Trait-Based Filtering of the Regional Species Pool to Guide Understory Plant Reintroductions in Midwestern Oak Savannas, U.S.A.

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Abstract

A common first step during ecological restoration is reestablishing the local species pool through active reintroduction of individual plant species. Unfortunately, the regional species pool is often far too large to be of practical use during restoration. Methods are needed to produce manageable lists of key species for directed reintroduction. We used life history traits to target species from the regional species pool ($n = 900$) for reintroduction to degraded Midwestern oak savanna remnants ($n = 8$) in central Iowa, U.S.A. Beginning with the full regional species pool, we first used a priori filters to remove exotic species, species that live in permanently wet habitats, and species already present at the degraded remnant savannas. Next, we created a set of filters to target species with high priority for reintroduction, based on comparisons between the degraded and regional species pools. By this process, we identified perennial forbs and grasses that may be dispersal limited (ant, passive, or heavy wind-dispersed seeds) and are conservative in habitat requirement or have affinities for high-light environments. By applying these filters, we were able to winnow down the regional species pool to a manageable number of species ($n = 111$) that we recommend for initial reintroduction efforts to the degraded savanna remnants. Furthermore, we specifically targeted members of the regional species pool that could fill under-represented ecological niches at the degraded savanna remnants and discuss potential benefits of adding these species for restoring ecosystem function.

Key words: **dispersal limitation, floristic quality, life history traits, Midwest, oak savanna, reference information, restoration planning, species list, species pool.**

Introduction

One major focus of ecological restoration is the reestablishment of plant communities at degraded sites, guided by the species composition of reference sites (Zobel et al. 1998; Bakker et al. 2000; van Diggelen & Marrs 2003; SER 2004; Ruiz-Jaen & Aide 2005). The first step toward achieving this goal is to reestablish plant species' populations (i.e., repopulate the local species pool, Zobel et al. 1998). For this to be successful, it is important to define the species pool for the ecosystem of interest (i.e., regional species pool; Zobel et al. 1998) and understand differences between this and composition at degraded sites. Targeted reintroductions might then restore degraded species pools more rapidly to the reference composition (SER 2004). Following species establishment, more specific goals might be pursued, such as restoration of species' relative abundances, species interactions, and ecosystem function; however, these later goals may be contingent upon first repopulating the local species pool (van Diggelen & Marrs 2003; SER 2004).

Unfortunately, the regional species pool is often too large to effectively guide initial species reintroductions. Species traits present a potential means for targeting a smaller list of high-priority species for reintroduction. Species traits have helped us to understand processes that are often key components of successful restoration. For example, trait-based analyses have shown that passive and ant-dispersed species have very limited capacity to disperse to restored sites and secondary woods (Singleton et al. 2001; Kirkman et al. 2004) and that ant-dispersed species do not persist well in woodlands that have been grazed by cattle (Mabry 2002). Generalist species (those that are good colonizers and competitors) and species that regenerate vegetatively may outperform other species when introduced to restored sites (Pywell et al. 2003). Furthermore, species traits have been important for understanding how communities response to disturbances (Lavorel et al. 1997) and assemble during restoration (Temperton et al. 2004).

In this paper, we use a set of plant traits to target a list of species for initial reintroduction to degraded Midwestern oak savannas. This ecosystem is a component of the North American forest/prairie transition zone (Anderson 1998) and is ideal for developing such an approach for

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doi: 10.1111/j.1526-100X.2007.00317.x

several reasons. Although historically widespread throughout the Midwest, less than 1% of oak savannas now remain in pristine condition and reference sites are rare (Nuzzo 1986; Asbjornsen et al. 2005). Historic vegetation of upland savannas was comprised of a sparse overstory dominated by the genus *Quercus* and a continuous understory of graminoids and forbs with both prairie and woodland affinities (Anderson 1998). Following European settlement, fire suppression led to woody encroachment and a shift in the understory toward species more typical of closed-canopy forests (Cottam 1949; Curtis, 1959; Anderson 1998). An unknown amount of remnant savanna that is degraded by woody encroachment may have high potential for restoration, which typically involves mechanical removal of encroaching trees followed by prescribed understory fire (Packard 1993). In this paper, we focus on the understory because it contains the majority of this ecosystem's plant biodiversity (Leach & Givnish 1999). It is not clear whether fire and thinning are sufficient for reestablishing this stratum and there is evidence for significant dispersal limitations among understory savanna species (Tilman 1997; Kirkman et al. 2004), raising the possibility that restoring understory diversity will necessitate active reintroduction. Lists of species, which are commonly compiled by conservation agencies and land managers, may be the only source of reference information for rare ecosystems, like Midwestern oak savannas (Bakker et al. 2000).

To assemble a list of species for the regional pool, we use three categories of reference lists that are often commonly available to land managers: (1) a list of species proposed to historically occur in the habitat of interest, based on their suitability for the ecosystem's abiotic conditions (Zobel et al. 1998), (2) a species list from a working restoration effort, and (3) a list of species found at a pristine reference site. In our study, the proposed list included species with habitat requirements that match the mixed-light conditions found in Midwestern oak savannas (Delong & Hooper 1996). The working list was from an ongoing Midwestern oak savanna restoration effort at the University of Wisconsin, Madison, Arboretum (Bader 2001). It represents an experimental approach (Zobel et al. 1998), where the species pool was determined by exhaustively adding propagules of many species to the desired community and recording those that survive. Finally, the list from a pristine reference site came from a privately owned and restored Midwestern oak savanna in southern Iowa (hereafter, Timberhill savanna). This list of species was derived from the classic method of determining the species pool, whereby any species inhabiting predetermined "pristine" sites are included on the list (SER 2004).

Combined, these lists represent the regional pool of species that would likely have been present at historic savannas in the region. Additionally, we obtained a second set of species lists for degraded savannas by inventorying eight degraded remnants. Our aim in this paper is to provide a list of candidate species for reintroduction at the degraded remnants. Our approach is to first compare degraded ($n = 8$) and reference savanna species lists ($n = 3$) to determine important differences in species composition. To resolve differences, we then use species traits as filters to narrow the regional species pool down to a manageable list of target species for reintroduction. Through this approach, we identify species that may fill important, but underfilled ecological niches at the degraded sites (i.e., species with high priority for reintroduction).

Methods

Site Descriptions and Data Collection

As part of a larger research project, eight Midwestern oak savanna remnants in central Iowa, U.S.A., are undergoing restoration to reverse woody encroachment. Six of the eight remnants were located along the southwestern shore of Saylorville Lake, a reservoir of the Des Moines River (lat 41°76′N, long 93°82′W). These white oak (*Quercus alba*) savanna remnants have never been plowed, ranged in size from 2.1 to 3.3 ha, and were located on dry uplands (Asbjornsen et al. 2005). Prior to purchase by the U.S. Army Corps of Engineers in the late 1960s to early 1970s, this area was privately owned and used for livestock pastures. Following acquisition, the cessation of pasturing, and ≥35 years of fire suppression, these remnants experienced heavy woody encroachment by shade tolerant trees such as American elm (*Ulmus american*) and ironwood (*Ostrya virginiana*) (Karnitz & Asbjornsen 2006).

The remaining two remnants were located within the Neal Smith National Wildlife Refuge (lat 41°33′N, long 93°17′W). These bur oak (*Q. macrocarpa*) savanna remnants have never been plowed, ranged in size from 2.0 to 2.5 ha, and were located on moderately moist uplands. Prior to purchase by the U.S. Fish and Wildlife Service in the early to mid-1990s, these sites were privately owned. One of the two remnants was pastured by domestic livestock, whereas the other was historically used as a game preserve and was never pastured (P. Drobney 2004, Neal Smith National Wildlife Refuge, Head Biologist, personal communication). Both sites have experienced heavy woody encroachment by shade tolerant trees species such as American elm (*U. american*) and slippery elm (*U. rubra*).

As part of the larger study, permanently marked 1 × 1–m quadrats were established every 10 m along 100- to 200-m linear sampling transects within each of the eight degraded savanna remnants. In addition, quadrats were established every 10 m along 50-m linear transects, which ran perpendicular to the original transect, every 25 m. The perpendicular transects were established so that a sampling bias did not exist for extreme upland areas of the ridge/ravine topography at the Saylorville Lake sites. All vegetation quadrats ($n = 25$–50 per site) were sampled for plant species *prior to restoration* during May, June, and September 2003 and data were compiled into a species list for each site. We did not consider seed banks because evidence consistently indicates that soil seed bank persistence is poor for sites that have been degraded for longer than a few decades (van Diggelen & Marrs 2003) and for forest/woodland species in general (Schiffman & Johnson 1992; Graae & Sunde 2000).

We obtained the potential savanna species list (Delong & Hooper 1996; $n = 251$) and working species list (Bader 2001; $n = 484$) from their respective publications. The pristine reference site, Timberhill savanna, is located in south-central Iowa, U.S.A. (lat 40°45′N, long 94°00′W). This ~24-ha site ranges from dry uplands to moist bottomlands and has been actively managed as oak savanna for the last 15 years (S. Brown 2005, land owner, personal communication). Restoration has involved mechanical tree removal and prescribed fires; however, offsite seeds have never been intentionally added to this site (S. Brown, personal communication). Timberhill savanna's plant species ($n = 359$) were surveyed during four walk-through inventories by Dr. Gerould Wilhelm, during June and September 2003 and July 2004.

Traits Used to Develop the Restoration List

We used seven traits to winnow the regional species' pool down to a list of species to target for reintroduction: (1) status as exotic or native, (2) wetland indicator status, (3) life-form, (4) seed dispersal mode, (5) seed mass, (6) affinity for intact native habitat (coefficient of conservatism), and (7) light/shade affinity (habitat light coefficient). Although we recognize that there are many additional life history traits, we choose these for their pertinence to savanna ecology and restoration and because we were not able to obtain complete datasets for other traits.

Native/exotic status is an important trait for our reintroduction list because ecological restoration focuses on promoting native species (SER 2004). Wetland indicator status was important to consider because savannas range from moist lowlands to dry uplands (Curtis 1959). Species characteristic of the wettest sites in lowland savannas would likely not survive introduction and, thus, not be appropriate for the upland savannas considered in this study. Life-form is an easily measured "soft" trait that can serve as a proxy for more difficult to measure functional characteristics such as response to fire and primary productivity (Lavorel & Garnier 2002). In savannas, fire has been shown to favor graminoids and prairie forbs (Tester 1996; Kirkman et al. 2004). At the same time, the shade cast by trees in savannas is sufficient to suppress dominant prairie grasses, promoting forb species richness (Leach & Givnish 1999). Thus, life-form is related to resource partitioning in savannas and is important to consider in our analysis because this might account for maintenance of biodiversity (Leach & Givnish 1999; Meisel et al. 2002). We considered seed mass and dispersal mechanism to understand which species might require active reintroduction and which might passively recolonize our sites during restoration (Pausas & Lavorel 2003). Predicting dispersal capacity is generally based on morphological characters (Willson 1993). Evidence is accumulating that propagule mass and number are also key components of dispersal distance, with a trade-off occurring between many small, therefore dispersible, seeds versus few heavier seeds (Baker 1972; Eriksson 1995; Rees 1995; Henery & Westoby 2001; Mabry 2004). Coefficient of conservatism is a measure of species' affinity for intact native sites (Swink & Wilhelm 1994). In our study, this metric provides insight into whether woody encroachment has changed floristic quality as well as composition. This is an important consideration given the evidence that habitat specialists are particularly vulnerable to disturbance (Drayton & Primack 1996; Rooney et al. 2004) and perform poorly in some restorations (Pywell et al. 2003). However, although woody encroachment can result in replacement of savanna understory species with a woodland flora (Cottam 1949; Curtis 1959), it is unknown whether this might alter species quality. For example, it is possible that woody encroachment might result in replacement of a high- (or low-) quality savanna flora with equally high- (or low-) quality woodland species. As described above, understory light environment is an important gradient maintaining diversity in Midwestern oak savannas (Leach & Givnish 1999; Meisel et al. 2002), which becomes significantly shadier with woody encroachment (Cottam 1949), making species affinities for sunny and shady microhabitats important for us to consider.

We obtained species' native/exotic status, life-form, light/shade affinity, and dispersal mode from Great Plains Flora Association (1986) or Gleason and Cronquist (1991) if a species was not present in the former. Dispersal mode was in some cases supplemented by examining specimens in the Ada Haydon Herbarium at Iowa State University. Seed mass data (seeds/g) were obtained from the Kew Royal Botanical Gardens online database (http://www.rbgkew.org.uk/, accessed 8 January 2007) and catalogue of the Prairie Moon Nursery, a native seed supplier located in Winona, MN, U.S.A. We obtained wetland indicator status from the NRCS plants database (http://www.plants.usda.gov, accessed 8 January 2007). Coefficients of conservatism were available electronically for Iowa (http://www.public.iastate.edu/~7Eherbarium/coeffici.html, accessed 8 January 2007) and Wisconsin (http://www.botany.wisc.edu/wisflora/, accessed 8 January 2007).

Species were classified as exotic if they were not present in the state of Iowa prior to settlement by Europeans. Wetland indicator categories range from −5 (permanent wetland obligate) to +5 (xeric upland obligate). Life-form categories were annual/biennial forbs, perennial forbs, annual grasses, perennial grasses, sedges, ferns, herbaceous vines, woody vines, shrubs, and trees. To understand species' dispersal capacities, we considered seed mass (seeds/g) and classified species into dispersal modes using the following categories and criteria (Flinn & Vellend 2005): *Wind*-dispersed seeds either had feathery protrusions, such as a pappus, or were $\leq$0.5 mm in size and light enough to be carried by wind without dispersal structures. Seeds dispersed *externally* on the coats of vertebrate animals had barb-like protrusions. Seeds that are ingested and dispersed *internally* by vertebrate animals had fleshy fruits. *Cached* seeds were those intentionally distributed and buried by small mammals (van der Linden & Farrar 1993). *Ant*-dispersed seeds had elaiosomes, lipid-rich appendages that attract ants. All other seeds were classified as having *passive* dispersal, meaning that no special mechanism for dispersing seeds was evident. Coefficients of conservatism are commonly used by land managers in North America (e.g., Swink & Wilhelm 1994; Francis 2000; Mushet et al. 2002) and are assigned to all species in a region by local botanists, who rank species by their affinity for intact native habitat on a scale of 0–10 (Swink & Wilhelm 1994). The most conservative species can survive only in areas where ecological processes remain intact and are assigned a value of 10. The most generalist species can persist in any habitat and receive a value of 0. Use of coefficients has been objectively evaluated as ecologically meaningful indicators of floristic quality (Francis et al. 2000; Lopez & Fennessy 2002; Mushet et al. 2002; Cohen et al. 2004). To classify species for their affinity for light along the continuum from sunny to shaded habitats, we created the "habitat light coefficient" by coding each species habitat description from published flora on a scale from 1 (least understory light, e.g., "moist forest") to 10 (most understory light; e.g., "prairie"; Appendix 1). Because most species had multiple habitats listed, we used the mean value for each species in our analyses.

Data Analysis

We used a two-step process to select, from the regional species pool, a manageable number of species with high priority for reintroduction to the degraded remnants: (1) a priori filters and (2) filters based on comparison of the degraded and reference species lists.

According to our a priori filters, species were removed from the regional species pool if they were (1) already present at the degraded sites, (2) exotic, or (3) wetland obligates (wetland indicator −5). Wetland obligates were defined as species with wetland indicator status −5. Species with values −4 through 5 are found outside of wetlands (http://www.plants.usda.gov, accessed 8 January 2007), occur at the degraded remnants (Brudvig, unpublished data) and, thus, might be appropriate for reintroduction to our upland sites.

To form the second set of filters, we compared trait abundances between the reference and degraded species lists to determine whether there were under-represented life-forms and dispersal modes and whether differences existed in coefficient of conservatism and/or habitat light coefficient. This approach has at least two benefits: (1) It identifies under-represented ecological niches that, if filled, might have effects on ecosystem function (Hooper et al. 2005). (2) It promotes functional redundancy, which is a goal of ecological restoration because it may provide ecosystem resiliency (SER 2004; Hooper et al. 2005). We used t tests to compare degraded ($n = 8$) and reference lists ($n = 3$) for the above mean trait values. In addition, because coefficients of conservatism and habitat light coefficients are data represented across a spectrum, we used tests of skewness and kurtosis (SAS Institute 2002) to identify specific portions of these distributions that differed between degraded and reference lists. Positive or negative skewness indicates longer than expected tails, that is, more high or low values than expected. Positive or negative kurtosis indicates fewer or greater values in the middle than expected, that is, a peaked or flat middle portion of the distribution. We defined results as significant at $\alpha < 0.05$; however, we corrected this to $\alpha < 0.005$ for life-form and 0.008 for dispersal, to account for the number of nonindependent tests in these analyses ($n = 10$ and $n = 6$, respectively). We performed all statistical analyses in SAS Institute (2002).

Results

Overall, reference lists contained 893 species, of which 110 were present at eight degraded Midwestern oak savanna remnants. The remnants had a cumulative list of 136 species of vascular plants (Appendix 2). Forty-three (31.6%) of the species were present on the Delong and Hooper (1996) list of 251 potential savanna species, 66 (48.5%) were found on the Bader (2001) working list of 484 species, and 91 (66.9%) were found on the Timberhill savanna pristine reference site list of 357 species. Conversely, 783 species (~88%) from the regional species pool were absent from the degraded sites.

Life-Form Groups

Relative to reference lists, degraded remnants had fewer native perennial forbs ($t = 5.22$, $p = 0.0006$) and native perennial grasses ($t = 3.79$, $p = 0.0043$) (Fig. 1), making these traits targets for reintroduction. Degraded remnants had greater proportions of woody vines ($t = 5.35$, $p = 0.0005$) and tree species ($t = 7.40$, $p < 0.0001$) (Fig. 1), whereas annual/biennial forbs, annual grasses, sedges, ferns, herbaceous vines, and shrubs did not differ between lists (maximum $t = 2.36$, $p = 0.0429$; shrubs). Thus, we excluded these life-forms from the reintroduction list.

Dispersal Mode and Seed Mass

Degraded remnants had fewer species with passively dispersed seeds ($t = 7.51$, $p < 0.0001$) and evidence for fewer species with wind-dispersed seeds ($t = 2.98$, $p = 0.0155$) (Fig. 2), suggesting that species with these traits would be good targets for reintroduction. We further filtered wind-dispersed species by considering only those with heavier seeds (<2,000 seeds/g; we chose this cutoff because seed data were continuous, except for a break between 2,000 and 2,800 seeds/g; data not presented) because these species may be more dispersal limited than those with small

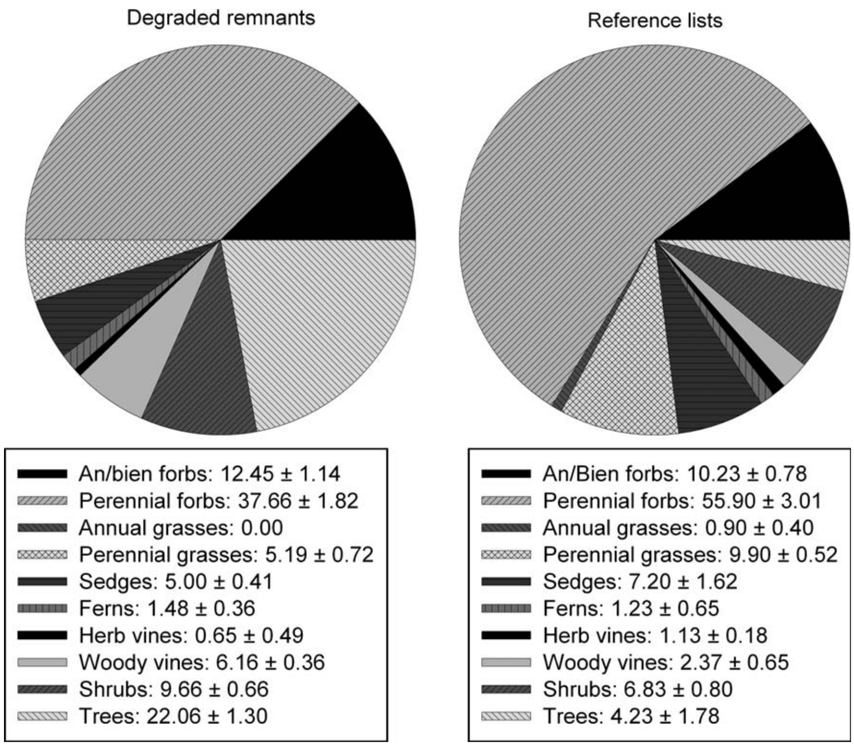

Figure 1. Percentage of species by life-forms from eight central Iowa degraded oak savannas (degraded remnants; mean ± 1 SE) and the regional species pool (reference lists; mean ± 1 SE). The percentage of perennial forbs, perennial grasses, woody vines, and shrubs differed between degraded and reference lists at the $\alpha < 0.005$ level.

wind-dispersed seeds (Higgins et al. 2003). Degraded sites also had higher proportions of ant ($t = 4.60$, $p = 0.0013$), externally ($t = 6.24$, $p = 0.0002$), internally ($t = 4.64$, $p = 0.0012$), and cache-dispersed seeds ($t = 4.27$, $p = 0.0021$) (Fig. 2). Although the degraded sites had more ant-dispersed species, we chose to retain this group because of the well-documented dispersal limitation associated with this trait and its association with pristine sites (Matlack 1994; Graae & Sunde 2000; Mabry 2002; Flinn & Vellend 2005). We excluded externally, internally, and cache-dispersed species from the reintroduction list.

Coefficients of Conservatism

Degraded remnant lists had a lower mean coefficient of conservatism (3.18 ± 0.12 SE) than the reference lists (5.66 ± 0.36 SE; $t = 5.47$, $p = 0.0004$). Skewness did not differ between degraded and reference lists ($t = 0.63$, $p = 0.5463$), with all lists displaying relatively normal distributions (0.062 for degraded remnants and ~0.00 for reference lists). However, degraded remnants displayed significantly flatter distributions than any of the reference lists ($t = 6.02$, $p = 0.0002$), with mean kurtosis of −1.24 for degraded remnants and −0.64 for the reference lists. Visually, the difference appears to be due to a marked absence of species with high coefficient of conservatism (8 and above) on degraded lists (Fig. 3), making this trait group a target for reintroduction.

Habitat Light Coefficients

Mean habitat light coefficient for degraded remnant lists (4.07 ± 0.07 SE) was significantly lower than that of reference lists (5.66 ± 0.30 SE; $t = 7.97$, $p < 0.0001$), indicating that degraded sites had substantially fewer species specializing in high-light environments. Degraded remnants were significantly more left skewed than the reference lists (degraded mean = 0.11, reference mean = −0.28; $t = 4.86$, $p = 0.0009$). Visually, this appears to be due to a paucity of species with high habitat light coefficient (7–9) on degraded remnants relative to the reference lists (Fig. 4), making this trait group a target for reintroduction. Lists did not differ in kurtosis values for habitat light coefficients (degraded mean = −0.69, reference mean = −0.37; $t = 1.34$; $p = 0.2136$).

Assembling the List

To our regional species pool ($n = 893$), we first applied three a priori filters: we excluded species already present at degraded sites ($n = 110$), exotic species ($n = 34$), and obligate wetland species ($n = 54$). Thus, our a priori filters resulted in a reduced list of 695 species. Next, we applied filters based on comparisons between degraded and reference lists. Our analyses indicated that perennial forbs and grasses (Fig. 1), and species with passively and wind-dispersed seeds (Fig. 2) were under-represented at the degraded remnants. Thus, we retained perennial grasses

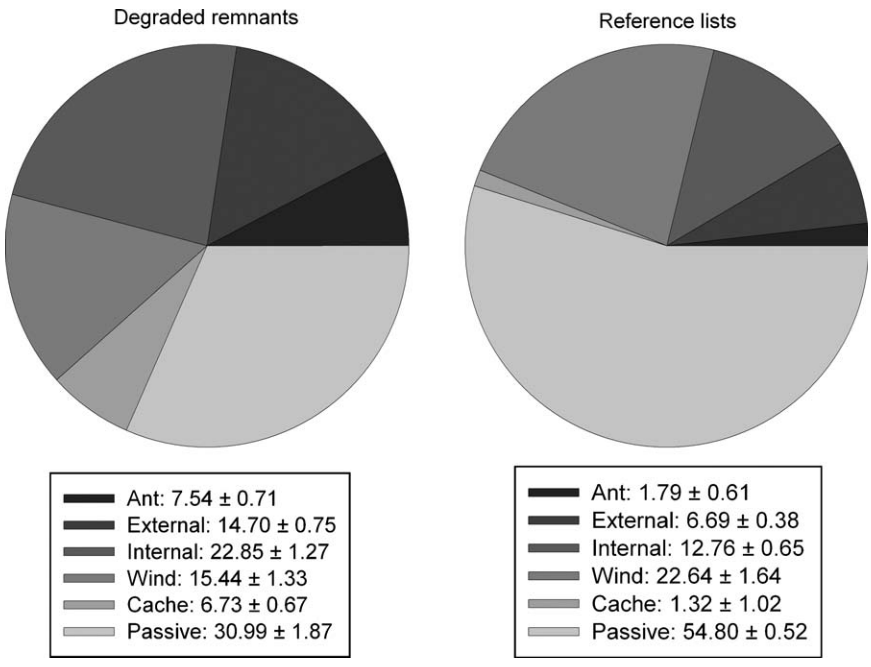

Figure 2. Percentage of species by seed dispersal modes from eight central Iowa degraded oak savannas (degraded remnants; mean ± 1 SE) and the regional species pool (reference lists; mean ± 1 SE). The proportion of all modes except wind dispersal differed between degraded and reference lists at the $\alpha < 0.008$ level.

and perennial forbs that were passively or ant-dispersed (see above) or with heavy (<2,000 seeds/g) wind-dispersed seeds ($n = 46$ grasses, 193 forbs). Remnants also had fewer conservative species (Fig. 3) and species that occur in high-light environments (Fig. 4). Thus, our final filter was to retain species with either coefficient of conservatism values of 8–10 or habitat light coefficient values 7–9. This resulted in a final list of 111 species (20 grasses, 91 forbs).

For those species with data available, we supply seed mass (Table 1). These data might be useful as a final filter due to the trade-off between seed size and production, making larger seeded species potentially more dispersal limited and, thus, better targets for restoration (Baker 1972; Eriksson 1995; Rees 1995; Henery & Westoby 2001).

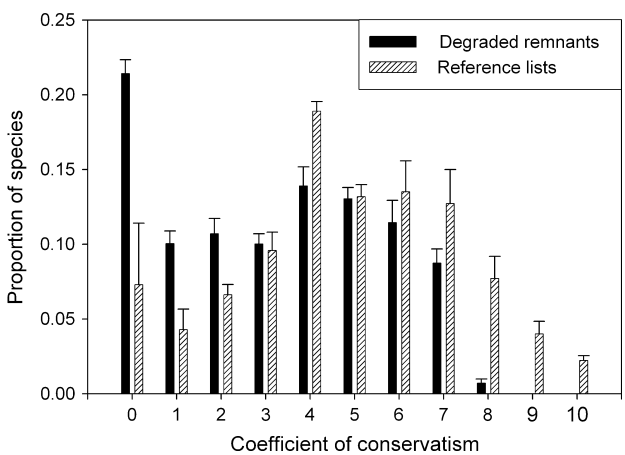

Figure 3. Coefficient of conservatism (C.C.) values (an index of affinity for undegraded habitat, with 10 being the greatest affinity), for species from eight central Iowa degraded oak savannas (degraded remnants; mean + 1 SE) and three reference lists (mean + 1 SE). Mean C.C. values are significantly greater for the reference lists than the degraded savanna remnants ($t = 5.47$, $p = 0.0004$).

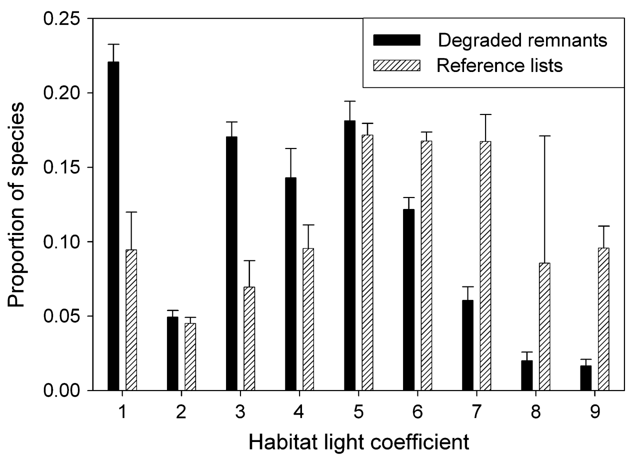

Figure 4. Understory species light requirements for eight central Iowa degraded oak savannas (degraded savanna remnants; +1 SE) and three reference lists (mean +1 SE). Species are coded for habitat light coefficients on a scale of 1 (occur at lowest understory light levels) to 10 (occur at highest understory light levels) and binned into the categories shown on the horizontal axis. Species' mean habitat light coefficient is significantly greater for the reference lists than the degraded savanna remnant's lists ($t = 7.97$, $p < 0.0001$).

Table 1. Species recommended for addition to eight degraded oak savanna remnants in central Iowa, U.S.A. ($n = 111$), based on a species-trait filtering of the regional species pool ($n = 893$).

Species	*Family*	*No. of Lists*[a]	*C.C.*	*Habitat Light Coefficient*	*Dispersal*	*Seeds/g*
Agrostis hyemalis	Poaceae	1	4	8.33	Passive	18,739
Allium canadense	Liliaceae	3	6	7.00	Passive	20
A. cernuum	Liliaceae	1	10	6.00	Passive	268
A. tricoccum	Liliaceae	1	9	1.00	Passive	49
A. gerardii	Poaceae	3	4	9.33	Passive	353
Anemone cylindrical	Ranunculaceae	2	7	8.50	Wind	917
A. quinquefolia	Ranunculaceae	1	8	1.00	Ant	883
Asclepias amplexicaulis	Asclepiadaceae	1	4	9.00	Wind	85
A. hirtella	Asclepiadaceae	2	5	9.00	Wind	152
A. speciosa	Asclepiadaceae	1	6	8.33	Wind	159
A. sullivantii	Asclepiadaceae	2	7	9.00	Wind	159
A. tuberosa	Asclepiadaceae	2	6	8.67	Wind	152
A. viridiflora	Asclepiadaceae	1	6	10.00	Wind	127
Aster laevis	Asteraceae	3	7	10.00	Wind	1,940
A. oblongifolius	Asteraceae	1	10	8.5	Wind	1,799
A. sericeus	Asteraceae	2	10	7.00	Wind	1,975
A. turbinellus	Asteraceae	1	8	4.00	Wind	1,235
Aureolaria grandiflora pulchra	Scrophulariaceae	2	9	1.00	Passive	8,113
Baptisia bracteata glabrescens	Fabaceae	3	7	7.00	Passive	49
B. lactea	Fabaceae	3	6	7.60	Passive	60
Besseya bullii	Scrophulariaceae	1	5	8.00	Passive	—
Bouteloua curtipendula	Poaceae	2	6	8.00	Passive	212
B. hirsute	Poaceae	1	7	8.5	Passive	2,469
Brachyelytrum erectum	Poaceae	2	8	1.00	Passive	—
Brickellia eupatorioides	Asteraceae	2	5	10.00	Wind	1,129
Bromus kalmii	Poaceae	2	10	7.00	Passive	282
B. pubescens	Poaceae	3	9	2.00	Passive	268
Cacalia muhlenbergii	Asteraceae	1	7	4.00	Wind	141
C. plantaginea	Asteraceae	1	4	10.00	Wind	166
Camassia scilloides	Liliaceae	3	9	7.00	Passive	148
Campanula rotundifolia	Campanulaceae	1	10	5.75	Passive	31,747
Castilleja sessiliflora	Scrophulariaceae	1	10	6.50	Passive	7,055
Cirsium altissimum	Asteraceae	3	4	8.50	Wind	247
Dalea candida	Fabaceae	3	10	7.50	Passive	613
D. purpurea	Fabaceae	3	8	7.00	Passive	661
Dichanthelium acuminatum villosum	Poaceae	1	3	10.00	Passive	—
D. latifolium	Poaceae	2	8	1.00	Passive	463
D. leibergii	Poaceae	2	6	7.00	Passive	—
Echinacea pallida	Asteraceae	2	7	10.00	Passive	183
E. purpurea	Asteraceae	2	9	7.00	Passive	233
Eryngium yuccifolium	Apiaceae	3	8	7.00	Passive	265
Euphorbia corollata	Euphorbiaceae	3	3	8.00	Passive	282
Helianthemum bicknellii	Cistaceae	1	7	7.00	Passive	—
Helianthus grosseserratus	Asteraceae	2	4	10.00	Passive	529
H. occidentalis	Asteraceae	1	8	5.00	Passive	385
H. rigidus	Asteraceae	2	8	10.00	Passive	—
Hepatica nobilis obtuse	Ranunculaceae	1	10	1.00	Ant	333
Hierochloe odorata	Poaceae	1	7	9.00	Passive	1,411
Hypoxis hirsuta	Liliaceae	3	7	8.00	Passive	2,822
Ipomoea pandurata	Convolvulaceae	1	4	10.00	Passive	23
Koeleria macrantha	Poaceae	2	7	7.00	Passive	5,104
Lechea intermedia	Cistaceae	1	10	7.00	Passive	—
Liatris aspera	Asteraceae	3	8	7.00	Wind	564
L. cylindracea	Asteraceae	1	10	10.00	Wind	494
L. pycnostachya	Asteraceae	2	6	10.00	Wind	388
L. squarrosa	Asteraceae	2	8	7.00	Wind	247
Lilium philadelphicum andinum	Liliaceae	2	9	7.00	Passive	529
Linum sulcatum	Linaceae	2	7	7.00	Passive	1,482
Lithospermum canescens	Boraginaceae	3	7	7.00	Passive	345

Table 1. Continued

Species	*Family*	*No. of Lists*[a]	*C.C.*	*Habitat Light Coefficient*	*Dispersal*	*Seeds/g*
L. caroliniense	Boraginaceae	1	6	7.00	Passive	175
L. incisum	Boraginaceae	1	5	7.00	Passive	213
Lupinus perennis	Fabaceae	1	10	6.63	Passive	39
Luzula acuminate	Juncaceae	1	10	5.00	Passive	—
Lysimachia quadriflora	Primulaceae	1	7	10.00	Passive	3,175
Minuartia michauxii	Caryophyllaceae	1	10	5.00	Passive	—
Moehringia lateriflora	Caryophyllaceae	1	10	4.40	Passive	—
Monarda punctata villicaulis	Lamiaceae	1	6	8.50	Passive	3,175
Muhlenbergia cuspidate	Poaceae	1	10	10.00	Passive	6,349
Oenothera perennis	Onagraceae	1	8	7.67	Passive	—
Oxalis violacea	Oxalidaceae	3	7	7.50	Passive	2,500
Parthenium integrifolium	Asteraceae	3	9	4.00	Passive	247
Pedicularis lanceolata	Scrophulariaceae	1	7	9.00	Passive	1,552
Penstemon digitalis	Scrophulariaceae	3	4	7.67	Passive	4,586
P. gracilis	Scrophulariaceae	1	5	7.50	Passive	21,164
P. grandiflorus	Scrophulariaceae	1	5	10.00	Passive	494
Poa sylvestris	Poaceae	1	10	2.00	Passive	1,764
Polygala senega	Polygalaceae	2	7	7.00	Passive	417
Polytaenia nuttallii	Apiaceae	2	8	7.00	Passive	141
Potentilla arguta	Rosaceae	2	8	7.33	Passive	8,113
Prenanthes aspera	Asteraceae	1	9	7.50	Wind	494
P. racemosa	Asteraceae	1	7	7.33	Wind	705
Psoralidium batesii	Fabaceae	1	9	7.33	Passive	35
Pulsatilla patens multifida	Ranunculaceae	2	8	8.00	Wind	635
Pycnanthemum tenuifolium	Lamiaceae	2	6	7.50	Passive	13,334
P. virginianum	Lamiaceae	2	4	7.00	Passive	7,760
Ranunculus rhomboideus	Ranunculaceae	1	10	7.00	Passive	705
Ratibida pinnata	Asteraceae	3	4	8.00	Passive	1,058
Rudbeckia subtomentosa	Asteraceae	2	4	10.00	Passive	1,517
Schizachyrium scoparium	Poaceae	3	5	10.00	Passive	529
Silphium integrifolium	Asteraceae	3	4	10.00	Passive	42
S. laciniatum	Asteraceae	2	7	10.00	Passive	23
Sisyrinchium angustifolium	Iridaceae	1	6	7.00	Passive	1,058
S. campestre	Iridaceae	3	4	7.00	Passive	1,587
Solidago rigida	Asteraceae	2	4	10.00	Wind	1,446
Sorghastrum nutans	Poaceae	3	4	10.00	Passive	423
Spartina pectinata	Poaceae	2	4	8.67	Passive	233
Sphenopholis obtusata	Poaceae	2	8	6.20	Passive	11,111
Sporobolus cryptandrus	Poaceae	1	3	7.50	Passive	12,346
S. heterolepis	Poaceae	1	9	7.00	Passive	564
Taenidia integerrima	Apiaceae	3	9	4.67	Passive	212
Talinum rugospermum	Portulacaceae	1	10	10.00	Passive	2,822
Tephrosia virginiana	Fabaceae	1	7	8.00	Passive	88
Uvularia sessilifolia	Liliaceae	1	9	1.00	Ant	—
Veratrum woodii	Liliaceae	1	8	1.00	Passive	—
Vernonia missurica	Asteraceae	1	4	8.33	Wind	776
Viola adunca	Violaceae	1	10	4.67	Ant	—
V. pedata	Violaceae	2	8	7.33	Ant	917
V. pedatifida	Violaceae	2	8	7.00	Ant	988
Zigadenus elegans	Liliaceae	2	8	8.00	Passive	1,482
Zizea aptera	Apiaceae	1	8	6.33	Passive	423

Species are perennial forbs and grasses that lack means for long-distance dispersal (species are dispersed passively or by ants, or are wind dispersed with heavy seeds, <1,000 seeds/g) and are highly conservative (Iowa coefficient of conservatism [C.C.] 8–10), and/or high-light specialists (habitat light coefficient 7–10). Seed weights are also provided as a potential additional filter for reintroduction order, with heavier seeds given higher priority.
[a]Number of reference lists on which species was present.

Discussion

For rare ecosystems, extant reference information may also be rare. Midwestern oak savanna is a rare ecosystem and lists of species that represent the regional species pool may be the most complete modern reference information available. Our study examined the potential for using species traits as filters to prioritize species for reintroduction to degraded sites. Using seven traits, we reduced a regional list of 893 species to a list of 111 species that included native species of upland habitats with passive or ant-dispersed seeds or heavy wind-dispersed seeds. Priority species were further defined as native perennial forbs or grasses, and conservative in habitat requirement or characteristic of high-light environments. This process targeted a group of species that are least likely to recolonize through natural succession and play key functional roles through filling important, but under-represented savanna niches.

The remnants in our study are currently under-represented in species that define the understories of upland savanna, and that appear on all three reference lists. Addition of species with these traits might improve the structure, function, and conservation value of restored sites and promote high site-level diversity and functional redundancy, ensuring that critical ecosystem processes are effectively promoted during restoration (SER 2004). Under-representation of an ecosystem's characteristic life-forms may impair nutrient cycling, primary productivity, and ecosystem response to fire (Lavorel & Garnier 2002). In our case, we identified under-representation of perennial grasses such as *Andropogon gerardii*, *Bouteloua curtipendula*, and *Schizachyrium scoparium* and perennial forbs, including prominent species in the genera *Baptisia*, *Dalea*, *Echinacea*, *Helianthus*, *Lithospermum*, *Penstemon*, and *Silphium*. Without the addition of perennial grasses, the restored sites are unlikely to function as savannas, particularly, in the capacity to carry understory fires (Kirkman et al. 2004). Without the additional of prairie forbs, the restored savannas could lack the characteristic turnover of species along gradients of light and shade (Leach & Givnish 1999; Meisel et al. 2002; Ludwig et al. 2004).

Our analyses also elucidated the under-representation of species that typically inhabit high-light environments. Following initial restoration (removal of encroaching woody vegetation) and the ensuing reestablishment of sunny, shady, and mixed-light habitats, reintroduction of this group will supplement the low and mid-light specialists that currently persist at the remnants. Reintroduction of this group is particularly important for promoting site-level species richness, given the importance of light as a gradient that maintains high diversity in savannas (Leach & Givnish 1999; Meisel et al. 2002).

We also targeted species with high coefficient of conservatism values. Woody encroachment can transform open-canopy savannas to closed-canopy woodlands, which can result in a conversion of understory flora from savanna to woodland species (Cottam 1949). Prior to this study, however, it was unknown whether woody encroachment might also alter species quality (coefficient of conservatism). We found support for reduced species quality on remnant lists, which might be due to woody encroachment, historical logging, and/or past cattle grazing at our sites (Karnitz & Asbjornsen 2006).

Our paper uses a well-established framework for approximating species dispersal capabilities (Flinn & Vellend 2005), with evidence for dispersal limitation among passively dispersed species over a wide range of systems (Saunders et al. 1991; Tilman 1997; Graae & Sunde 2000; Tofts & Silvertown 2002; Kirkman 2004; Flinn & Vellend 2005). There is also evidence that animal and some wind-dispersed species are good early colonists of secondary woodlands and disturbed sites (Robinson & Handel 1993; Matlack 1994; Graae & Sunde 2000; McLachlan & Bazely 2001), suggesting that species with these characters are more likely to recolonize through natural succession. Furthermore, heavy (e.g., large) seeds are often associated with high-site persistence due to greater abilities to deploy resources in the face of drought, litter deposition, herbivory, and other "hazards" (Gross 1984; Leishman & Westoby 1994; Eriksson 1995; Bond et al. 1999; Maurer et al. 2003). Thus, we suggest that if an additional filter of our reintroduction list is desired, species with heavier seeds may be particularly good candidates for reintroduction, due to potentially higher propagation and survival of new recruits.

However, it remains an open question whether simple addition of seeds will be sufficient to permanently alter the composition and structure of the degraded sites. As Saunders et al. (1991) point out, presence of a species at a site is not a guarantee that it will persist—persistence requires reproduction and successful recruitment. In fact, high initial germination may not reflect adult establishment due to unfavorable site conditions (Turnbull et al. 2000). However, several lines of evidence suggest that reintroduction can be a successful strategy for overcoming dispersal limitations and reestablishing key species at the sites in this study. Propagule addition experiments in Minnesota oak savannas (Foster & Tilman 2003) and open Iowa woodlands (Mottle et al. 2006) demonstrated that dispersal, not site factors, limited community composition. In both cases, introduced species established reproductive populations over the duration of the 7- to 8-year studies.

We concur with Kirkman et al. (2004) that traits can help us understand mechanisms that govern the diversity and abundance of plant species, but they do not "provide a simple prescription for restoring a damaged or destroyed community." Future research should include long-term monitoring of the oak savanna understory during restoration to document which species return without reintroduction, and the traits associated with these. More work is also needed to determine how traits such as life-form, seed size, capacity for vegetative spread (Singleton et al. 2001), and the order that species are reintroduced influence reestablishment success (Fukami et al. 2005). We also need to know to what extent reintroduction ultimately moves degraded sites toward reference conditions for a range of criteria—species richness, diversity, wildlife habitat, and ecosystem level processes such as nutrient cycling. In sum, long-term monitoring during restoration of the remnants in this study will provide a laboratory for investigating community assembly rules within restoration contexts (Temperton et al. 2004).

Finally, in contrast to Europe (e.g., Ecological Flora of the British Isles online database at http://www.york.ac.uk/res/ecoflora/cfm/ecofl/index.cfm) species trait databases do not currently exist for most North American plant species, leaving the process of species coding up to individual researchers and land managers. Priority should be given to developing an equivalent North American database so that this and similar approaches can be readily applied to on-the-ground restorations.

Implications for Practice

Midwestern oak savannas may require species reintroductions as part of the restoration process; however, the regional species pool is too large to be of practical use as a reference (893 species).

- Coding species lists for life history traits (e.g., life-form, method of seed dispersal) resulted in a smaller targeted list of species for reintroduction (111 species).
- Important traits of species from this list included dispersal limitation, specialization for high-light environments, high coefficient of conservatism, and species with perennial native forb and grass life-forms.
- Reintroduction of species from our list may improve remnant composition, structure, and function and provides an opportunity to test oak savanna assembly rules.

Acknowledgments

We thank the U.S. Fish and Wildlife Service and U.S. Army Corps of Engineers for allowing us to survey remnant savannas on their lands, Sybilla Brown for making Timberhill savanna's species list available to us, and Greg Curler, Chris Evans, Allison Hopkins, and Holly Karnitz for assisting with field data collection. Comments by Heidi Asbjornsen, Vicky Temperton, and two anonymous reviewers helped to revise earlier versions of this paper. This project was funded by U.S. Forest Service grants 03JV11231300012 and 03JV11231300023 and the Iowa State University Department of Natural Resource Ecology and Management.

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Appendix 1. Habitat descriptions from published flora, for species from degraded Midwestern oak savannas ($n = 8$), a proposed list of savanna species (Delong & Hooper 1996), a working savanna restoration species list (Bader 2001), and at a pristine reference site (Timberhill savanna).

Habitat	*Light Value*	*Habitat*	*Light Value*	*Habitat*	*Light Value*
Bottomland forests	1	Banks of rivers	5	Along ditches	8
Forests	1	Banks of waterways	5	Along marshes	8
Rich-wooded hillsides	1	Boarders	5	Around marshes	8
Rich woodlands	1	Brushy places	5	Banks of marshes	8
Rich woods	1	Disturbed sites	5	Cliffs	8
Shaded habitats	1	Edges of ponds	5	Ditches	8
Shaded places	1	Edges of woods	5	Dry sterile sandy soil	8
Shaded stream banks	1	Flood plains	5	Field margins	8
Wooded areas	1	Forest edge	5	Forest clearings	8
Wooded hillsides	1	Forest margins	5	Gardens	8
Wooded regions	1	Lake margins	5	Lawns	8
Wooded slopes	1	Lakeshores	5	Marshy areas	8
Woods	1	Near forest edge		Open swampy sites	8
Bottomlands	2	Near old dwellings	5	Prairie ditches	8
Dry upland woods	2	Partial shade	5	Roadside banks	8
Flood plain forests	2	Pond banks	5	Roadsided itches	8
Riparian woodlands	2	Pond shores	5	Roadsides	8
Riverbank forest	2	Ravine thickets	5	Sand bars	8
Wooded bluffs	2	Ravines	5	Sloughs	8
Wooded stream valleys	2	Rocky ridges	5	Swales	8
Woodlands	2	Rocky or sandy hillsides	5	Waste areas	8
Disturbed woodlands	3	Savannas	5	Waste ground	8
Hillsides	3	Seepage areas	5	Waste places	8
Partly open wooded areas	3	Shaded lawns	5	Fens	9
Springs	3	Shores	5	Meadows	9
Stream beds	3	Sparse woods	5	Old fields	9
Stream valleys	3	Thickets	5	Clearings	10
Valley floors	3	Transitional prairie woods	5	Cultivated fields	10
Valleys	3	Variety of disturbed habitats	5	Cultivated ground	10
Wooded waterways	3	Variety of habitats	5	Cutover areas	10
Along streams	4	Wet places	5	Feedlots	10
Along wooded riparian sites	4	Wetland sites	5	Fields	10
Around springs	4	Woodland edges	5	Grasslands	10
Banks of streams	4	Woodland–prairie borders	5	Hay fields	10
Banks of swamps	4	Barrens	6	In the open	10
Base of bluffs	4	Brushy pastures	6	Marshes	10
Bluffs	4	Ledges	6	Open areas	10
Creek banks	4	Openings in woods	6	Open ground	10
Dry rocky hillside	4	Outcrops	6	Open habitats	10
Open scrubby woods	4	Parks	6	Open hillsides	10
Open to rocky woods	4	Sparsly wooded areas	6	Open marshy sites	10
Open wooded areas	4	Wooded damp prairies	6	Open places	10
Open wooded hillsides	4	Bogs	7	Open sites	10
Open woodland	4	Border of open woods	7	Open slopes	10
Open woods	4	Bushy prairie ravines	7	Open sterile places	10
Shaded hillsides	4	Dry rocky sites	7	Open waste ground	10
Shaded ledges	4	Exposed ledges	7	Plains	10
Stream banks	4	Exposed sites	7	Prairie	10
Stream margins	4	Exposed stream banks	7	Prairie hillsides	10
Swamps	4	Fence rows	7	Prairie swales	10
Woodland thickets	4	Old farmsteads	7	Railroad embankments	10
Along lakes	5	Open waterways	7	Sand dunes	10
Along ponds	5	Pastures	7	Stripmine tailings	10
Banks	5	Prairie ravines	7	Weedy lots	10
Banks of lakes	5	Ravines in prairies	7		
Banks of ponds	5	Seral communities	7		

Light values rank habitats' available understory light, on a scale of 1 to 10 (least to most).

Appendix 2. Understory plant species recorded during 2003 sampling of eight degraded savanna remnants in central Iowa, species traits (C.C., Iowa coefficient of conservatism; Light, habitat light coefficient; Life-form; Native, native (x)/exotic status; Disp, seed dispersal mechanism), and indication (x) of whether the species appears on a proposed list of savanna species (D&H, Delong and Hooper 1996), a working savanna restoration species list (Bader, Bader 2001), and at a pristine reference site (Tim, Timberhill savanna).

Species	*C.C.*	*Light*	*Life-form*[a]	*Native*	*Disp*[b]	*# Sites*[c]	*D&H*	*Bader*	*Tim*
Acalypha rhomboidea	6	6.33	A-FORB	x	P	5			x
Acer negundo	0	5	TREE	x	W	2			x
Acer nigrum	5	1	TREE	x	W	3			
Acer saccharum	5	2.5	TREE	x	W	2			
Actaea rubra	7	1	P-FORB	x	I	1		x	
Agastache nepetoides	4	4.33	P-FORB	x	P	2	x	x	x
Amaranthus albus	0	7.8	A-FORB	x	P	5			
Ambrosia artemisiifolia	0	10	A-FORB	x	P	2	x		x
Ambrosia trifida	0	5.75	A-FORB	x	P	4			x
Amelanchier arborea	8	4	TREE	x	IN	4		x	
Amphicarpaea bracteata	4	5.5	H-VINE	x	EX	2	x	x	x
Anemone virginiana	4	1	P-FORB	x	W	1	x	x	x
Aquilegia canadensis	6	1	P-FORB	x	P	2	x	x	x
Arctium minus	0	6	B-FORB		EX	1	x		
Arisaema triphyllum	4	1	P-FORB	x	I	3		x	x
Asclepias syriaca	0	5.9	P-FORB	x	W	1	x	x	x
Aster cordifolius	7	5.5	P-FORB	x	W	5			
Bidens frondosa	3	5.25	A-FORB	x	EX	1			x
Botrychium virginianum	6	1	FERN	x	W	5		x	x
Bromus inermis	0	7.33	P-GRASS		P	7			
Campanula americana	4	5.25	A-FORB	x	P	7	x	x	
Cannabis sativa	0	7	A-FORB		P	1			
Carex amphibola v. *turgida*	4	3.17	P-SEDGE	x	P	6			x
Carex blanda	2	4	P-SEDGE	x	P	7		x	x
Carex cephaloidea	6	4	P-SEDGE	x	P	1			
Carex jamesii	6	1	P-SEDGE	x	A	6			x
Carex pensylvanica	6	4.5	P-SEDGE	x	P	6	x	x	
Carya cordiformis	5	1	TREE	x	C	7			x
Carya ovata	5	1	TREE	x	C	6			x
Celastrus scandens	1	5.2	W-VINE	x	IN	1	x	x	x
Celtis occidentalis	2	4	TREE	x	I	7			
Chenopodium album	0	10	A-FORB		P	1			
Circaea lutetiana	5	3	P-FORB	x	EX	7		x	x
Claytonia virginica	4	5.33	P-FORB	x	A	3		x	
Conyza canadensis	0	9	A-FORB	x	W	1			x
Cornus foemina	1	5.33	SHRUB	x	I	8	x	x	x
Crataegus sp.	3	5	TREE	x	I	2	x	x	x
Cryptotaenia canadensis	4	3.5	P-FORB	x	EX	7		x	x
Dactylis glomerata	0	6	P-GRASS		P	1			
Cardamine concatenata	7	1	P-FORB	x	A	2			
Desmodium glutinosum	5	3	P-FORB	x	EX	4		x	x
Dicentra cucullaria	7	1	P-FORB	x	A	4			
Dichanthelium acuminatum	3	6	P-GRASS	x	P	2	x	x	x
Elymus canadensis	5	7	P-GRASS	x	P	3	x	x	
Hystrix patula	5	1	P-GRASS	x	P	1	x	x	x
Elymus villosus	5	5.25	P-GRASS	x	P	3	x	x	x
Erigeron strigosus	2	7.5	P-FORB	x	W	1	x	x	x
Erythronium albidum	6	3	P-FORB	x	A	5	x	x	
Euonymus atropurpureus	7	3.5	SHRUB	x	IN	1			
Eupatorium purpureum	6	4	P-FORB	x	W	1		x	x
Eupatorium rugosum	2	4	P-FORB	x	W	8			x
Festuca obtusa	7	2	P-GRASS	x	P	4		x	x
Fraxinus americana	6	3.33	TREE	x	W	2			x
Fraxinus pennsylvanica	1	4.5	TREE	x	W	7			x
Galium aparine	1	6.4	A-FORB	x	EX	8			
Galium circaezans	6	3.33	P-FORB	x	EX	7		x	x

Appendix 2. Continued

Species	*C.C.*	*Light*	*Life-form*[a]	*Native*	*Disp*[b]	*# Sites*[c]	*D&H*	*Bader*	*Tim*
Galium concinnum	7	6.14	P-FORB	x	EX	7	x	x	x
Galium triflorum	7	4.86	P-FORB	x	EX	7		x	x
Geum canadense	2	3.33	P-FORB	x	EX	3	x	x	x
Gleditsia triacanthos	0	2.5	TREE	x	P	8			x
Gymnocladus dioica	5	3.25	TREE	x	P	1			
Hackelia virginiana	0	3	P-FORB	x	EX	7			x
Helianthus strumosus	5	4	P-FORB	x	P	1	x	x	x
Hepatica acutiloba	6	1	P-FORB	x	A	2		xx	
Hydrophyllum virginianum	3	1	P-FORB	x	P	6			x
Impatiens pallida	5	3.67	A-FORB	x	P	3			x
Ipomoea coccinea	0	6.5	H-VINE		P	1			
Juglans nigra	4	1	TREE	x	C	4			x
Juniperus virginiana	1	8	TREE	x	IN	1			x
Lactuca canadensis	1	6.5	B-FORB	x	W	4	x	x	x
Laportea canadensis	3	1	P-FORB	x	P	3			x
Leonurus cardiacea	0	5.8	P-FORB		P	1			
Lonicera tatarica	0	4.67	SHRUB		IN	2			
Maclura pomifera	0	5.8	TREE		P	1			
Pyrus ioensis	4	5	TREE	x	IN	1	x	x	
Melilotus alba	0	8.67	B-FORB		P	1			
Menispermum canadense	5	3.67	W-VINE	x	IN	1	x	x	
Monarda fistulosa	2	7.11	P-FORB	x	P	2	x	x	x
Osmorhiza claytoni	3	1	P-FORB	x	EX	7		x	x
Ostrya virginiana	5	1	TREE	x	W	6			x
Oxalis stricta	0	6.2	P-FORB	x	P	6	x		x
Parthenocissus quinquefolia	2	4.43	W-VINE	x	IN	8	x	x	x
Pedicularis canadensis	7	7	P-FORB	x	P	1	x	x	x
Phlox divaricata	5	3.5	P-FORB	x	P	7		x	x
Phryma leptostachya	4	3.33	P-FORB	x	P	8		x	x
Pilea pumila	3	1	A-FORB	x	P	6			x
Plantago major	0	8.6	P-FORB		P	1			
Poa pratensis	0	5	P-GRASS		P	7			x
Podophyllum peltatum	4	1	P-FORB	x	IN	5		x	x
Polygonatum biflorum	4	1	P-FORB	x	IN	4	x	x	x
Polygonum erectum	1	9	A-FORB	x	P	1			
Polygonum persicaria	0	7.5	A-FORB		P	3			
Populus grandidentata	4	1	TREE	x	W	1			
Potentilla recta	0	8.22	P-FORB		P	4			x
Potentilla simplex	3	5.86	P-FORB	x	P	2	x	x	x
Prunus americana	2	5.33	TREE	x	IN	2	x	x	x
Prunus serotina	3	5	TREE	x	IN	8			x
Prunus virginiana	2	6.6	SHRUB	x	IN	1	x		
Pteridium aquilinum v. *latiusculum*	4	6.29	FERN	x	P	4		x	
Quercus alba	6	1	TREE	x	C	6			x
Quercus macrocarpa	4	3	TREE	x	C	2			x
Quercus borealis	6	1	TREE	x	C	8			
Quercus velutina	4	1	TREE	x	C	3			x
Ranunculus abortivus	0	5.33	A-FORB	x	P	2		x	x
Ribes missouriense	3	5.33	SHRUB	x	IN	8	x	x	x
Rosa carolina	4	6.8	SHRUB	x	IN	2	x	x	x
Rosa multiflora	0	6	SHRUB		IN	5			x
Rubus occidentalis	1	6	SHRUB	x	IN	7	x	x	x
Sambucus canadensis	1	5.75	SHRUB	x	IN	1		x	x
Sanguinaria canadensis	7	2	P-FORB	x	A	4		x	x
Sanicula marilandica	5	5.33	P-FORB	x	EX	8		x	
Scutellaria parvula	7	6.67	P-FORB	x	P	1		x	x
Silene stellata	4	5.33	P-FORB	x	P	1	x	x	x
Smilax herbacea	5	3	H-VINE	x	IN	3	x	x	x
Smilax hispida	4	2.67	W-VINE	x	IN	8			x

Appendix 2. Continued

Solanum ptycanthum	0	6.5	A-FORB	x	IN	5			
Solidago canadensis	0	9	P-FORB	x	W	3	x	x	x
Solidago ulmifolia	6	4	P-FORB	x	W	5		x	x
Sonchus oleraceus	0	7.5	A-FORB		W	1			
Sporobolus asper	3	7.67	P-GRASS	x	P	1	x		
Symphoricarpos orbiculatus	0	4.25	SHRUB	x	IN	8		x	x
Taraxacum officinale	0	7	P-FORB		W	5			x
Anemonella thalictroides	7	1	P-FORB	x	P	4		x	
Tilia americana	5	1	TREE	x	W	4			x
Torilis arvensis	0	8.67	A-FORB		Ex	3			
Toxicodendron radicans	0	5.29	W-VINE	x	IN	8	x	x	x
Trifolium repens	0	7.5	P-FORB		P	3			x
Triosteum perfoliatum	4	1	P-FORB	x	IN	1		x	x
Ulmus americana	2	4	TREE	x	W	8			x
Ulmus rubra	2	3	TREE	x	W	8			x
Urtica dioica	0	4.67	P-FORB	x	P	2			
Uvularia grandiflora	7	1	P-FORB	x	A	7		x	x
Verbascum thapsus	0	9.33	B-FORB		P	1			x
Viola sororia	1	3.67	P-FORB	x	A	8		x	x
Vitis riparia	1	5.5	W-VINE	x	IN	6	x	x	x
Zanthoxylum americanum	3	6	SHRUB	x	P	6	x	x	x

[a]Life-form groups: A-FORB, annual forb; B-FORB, biennial forb; P-FORB, perennial forb; A-GRASS, annual grass; P-GRASS, perennial grass; P-SEGE – perennial sedge; FERN; H-VINE, herbaceous vine; W-VINE, woody vine; SHRUB; TREE.
[b]Seed dispersal mechanisms determined from published flora and herbarium specimens: W, wind; EX, vertebrate, externally; IN, vertebrates, internally; A, ant; C, cache; P, passive.
[c]No. of Sites: number of degraded remnants (maximum $n = 8$) species occupied.