natural Resources Wildlife Preservation #04-008W, and the Lewis Hanford Tiffany Botany Graduate Research Fund. The author appreciates the support of her committee members, Dr. Anne Fritz and Dr. Eric Bollinger. Above all the author would like to thank her master's thesis advisor, Dr. Scott Meiners for taking her in as a graduate student, having a backup plan when her first research project failed, guiding her through her final project, and prodding her along till the end.

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Introduction

Prior to European settlement, central North America was a vast grassland that stretched from Indiana west to Nebraska, south to Texas, and north to the Canadian provinces of Alberta and Saskatchewan (Transeau, 1935; Sampson and Knopf, 1994). This grassland encompassed approximately 162 million hectares before conversion to European agriculture (Mather, 1972; Sampson and Knopf, 1994). As early as 1830, homesteading in Indiana and Illinois began to alter the extent of the grasslands (Sampson and Knopf, 1994). Because tallgrass prairie areas were so productive for agriculture, they were almost eliminated in North America after European settlement, resulting in substantial changes in community composition and ecosystem processes (Camill et al., 2004). Most of this conversion to agriculture has occurred within the last 100 years (Cully et al., 2003). Today, less than 1% of the original prairie remains throughout much of the Great Plains, and in many states less than 0.1% of the original prairie remains (Sampson and Knopf, 1994).

A major consequence of this extensive habitat loss has been a significant increase in the degree of fragmentation of the remaining grasslands. When continuous habitats with large plant populations become fragmented, what remains are smaller separate remnants with smaller, isolated populations. Fragments also have more edge per unit of habitat and so populations within these fragments have a greater chance of experiencing edge effects. Changes in soil moisture, humidity, light, temperature, and wind all commonly vary along edges, all of which may affect resources available for reproduction (Saunders et al., 1991; Noss and Cooperrider, 1994; Camargo and Kapos, 1995; Gehlhausen et al., 2000). This fragmentation and loss of habitat is not unique to prairie ecosystems. As a consequence of human activities, many ecosystems throughout the world have become small, fragmented, and isolated. Habitat loss and fragmentation due to human activities have been identified as the most important factors contributing to the decline and loss of species worldwide (Noss and Cooperrider, 1994; Primack, 2008).

There is a high risk of local extinction associated with small, isolated populations (Heschel and Paige, 1995; Groom, 1998; Paschke, 2002) because population size is important in maintaining genetic diversity (Heschel and Paige, 1995; Frankham, 1996; Luijten et al., 2000; Montgomery et al., 2000; Paschke et al., 2002). Larger populations contain more individuals and typically greater genetic diversity (Frankham, 1996). There is often a correlation between fitness and genetic diversity; larger, more genetically diverse populations have greater reproductive success and are better able to adapt to changes in the environment (Heschel and Paige, 1995; Frankham, 1996; Reed and Frankham, 2003; Primack, 2008). Reproductive success and future adaptability are reduced in smaller populations due to genetic drift and inbreeding depression (Heschel and Paige, 1995; Frankham, 1996; Paschke, 2002; Reed and Frankham, 2003). Genetic drift, a process by which allele frequencies change from one population to the next due to chance, can lead to a loss of potentially beneficial alleles. In natural populations, mechanisms may exist to prevent inbreeding but when population size is small and no other mates are available, these mechanisms fail to prevent inbreeding (Primack, 2008). Mating with close relatives may result in inbreeding depression, a condition characterized by higher mortality of offspring, fewer offspring, or offspring that are weak, sterile or have low mating success (Willi et al., 2006). Because variation is lost due to genetic drift and inbreeding depression, these fragmented populations are then further vulnerable to local extinction due to demographic stochasticity: demographic fluctuations due to random variation in birth and death rates, and environmental stochasticity: environmental fluctuations such as variation in predation, competition, disease, food supply, or natural disasters such as fires, storms or drought (Heschel and Paige, 1995; Newman and Tallmon, 2001; Paschke, 2002; Primack, 2008).

Genetic variation is a primary mechanism in maintaining high levels of fitness within populations (Reed and Frankham, 2003). Genetic drift and inbreeding depression reduce the heterozygosity of a population (Luijten et al., 2000; Paschke et al., 2002; Primack, 2002). This in turn typically reduces various fitness related traits (Fischer and Matthies, 1998; Fischer et al., 2000; Paschke et al., 2002; Van Rossum et al., 2002; Reed and Frankham, 2003). Reduced fitness may result in reduced levels of growth, survival, and reproduction (Primack, 2002; Reed and Frankham, 2003) as well as increased susceptibility to stress (Heschel and Paige, 1995). Sufficiently high genetic diversity is therefore important in maintaining healthy, viable, and sustainable plant populations that are able to adapt to a changing environment.

The fitness of plants in small fragments may be further reduced by the interruption of critical biotic interactions, *i.e.* Allee effects (Groom, 1998). Changes in the fragmented animal/insect community may affect pollination (Fritz and Nilsson, 1994; Cunningham, 2000; Murren, 2002). As the distance increases between plant populations, the distance between individual plants increases. Pollinating insects may not visit widely scattered plants resulting in insufficient transfer of pollen and a decline in seed production (Primack, 2008). A decline in the population of potential mates might affect the genetic quality of pollinators and thereby reduce the production of seed (Menges, 1991). Small isolated fragments may be less attractive to pollinating insects which may also result in pollen limitation and lower seed set (Fritz and Nilsson, 1994; Agren, 1996; Murren, 2002). In self-incompatible or dioecious species, the pool of potential mates may be even more reduced.

Numerous studies have documented the effects of population size, fragmentation, and inbreeding depression on rare or endemic plant species (Heschel and Paige, 1995; Fischer and Matthies, 1998; Morgan, 1999; Eisto et al., 2000; Luijten et al, 2000; Paschke, et al., 2002). But relatively few have investigated the effects of habitat fragmentation on the fitness of common plant species (Hooftman et al., 2003). This may be an important line of inquiry given that common species make up the matrix of most communities and are the primary components of restoration projects. Hooftman et al. (2003) found that plants of a common calcareous fen species in Sweden, *Carex davalliana*, that originated from small, isolated habitat islands yielded less biomass, fewer tillers and fewer flowering tillers than plants from larger habitats. Populations of common species face the same challenges of habitat isolation and fragmentation as rare species. This study highlights the need for more research on common species in fragmented and isolated populations, especially considering the fragmented nature of many native communities.

This study investigated the effects of habitat fragmentation and isolation on common plant species, which are usually not of conservation concern. Fitness traits of five common prairie species were examined to determine whether common species suffer the effects of habitat fragmentation and isolation. The objectives of this study were to determine whether plants in small isolated remnants have reduced fitness as compared to species in a large remnant. If this is the case, then land and resource managers must take steps to insure the health of common, as well as rare species in small isolated populations.

Methods

Study Species

Five prairie species were chosen for this study based on their common occurrence across tallgrass prairies and their presence in at least two of the four prairie sites used in this study. Lead plant, *Amorpha canescens* Pursh. (Fabaceae) is a perennial sub-shrub of prairies and sandy dry areas (Gleason and Cronquist, 1991; Mohlenbrock, 2002). *Amorpha canescens* is a strongly rhizomatous woody legume (up to 1.2 m tall), that flowers from June through August (Hickman and Hartnett, 2002). Purple prairie clover, *Dalea purpurea* Vent. (Fabaceae) is a self-compatible perennial herb found in prairies and dry, sandy, or gravelly soil in open woods or along roadsides (Gleason and Cronquist, 1991; Yatskievych, 2000; Molano-Flores, 2004). It flowers from June through September (Yatskievych, 2000; Mohlenbrock, 2002). Rattlesnake master, *Eryngium yuccifolium* Michx. (Apiaceae) is a self-incompatible perennial herb commonly found in prairies, barrens, and woodland openings (Gleason and Cronquist, 1991; Yatskievych, 2000; Mohlenbrock, 2002; Molano-Flores, 2004). It is reported from virtually every state from the 98th meridian to western Connecticut (Trent, 1938). Rattlesnake master flowers from June through September (Yatskievych, 2000; Mohlenbrock, 2002). Wild quinine, *Parthenium integrifolium* L. (Asteraceae), is a self-incompatible perennial herb (Molano-Flores, 2004; Gleason and Cronquist, 1991). Wild quinine flowers from June to October and is often found in prairies, dry woods, and glades (Yatskievych, 2000; Mohlenbrock, 2002; Molano-Flores, 2004). Mountain mint, *Pycnanthemum virginianum* Dur. & B. D. Jacks (Lamiaceae) is a perennial herb found in marshes, calcareous fens, and prairies (Molano-Flores, 2004; Gleason and Cronquist, 1991). It flowers from July through September (Yatskievych, 2000; Mohlenbrock, 2002). The breeding system for *Pycnanthemum virginianum* is not known.

Study Sites

Four tall grass prairie remnants, one large and three small, were chosen for this study (Figure 1). Three of the sites studied, Loda Cemetery Prairie, Prospect Cemetery Prairie and Highway 45 Railroad Prairie, were remnants of a once continuous black soil prairie that was fragmented by conversion to agricultural land approximately 150 years ago. These three areas are within the Grand Prairie Section of the Grand Prairie Natural Division of Illinois bordering the Southern Uplands Section of the Wabash Border Natural Division (Schwegman et al., 1973), an area of very fertile, poorly drained soils formerly dominated by tall grass prairie.

Capel Hill Prairie (CHP), the fourth study area, is a 0.5 hectare, natural prairie opening in an oak hickory forest and completely isolated from any other prairie patches. It has been chronically isolated from other grasslands for several thousand years (Long Heikens and Robertson, 1994). Hill prairies in this area occur on south-facing slopes within a largely forested matrix and would predate European colonization of the area.

Loda Cemetery Prairie (LCP) is a 1.5 hectare remnant of the original mesic black soil prairie in the Grand Prairie Section of the Grand Prairie Natural Division (Heidorn, 2009a; Stanton and Meissen, 2009a). This preserve was protected by The Nature Conservancy has been managed by them since 1983 (Heidorn, 2009a). It is currently isolated within an agricultural (row crop) matrix with the nearest prairie remnant, 9 kilometers away.

Prospect Cemetery Prairie (PCP) is a 3.5 hectare fragment of mesic black soil prairie of the Grand Prairie Section of the Grand Prairie Natural Division (Heidorn, 2009b; Stanton and Meissen, 2009c). The cemetery was created in 1859 and burials continued until 1914 and possibly later (Hiedorn, 2009b). The cemetery prairie is owned by the Paxton Township Cemetery Association and was dedicated as a nature preserve in October, 1976. The nearest prairie is 3 kilometers from this fragment.

The Highway 45 Railroad Prairie is a narrow stretch of remnant prairie along a railroad right of way owned by the Canadian National Railroad (Stanton and Meissen, 2009b). While this site is narrow, only 30 meters wide, it persists in a nearly continuous band for almost 11 kilometers throughout the study area, encompassing 270 hectares and was considered the large prairie remnant in this study. An area roughly equivalent to the small prairie remnants, 2 hectares, was used in this study. The sample area was 3 kilometers from Prospect and 9 kilometers from Loda Cemetery Prairie (Figure 1). Pollen movement in temperate plant communities is typically very spatially limited (Handel, 1983; Levin, 1988; Pleasants, 1991; Godt and Hamrick, 1993; Schmitt, 1980). Levin (1988) found that gene flow becomes extremely rare at distances beyond 1,000 meters. However, the isolation effects of fragmentation may be mitigated by increased gene flow (White et al., 2002). Given that the small isolated fragments were greater than 3 kilometers apart, the small prairie fragments may be effectively isolated. The Highway

45 Railroad Prairie was the only sizeable prairie within the study area, precluding replication of the unfragmented condition.

Population Estimates

Population estimates were obtained by counting flowering individuals (Table 1). Rhizomatous and clonal plants were assumed to be individual genets if they were found at least 1 meter from the next individual plant. In each population, the number of flowering plants was counted at the peak of the flowering season in the year (2005) following the collection of plant material. Population size was measured by direct counting in the smaller remnants (Capel Hill Prairie and HW 45 railroad prairie) and estimated in the larger remnants from subsamples.

Fitness Measures

Maternal Plant Performance

Plant materials were collected during late summer/early fall 2004 at one large and three small prairie remnants in central Illinois. Beginning in August, 2004, 20 to 30 maternal plants of each study species were located within each remnant site. The number of main stems, branches, and flowers/fruits per branch was recorded for each individual. Fruits with dehiscing capsules were bagged at that time to prevent seed loss. Total reproductive biomass, consisting of all plant material above the base of the inflorescence, was collected as fruits matured. Biomass was air dried over a period of four weeks in paper bags, cleaned to remove stems and leaves, and weighed. Samples were not oven dried to retain seed viability. Total reproductive biomass was only measured for two of the five species.

From each maternal plant, 25 seeds were weighed to determine average seed weight. Seeds of *Pycnanthemum virginianum* were not weighed due to their small size. Seeds were then treated to induce germination. Seeds from *Eryngium yuccifolium, Parthenium integrifolium,* and *Pycnanthemum virginianum* were stratified in moist perlite for 60 days at 5° C. Seeds from *Amorpha canescens* and *Dalea purpurea* were scarified with 200-grit sandpaper to break the seed coat. Seeds were then stratified in moist perlite for 14 days at 5° C. After stratification, seeds were placed on wet filter paper in petri dishes and exposed to a day/night regime of 14 hours of light at 25° C and 10 hours of dark at 23° C in a growth chamber.

Seedling Fitness Measures

To further assess fitness among the remnants, the growth and performance of seedlings were assessed in the greenhouse. Two seedlings per maternal plant were taken from the germination trials and transplanted into cell packs filled with Promix© (Premiere Horticulture, Dorval, Quebec, Canada). After 45 days, one randomly chosen seedling per maternal plant was removed from the potting mix, rinsed in a water bath, and immediately weighed. Length of longest leaf was measured for *Eryngium* and *Parthenium* (basal rosette species) while total above ground plant height was measured for *Amorpha*, *Dalea*, and *Pycnanthemum* (all upright plants). Total leaf area in cm^2 was also measured for each seedling using a leaf area meter (LI-1600; LiCor, Inc. Lincoln, NE.)

Data Analysis

Variation in seed mass, total reproductive biomass, percent germination, seedling biomass, seedling height/leaf length and seedling leaf area among remnants was analyzed for each species using one-way ANOVA (SPSS Version 12.5 SPSS Inc, Chicago, IL). Percent germination was arcsine transformed; seedling biomass and seedling leaf area were log transformed to conform to normality assumptions of ANOVA. Variation among individual species between remnants was analyzed with a Tukey post hoc test.

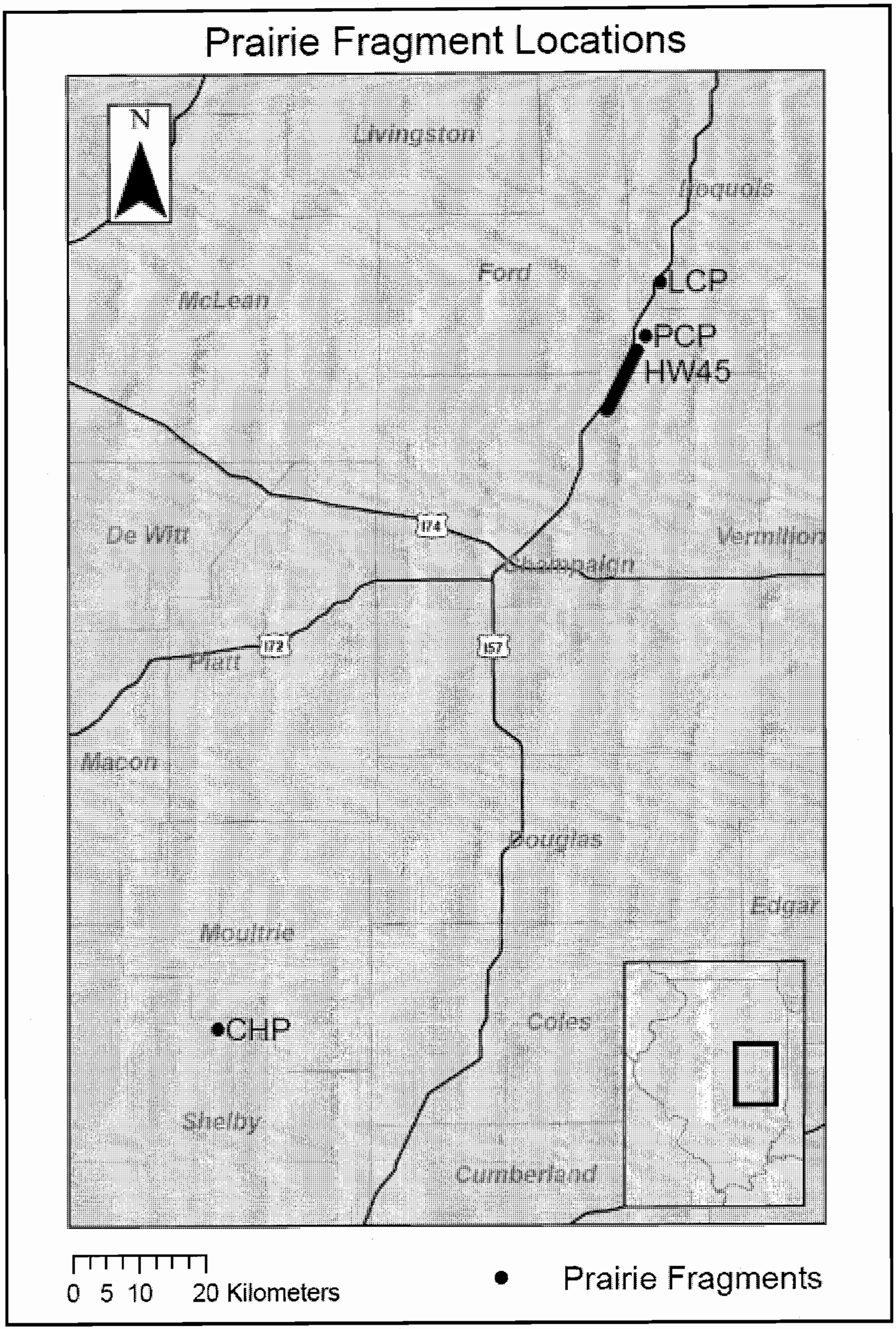

Figure 1. Map of prairie remnant locations.

Table 1. Fragment size and population estimates for five common prairie species.

Fragment	**HW 45**	**Prospect**	**Loda**	**Capel**
Hectares	2.0	3.5	1.5	0.5
Species				
Amorpha canescens	170	-	528	-
Dalea purpurea	125	1695	-	1293
Eryngium yuccifolium	86	6492	912	-
Parthenium integrifolium	191	1185	1912	-
Pycnanthemum virginianum	64	1000	1144	-

Results

(Population locations will be abbreviated as follows throughout the results, Capel Hill Prairie: CHP; Loda Cemetery Prairie: LCP; Prospect Cemetery Prairie: PCP; HW45 Railroad Prairie: HW45.)

Maternal Plant Performance

Seed Mass

Seed mass significantly varied among remnants in two of the four species in which it was measured (Figure 2). *Dalea purpurea* seeds were significantly smaller in the CHP and PCP remnants as compared to the larger HW45 remnant ($F_{2,57}$= 8.784; $P<0.001$ R^2= 0.242). *Parthenium integrifolium* seed mass was also significantly reduced in the smaller LCP remnant as compared to the PCP and HW45 remnant ($F_{2,58}$= 6.159; P=0.004; R^2= 0.178).

Total Reproductive Biomass

Total reproductive biomass was significantly less in the small remnants in the two species in which it was measured (Figure 3). Mean total reproductive biomass for *Dalea purpurea* was significantly different in all three remnants in which it was measured ($F_{2,55}$ = 75.127; $P<0.001$; R^2= 0.732), with the CHP remnant dramatically smaller than the other two remnants. *Pycnanthemum virginianum* also had significantly smaller total reproductive biomass ($F_{2,67}$ = 9.172; $P < 0.001$; $R^2 = 0.22$) in the PCP remnant as compared to the LCP and larger HW45 remnant. Total reproductive biomass for *Pycnanthemum virginianum* in the PCP remnant was nearly 40% lower than the other remnants.

Percent Germination

Percent germination significantly varied among remnants in three of the five species (Figure 4). *Dalea purpurea* had significantly lower percent germination in the small PCP remnant versus the HW45 remnant ($F_{2,54}$= 5.552; P=0.006; R_2= 0.171). Percent germination (arcsine transformed) for the PCP remnant was on average 0.88 versus 1.00 in the LCP remnant and 1.18 in the HW45 population. Percent germination was also reduced in one of the smaller prairie remnants of *Parthenium integrifolium* ($F_{2,55}$= 5.274; P=0.008; R_2= 0.161). *Pycnanthemum virginianum* had a significantly lower percent germination in the HW45 population compared to the two smaller remnants ($F_{2,56}$= 10.641; P<0.001; R_2= 0.275).

Seedling Fitness Measures

Seedling Biomass

After data transformation, none of the species had significant variation in seedling biomass among remnants (Figure 5).

Seedling Height and Leaf Length

Seedling height varied significantly among remnants in two of the five species (Figure 6). *Eryngium yuccifolium* had significantly lower seedling height in the small LCP remnant as compared to the larger HW45 remnant ($F_{2,37}$= 10.088; P<0.001; R^2= 0.353). Seedlings in the LCP remnant were 40% smaller than those from the larger HW45 remnant.

Pycnanthemum virginianum also had seedlings with significantly lower height in the small remnants. Seedlings in the smaller PCP remnant were 30% shorter than seedlings from the HW45 remnant ($F_{2,43}$= 8.585; P=0.001; R_2= 0.285).

Seedling Leaf Area

Seedling leaf area varied across remnants in only one of the species: *Eryngium yuccifolium*. Rattlesnake master had significantly smaller seedling leaf area in the small LCP remnant ($F_{2,37}$= 5.471; P=0.008; R_2= 0.228). Seedling leaf area in the LCP remnant was 40% less than the larger HW45 remnant.

Binomial Test

The comparison between HW45 and the small sites was significant 10 times out of 24 . In nine of these, at least one of the small remnants had significantly reduced performance relative to the HW45 site. The probability of obtaining this number of significant reductions in fitness in small remnants was sufficiently small (alpha 0.05; binomial probability <0.001) that the results were not an effect of multiple statistical tests.

Table 2. ANOVA of the influence of source remnant on various fitness measures in five common prairie species.

Species	Source	d.f.	F.	P	R2
Amorpha canescens	Seed mass	1,37	0.457	0.503	0.012
Dalea purpurea	Seed mass	**2,57**	**8.784**	**0.000**	**0.242**
Eryngium yuccifolium	Seed mass	2,56	1.353	0.267	0.046
Parthenium integrifolium	Seed mass	**2,58**	**6.159**	**0.004**	**0.178**
Pycnanthemum virginianum	Seed mass	-	-	-	-
Amorpha canescens	Reproductive biomass	-	-	-	-
Dalea purpurea	Reproductive biomass	**2,55**	**75.127**	**0.000**	**0.732**
Eryngium yuccifolium	Reproductive biomass	-	-	-	-
Parthenium integrifolium	Reproductive biomass	-	-	-	-
Pycnanthemum virginianum	Reproductive biomass	**2,65**	**8.104**	**0.001**	**0.200**
Amorpha canescens	Percent germination	1,25	3.524	0.072	0.124
Dalea purpurea	Percent germination	**2,54**	**5.552**	**0.006**	**0.171**
Eryngium yuccifolium	Percent germination	2,58	1.203	0.308	0.040
Parthenium integrifolium	Percent germination	**2,55**	**5.274**	**0.008**	**0.161**
Pycnanthemum virginianum	Percent germination	**2,56**	**10.641**	**0.000**	**0.275**
Amorpha canescens	Seedling biomass	1,37	1.678	0.203	0.043
Dalea purpurea	Seedling biomass	2,44	1.558	0.222	0.066
Eryngium yuccifolium	Seedling biomass	2,37	2.879	0.069	0.135
Parthenium integrifolium	Seedling biomass	2,24	2.498	0.103	0.172
Pycnanthemum virginianum	Seedling biomass	2,43	2.635	0.083	0.109
Amorpha canescens	Seedling height	1,37	0.002	0.883	0.001
Dalea purpurea	Seedling height	2,44	2.973	0.062	0.119
Eryngium yuccifolium	Longest leaf	**2,37**	**10.088**	**0.000**	**0.353**
Parthenium integrifolium	Longest leaf	2,23	0.978	0.391	0.078
Pycnanthemum virginianum	Seedling height	**2,43**	**8.585**	**0.001**	**0.285**
Amorpha canescens	Seedling leaf area	1,35	0.211	0.649	0.006
Dalea purpurea	Seedling leaf area	2,44	1.451	0.245	0.062
Eryngium yuccifolium	Seedling leaf area	**2,37**	**5.471**	**0.001**	**0.228**
Parthenium integrifolium	Seedling leaf area	2,24	1.776	0.191	0.129
Pycnanthemum virginianum	Seedling leaf area	2,43	0.522	0.597	0.024

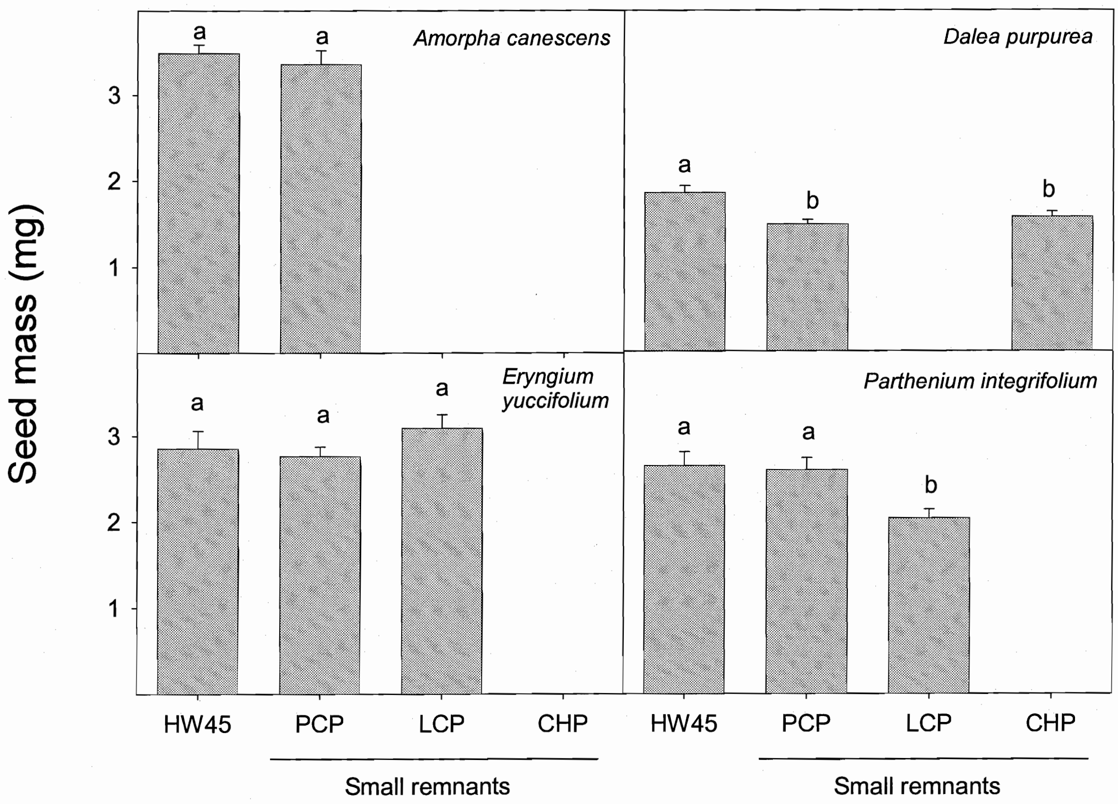

Figure 2. Effect of remnant size on mean seed mass in four common prairie species. Prospect, Capel and Loda are small remnants (< 3.5 ha) while HW 45 is a large railroad remnant. Data plotted are means +/- 1 SE. Means sharing the same letter are not significantly different (P>0.05) based on a Tukey post-hoc test.

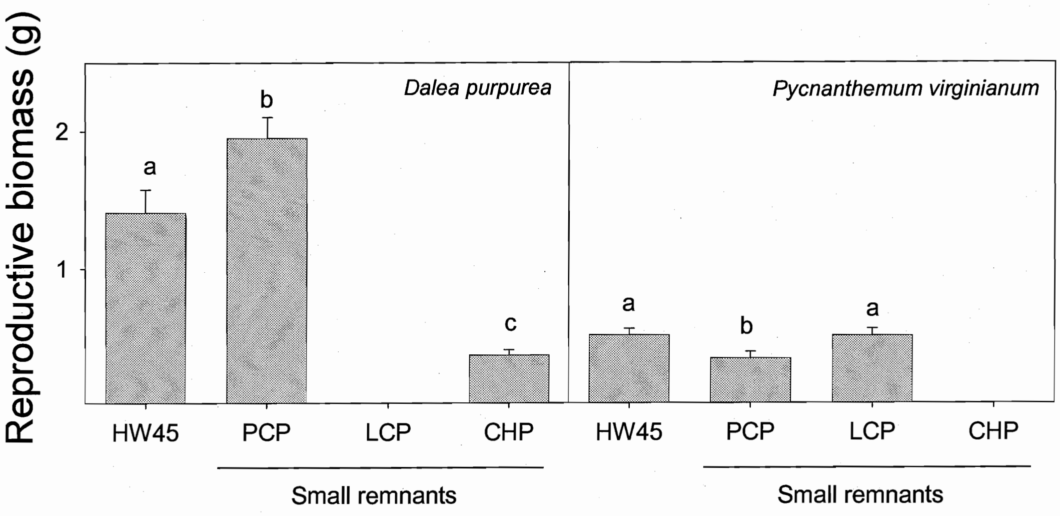

Figure 3. Effect of remnant size on mean reproductive biomass in four common prairie species. Data plotted are means +/- 1 SE. Means sharing the same letter are not significantly different (P>0.05) based on a Tukey post-hoc test.

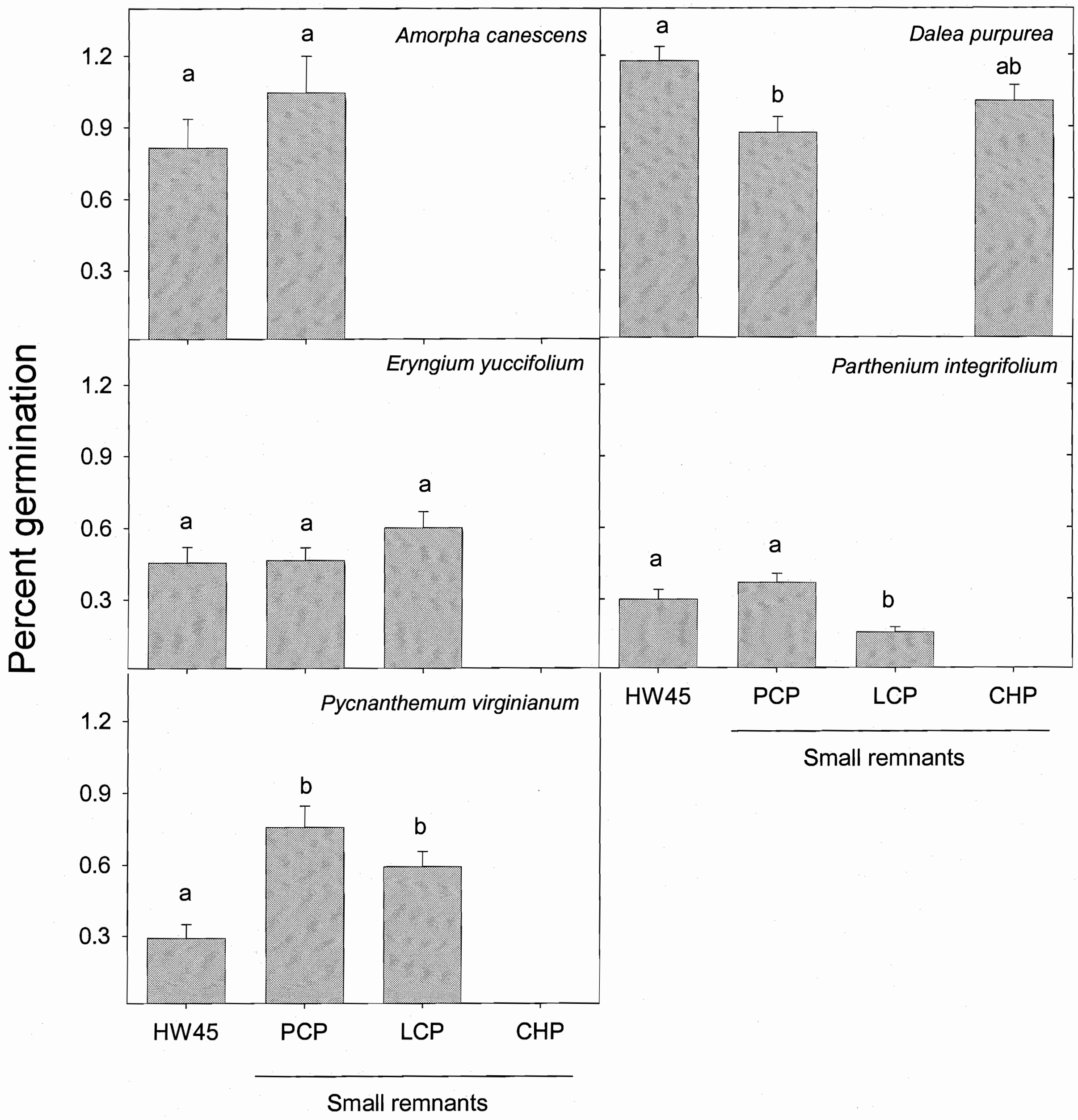

Figure 4. Effect of remnant size on percent germination (arcsine transformed) in four common prairie species. Data plotted are means +/- 1 SE. Means sharing the same letter are not significantly different (P>0.05) based on a Tukey post-hoc test. Note: scales vary among species.

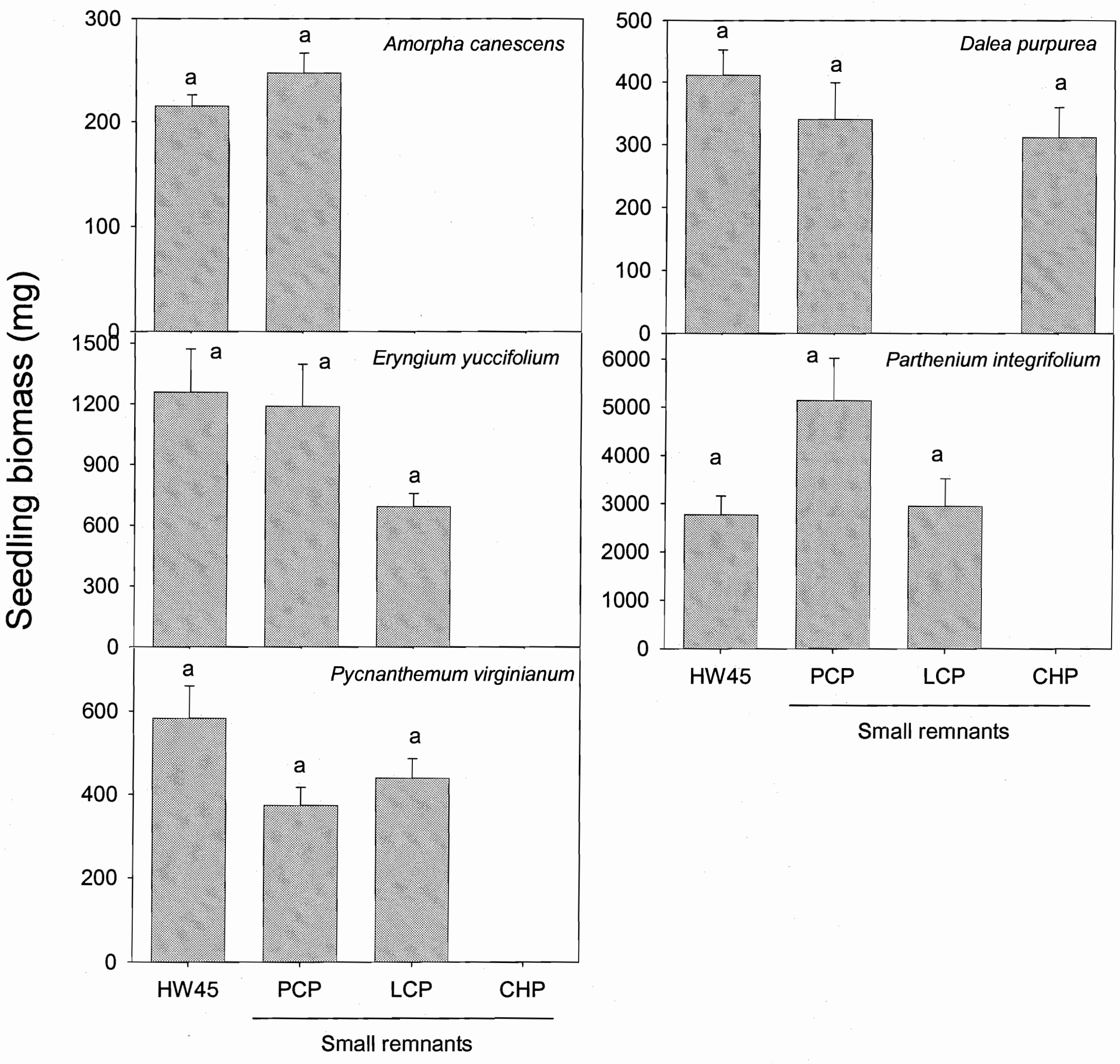

Figure 5. Effect of remnant size on mean seedling biomass in four common prairie species. Data plotted are means +/- 1 SE. Means sharing the same letter are not significantly different (P>0.05) based on a Tukey post-hoc test. Note: scales vary among species.

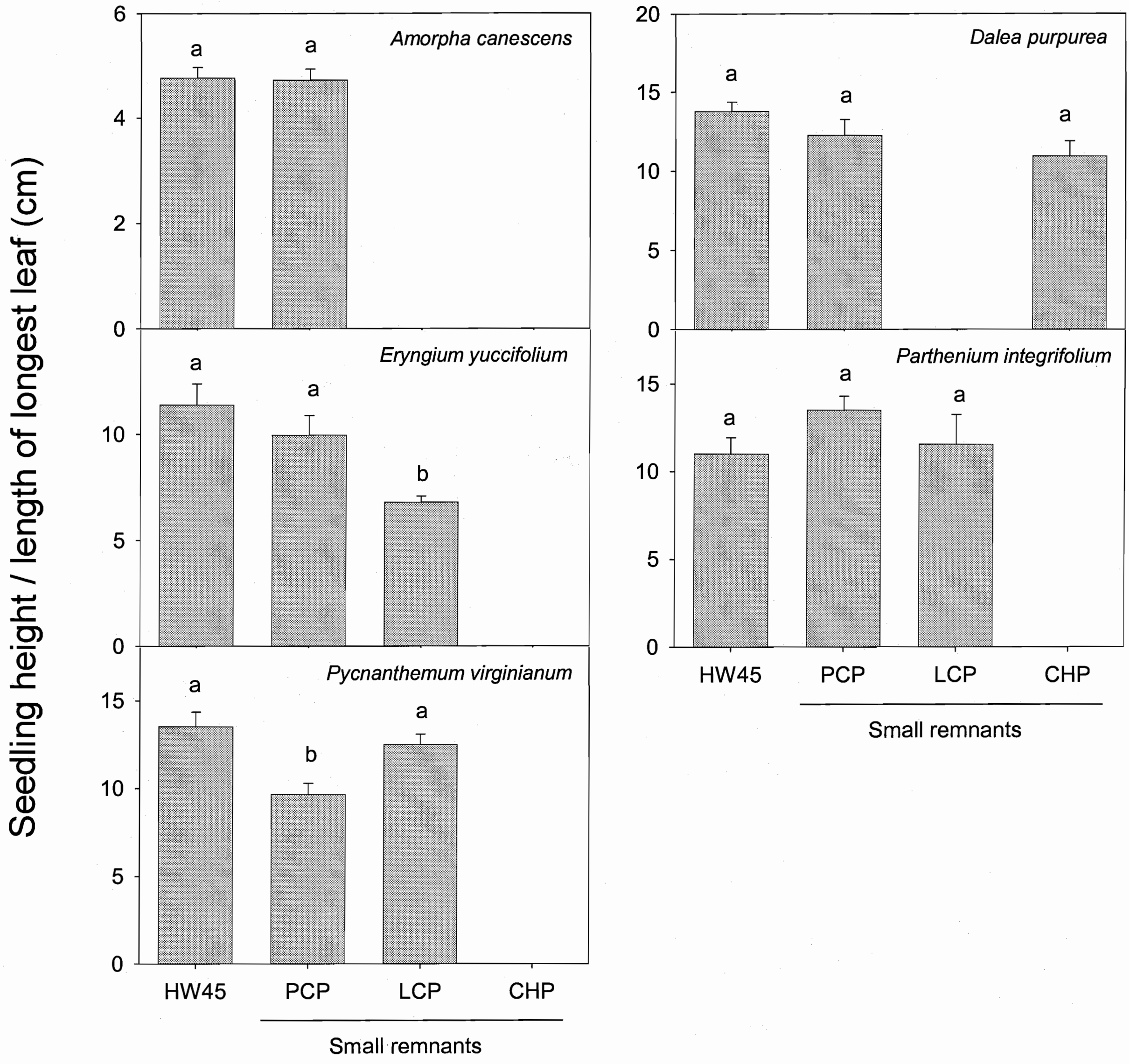

Figure 6. Effect of remnant size on seedling height and leaf length in four common prairie species. Data plotted are means +/- 1 SE. Means sharing the same letter are not significantly different (P>0.05) based on a Tukey post-hoc test. Note: scales vary among species.

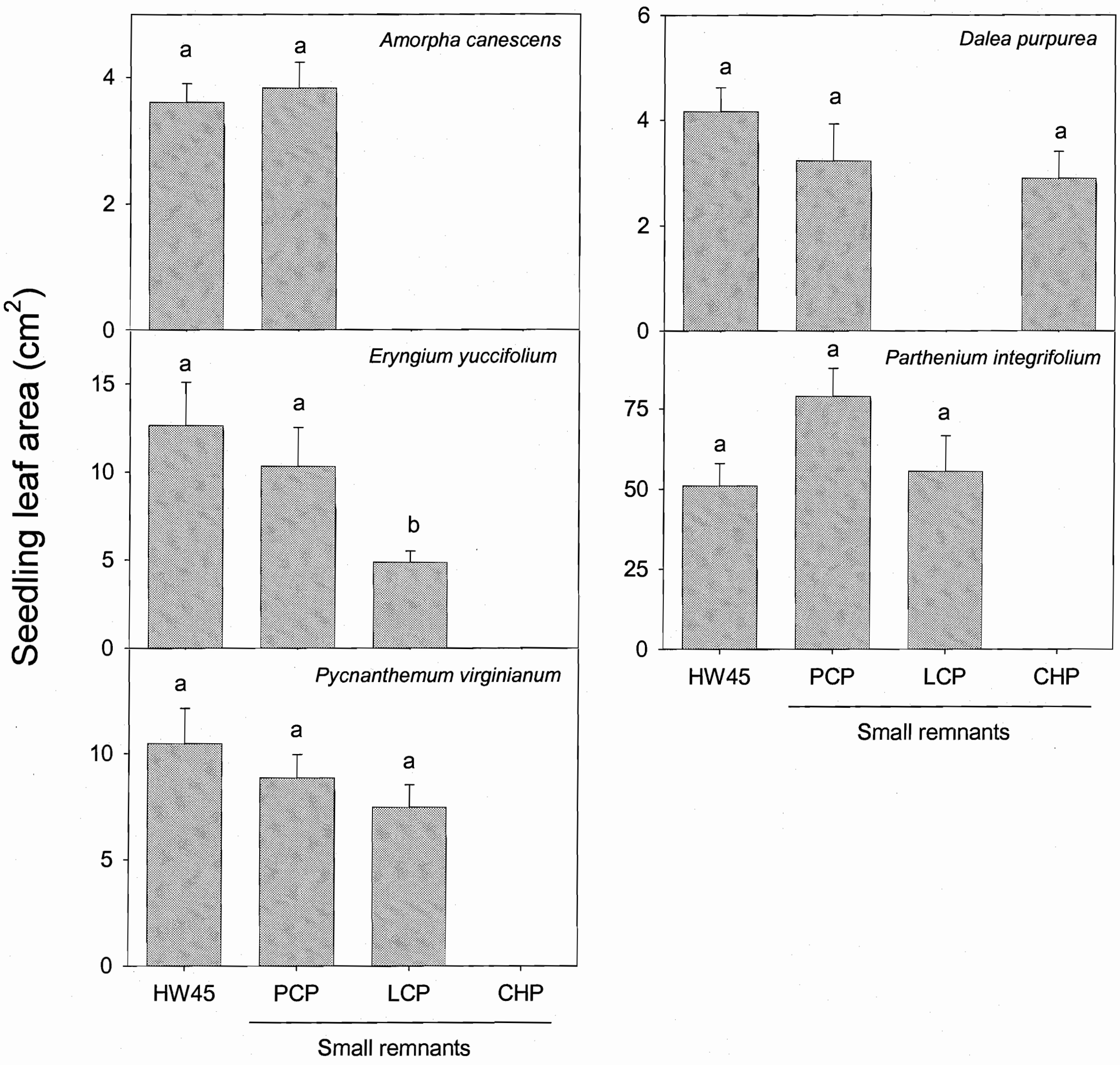

Figure 7. Effect of remnant size on seedling leaf area (cm^2) in five common prairie species. Data plotted are means +/- 1 SE. Means sharing the same letter are not significantly different (P>0.05) based on a Tukey post-hoc test. Note: scales vary among species.

Discussion

In five common prairie species, five out of six fitness measures had at least one plant species from a small remnant that had reduced fitness relative to the large remnant. Overall, species within the large remnant had greater fitness than those within smaller remnants, though not all small remnants showed reduced fitness. These results suggest that the common species in this experiment have suffered the effects associated with habitat fragmentation potentially driven by loss of genetic variation due to inbreeding depression and genetic drift. This conclusion is supported by similar investigations on rare species (Heschel and Paige, 1995; Fischer and Matthies, 1998; Morgan, 1999; Eisto et al, 2000; Luijten et al, 2000; Paschke, et al, 2002) as well as common species (Hooftman et al., 2003; Lienert and Fischer, 2003).

Three measures of maternal fitness were investigated in this study: seed mass, total reproductive biomass, and percent germination. Maternal effects of inbreeding can be defined as the fitness consequences on the offspring associated with the level of inbreeding of the maternal plant (Roach and Wulff, 1987; del Castillo, 1998). Maternal effects can have an important influence on plant fitness (Roach and Wulff, 1987). The maternal genotype may affect the quality of the offspring and may, therefore, affect the performance of the offspring. del Castillo (1998) found that inbreeding significantly reduced the individual contribution of seeds to the next generation. In my study, in two of the four species in which seed mass was measured, seed mass was significantly reduced in at least one of the smaller habitat fragments as compared to the larger fragment. *Dalea purpurea* and *Parthenium integrifolium* both had smaller seeds in at least one of the remnant populations as compared to the larger HW45 remnant (Figure 2).

Seed mass is important because larger seed mass increases the amount of resources available for the seedling. Large and well-resourced seeds have been shown to provide an advantage when seedlings are competing with neighbors, growing under shaded conditions, buried under litter, or during periods of drought (Stanton, 1984; Parrish and Bazzaz, 1985; Eriksson, 1999).

Total reproductive biomass, measured as the total weight of the inflorescence and seeds, reflects the amount of energy invested in reproduction. A greater number of flowers and branches within the inflorescence provide greater opportunities for seed production. In this study, total reproductive biomass was measured for *Dalea purpurea* and *Pycnanthemum virginianum*. In *D. purpurea*, the small hill prairie remnant had 75% less reproductive biomass than either of the other two remnants (Figure 2). However, this variation could reflect resource availability rather than population fitness. Hill prairies in Illinois are generally drier sites on south and west facing slopes. Stewart (2006) analyzed soils at the CHP site and found that overall soil fertility was reduced at the hill prairie site as compared to the three black soil prairie remnants (HW45, PCP, LCP). It is possible that resource limitations or environmental stress contributed to reduced reproductive allocation for *D. purpurea* in that site. A subsequent common garden study using the same source remnants and species found that total above ground biomass varied significantly among remnants though it was a smaller remnant that produced greater biomass (Stewart, 2006). Although the common garden experiment measured total above ground biomass in *D. purpurea*, these results suggest that the reduced levels of reproductive biomass seen in this study may be a result of environmental resource limitations rather than genotypic differences. *Pycnanthemum virginianum* had a 35%

reduction in reproductive biomass in PCP compared to the HW45 remnant. As *P. virginianum* was not collected from the hill prairie, environmental variation seems less likely to have generated its variation in reproductive biomass across remnants.

The percentage of seeds that germinated was significantly lower in small remnants in three of the five species (Figure 3). *Dalea purpurea* and *Parthenium integrifolium* both had reduced levels of germination in one of the small remnants when compared to the larger remnant. Seed mass was also reduced in both *D. purpurea* and *P. integrifolium*, which could suggest resource limitation for germination. Other studies have found varying results. Helenurm (1998) and Hooftman et al. (2003) found a correlation between germination rate and population size suggesting a genotypic effect of population size on seed quality. In contrast, Eisto et al. (2000) found that seed germination ability was independent of population size. Morgan (1998) found a similar lack of differences in seed germinability between populations of *Rutidosis leptorrhynchoides*, an endangered Australian grassland perennial.

Seed mass, total reproductive biomass and percent germination were reduced in the small remnants as compared to the larger remnant. These results suggest negative consequences of habitat fragmentation and isolation on the fitness of plants in small remnants, but some of these results may also be due to environmental effects. Interestingly, measures of maternal fitness were not consistent among sites within a species. For example, *D. purpurea* had the largest reproductive biomass at PCP, but the highest germination and seed mass at HW45.

Based on the results of the three seedling fitness measures, two of the species in small remnants had reduced fitness when compared to the larger remnant. Seedling mass did not differ significantly among any of the remnants but seedling height/leaf length and seedling leaf area were reduced in the smaller Loda Cemetery remnant for *Eryngium yuccifolium*. Seedlings were also 40% shorter and seedling leaf area was 60% less in the smaller remnant as compared the larger remnant. *Pycnanthemum virginianum* had 30% shorter seedlings in one of the small remnants compared to the larger remnant. The smaller seedling size and the tendency for some species to have smaller seeds, reduced reproductive biomass, and reduced germination rate in smaller remnants is in line with reports of reduced plant performance in small compared with large remnants (Menges, 1991; Heschel and Paige, 1995; Frankham, 1996; Fischer and Matthies, 1998; Paschke, 2002; Reed and Frankham, 2003). Taken together, the reductions in both maternal plant performance and seedling fitness across several measures and species indicate that these common prairie species are potentially suffering the consequences of habitat fragmentation as is often seen in rare plant species.

A follow up study by Stewart (2006) used a common garden experiment to test fitness of established plants in a restoration setting. Stewart documented significant variation in growth among remnants, but the HW45 remnant did not consistently have the greatest performance. The lack of consistent remnant effects could be attributed to the use of seedlings in the garden experiment rather than seeds. The reduced fitness seen in my experiment during germination and the initial stages of growth would have been partially eliminated through the use of seedlings in the common garden experiment.

Population size estimates for the species in this study varied from 500 to almost 6,500 plants in the smaller remnants. These large population sizes may be expected given that each species in this study was chosen because it was a common species within the remnants. The potential for clonal reproduction in some species and unknown genetic structure of these populations makes it possible that a large number of individuals in these populations were closely related. Given the apparently large population sizes, it is even more important that reduced fitness was observed.

The large remnant used in this study, a 11 kilometer long narrow band of prairie, may have been suffering from edge effects. Given the narrow width of the fragment, it would likely all be considered edge with no interior habitat. Edge effects consist of changes in soil moisture, humidity, light, temperature, and wind (Noss and Cooperrider, 1994; Camargo and Kapos, 1995; Gehlhausen et al., 2000). In the case of the HW45 remnant, which was bordered by a railroad and a county highway, the site may have been exposed to increased pollution levels as well. Reproductive effort could also be wasted along the edge where habitat is unsuitable for seeds which disperse into the surrounding matrix. It is possible that the large remnant in this study was not large enough and was not a suitable comparison to truly assess the impacts of fragmentation. Percent germination was reduced in *Pycnanthemum virginianum* in the larger HW45 remnant as compared to the smaller remnants. This could suggest that there may also be negative fitness consequences associated with the large remnant in this study.

The long and narrow nature of the HW45 prairie may have restricted gene flow and effectively fragmented the local populations. Unfortunately, no large tracts of tallgrass prairie exist within the study area and the approximately 270 hectare linear remnant was the only large prairie remnant available for comparison. Given the potential for the large remnant in this study to be affected by fragmentation, these results may be conservative estimates of the impacts of fragmentation.

Conclusions

Four out of five common prairie species in this study exhibited at least two measure of reduced fitness in a small remnant compared to a large remnant. The use of multiple measures of both maternal and seedling fitness allowed the detection of differences as fitness measures did not all respond similarly. The reduction in fitness in small remnants is surprising given that these species existed in populations of 500 to 6,500 plants. These results suggest that while these species are in no immediate danger of decline, there is reason for concern for the long term health of their populations. Since common species comprise the matrix of the community in most cases, a change in population viability for those species may affect the community as a whole. Land and resource managers must take steps to insure the health of common, as well as rare species in small isolated populations. This may include steps such as the introduction of new genetic material (seeds, plants, pollen) into the small populations. Neither threatened not common species appear to be immune to the effects of fragmentation. As habitat fragmentation continues around the world, this supports the need for additional research into common species in other habitats and the development of long-term monitoring programs for common as well as rare species.

References

Agren, J. 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. Ecology, 77(6):1779-1790.

Camargo, J.L.C. and V. Kapos. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. Journal of Tropical Ecology, 11(2):205-221.

Camill, P., M. McKone, S. Sturges, W. Severud, E. Ellis, J. Limmer, C. Martin, R. Navratil, A. Purdie, B. Sandel, S. Talukder, and A. Trout. 2004. Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. Ecological Applications, 14(6):1680-1694.

Cully, A.C., J.F. Cully, and R.D. Hiebert. 2003. Invasion of exotic plant species in tallgrass prairie fragments. Conservation Biology, 17(4):990.

Cunningham, S. A. 2000. Depressed pollination in habitat fragments causes low fruit set. Proceedings of the Royal Society of London, Series B, 267:1149-1152.

del Castillo, R.F. 1998. Fitness consequences of maternal and nonmaternal components of inbreeding in the gynodioecious *Phacelia dubia*. Evolution, 52(1):44-60.

Eisto, A.K., M. Kuitunen, A. Lammi, V. Saari, J. Suhonen, S. Syrjasuo, and P.M. Tikka. 2000. Population persistence and offspring fitness in the rare bellflower *Campanula pericardia* in relation to population size and habitat quality. Conservation Biology 14(5):1413-1421.

Eriksson, E. 1999. Seed size variation and its effect on germination and seedling performance in the clonal herb *Convallaria majalis*. Acta Oecologica, 20:61-66.

Fischer, M. and D. Matthies. 1998. Effects of population size on performance in the rare plant *Gentianella germanica*. Journal of Ecology, 86:195-204.

Fischer, M., M. van Kleunen, and B. Schmid. 2000. Genetic allee effects on performance, plasticity and developmental stability in a clonal plant. Ecology Letters, 3:530-539.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife Conservation Biology, 10:1500-1508.

Fritz, A. and L.A. Nillson. 1994. How pollinator-mediated mating varies with population size in plants. Oecologia, 100(4):451-462.

Gehlhausen, S.M., M.W. Schwartz and C.K. Augspurger. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. Plant Ecology, 147(1):21-35.

Gleason, H.A. and A. Cronquist. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. 2nd Ed. New York Botanical Garden, Bronx NY. 986 p.

Godt, M.J. and J.L. Hamrick. 1993. Patterns and levels of pollen-mediated gene flow in *Lathyrus latifolius*. Evolution, 7(1): 98-110.

Groom, M.J. 1998. Allee effects limit population viability of an annual plant. The American Naturalist, 151(6):487-496.

Handel, S.N. 1983. Contrasting gene flow patterns and genetic subdivision in adjacent populations of *Cucumis sativus* (Cucurbitaceae). Evolution, 37(4): 760 – 771.

Heidorn, R. 2009a. Loda Cemetery Prairie Nature Preserve, Iroquois County. Online posting. 2009 Jan. Illinois Department of Natural Resources. 2009 Oct 26. http://dnr.state.il.us/INPC/09/Area%203/Iroquois/LodaCemPrairie/LodaCemetery

Prairie.htm

Heidorn, R. 2009b. Prospect Cemetery Prairie Nature Preserve, Ford County. Online posting. 2009 Jan. Illinois Department of Natural Resources. 2009 Oct 26. http://dnr.state.il.us/INPC/09/Area%206/ Ford/ ProspectCemPrairie/ProspectCemPrairie.htm

Helenurm, K. 19998. Outplanting and differential success in *Lupinus guadalupensis*. Conservation Biology, 12(1):118-127.

Heschel, M.S. and K.N. Paige. 1995. Inbreeding depression, Environmental stress, and population size variation in scarlet gilia (*Ipomopsis aggregata*). Conservation Biology, 9(1):126-133.

Hickman, K.R. and D.C. Hartnett. 2002. Effects of grazing intensity on growth, reproduction, and abundance of three palatable forbs in Kansas tallgrass prairie. Plant Ecology, 159(1): 23-33.

Hooftman, D.A.P., M. van Kleunen, and M. Diemer. 2003. Effects of Habitat Fragmentation on the Fitness of Two Common Wetland Species, *Carex davalliana* and *Succisa pratensis*. Oecologia, 134(3):350-359.

Levin, D.A. 1988. Consequences of stochastic elements in plant migration. The American Naturalist, 132(5): 643-651.

Lienert, J. and M.A. Fischer. 2003. Habitat Fragmentation Affects the Common Wetland Specialist *Primula farinosa* in North- East Switzerland Fischer. Journal of Ecology, 91(4):587-599.

Long Heikens, A. and P. A. Robertson. 1994. Barrens of the Midwest: a review of the literature. Castanea, 59(3):184-194.

Luijten, S., A. Dierick, J. Gerard, B. Oostermeijer, L.E.L. Raijmann, and H.C.M. Den Nijs. 2000. Population size, genetic variation, and reproductive success in a rapidly declining, self-incompatible perennial (*Arnica montana*) in the Netherlands. Conservation Biology, 14(6):1776-1787.

Mather, E.C. 1972. The American Great Plains. Annals of the Association of American Geographers, 62(2):237-257.

Menges, E.S. 1991. Seed germination percentage increases with population size in a fragmented prairie species. Conservation Biology, 5(2):158-164.

Mohlenbrock, R.H. 2002. Vascular flora of Illinois. Southern Illinois University Press, Carbondale, IL, 500p.

Molano-Flores, B. 2001. Breeding systems of plants used for prairie restorations: a review. Transactions of the Illinois State Academy of Science, 97:95-102.

Montgomery, M.E., L.M. Woodworth, R.K. Nurthen, K.M. Gilligan, D.A. Briscoe, and R. Frankham. 2000. Relationships between population size and loss of genetic diversity: comparisons of experimental results with theoretical predictions. Conservation Genetics, 1:33-43.

Morgan, J.W. 1998. Effects of population size on seed production and germinability in an endangered, fragmented grassland plant. Conservation Biology, 13(2):266-273.

Murren, C.J. 2002. Effects of habitat fragmentation on pollination: pollinators, pollinia viability and reproductive success. Journal of Ecology, 90(1):100-107.

Newman, D. and D.A. Tallmon. 2001. Experimental evidence for beneficial fitness effects of gene flow in recently isolated populations. Conservation Biology, 15(4):1054-1063.

Noss, F.F. and A. Cooperrider. 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Covelo, California. 416 p.

Parrish, J.A.D. and F.A. Bazzaz. Nutrient content of *Abutilon theophrasti* seeds and the competitive ability of the resulting plants. Oecologia, 65(2):247-251.

Paschke, M., C. Abs, and B. Schmid. 2002. Effects of population size and pollen diversity on reproductive success and offspring size in the narrow endemic *Cochlearia bavarica* (Brassicaceae). American Journal of Botany, 89(8):1250-1259.

Pleasants, J.M. 1991. Evidence for short-distance dispersal of pollinia in *Asclepias syriaca* L. Functional Ecology 5: 75 – 82.

Primack, R.B. 2008. A primer of conservation biology. 4th ed. Sinauer Associates, Inc. Sunderland, Massachusetts. 349 p.

Reed, D.H. and R. Frankham. 2003. Correlation between fitness and genetic diversity. Conservation Biology, 17(1):230-237.

Roach, D.A. and R.D. Wulff. 1987. Maternal effects in plants. Annual Review of Ecology and Systematics, 18:209-235.

Samson, F. and F. Knopf. 1994. Prairie conservation in North America. BioScience, 44(6):418-421.

Saunders D.A., Hobbs R.J., Margules C.R. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5(1):18-32.

Schmitt, J. 1980. Pollinator foraging behavior and gene dispersal in *Senecio* (Compositae). Evolution 3(5): 934 – 943.

Schwegman, J.E., G.B. Fell, M.D. Hutchinson, G. Paulson, W.M. Shephard, and J.

White. 1973. Comprehensive plan for the Illinois Nature Preserve system. Part 2. The natural divisions of Illinois. Illinois Nature Preserves Commission, Rockford. 32 p.

Stanton, M.L. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. 1984. Ecology, 65(4): 1105-1112.

Stanton, R. and J. Meissen. 2009a. Loda Cemetery Prairie. Online posting. Grand Prairie Friends. 2009 Oct 26. http://grandprairiefriends.org/stewardsites/loda.html

Stanton, R. and J. Meissen. 2009b. Paxton Railroad Prairie. Online posting. Grand Prairie Friends. 2009 Oct 26. http://grandprairiefriends.org/stewardsites/paxtonrr.html.

Stanton, R. and J. Meissen. 2009c. Prospect Cemetery Prairie. Online posting. Grand Prairie Friends. 2009 Oct 26. http://grandprairiefriends.org/stewardsites/prospect.html

Stewart, W.L. 2006. The effects of remnant seed source size on plant performance in a prairie restoration. MS Thesis (EIU) 41p.

Transeau, E.N. 1935. The prairie peninsula. Ecology, 16(3):423-437.

Trent, J.A. 1938. *Eryngium yuccifolium*: ecological distribution and some morphological irregularities. Transactions of the Kansas Academy of Science, 41(Mar. 31 - Apr. 2, 1938):155-163.

White, G.M., D.H. Boshier, and W. Powell. 2002. Increased pollen flow counteracts fragmentation in a tropical dry forest: an example from *Swietenia humilis* Zuccarini. Proceedings of the National Academy of Sciences, 99(4): 2038 – 2042.

Willi, Y., J. Van Buskirk, and A.A. Hoffmann. 2006. Limits to the adaptive potential of small populations. Annual Review of Ecology, Evolution, and Systematics, 37: 433-458.

Van Rossum, F., G. Echchgadda, I. Szabadi, and L. Triest. 2002. Commoness and long-term survival in fragmented habitats: *Primula elatior* as a study case. Conservation Biology, 16(5):1286-1295.

Yatskievych, Kay. 2000. Field Guide to Indiana Wildflowers. Indiana University Press, Bloomington, Indiana. 357 p.