

The number and size of seeds in common versus restricted woodland herbaceous species in central Iowa, USA

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Few plants have widespread distributions and occur wherever there is suitable habitat. Most species are absent from seemingly suitable sites because of limited colonizing ability. At a landscape scale colonization is limited by lack of seeds or suitable microsites, and this limit is likely to be exacerbated by current human alteration of the landscape. To test the hypothesis that species with restricted distributions have a more limited capacity for dispersal compared to common species, I compared seed number in a group of seven common woodland herbaceous species compared to seven species in the same genus or family with more restricted distributions. Restricted species had nearly an order of magnitude fewer seeds compared to closely related common species. They also produced over an order of magnitude larger seeds. These results support dispersal limitation. The ability to detect these differences was reduced when taxonomic information was not included. The data suggest that these species can not maximize both seed size and seed number. The results are interpreted in light of the human disturbance history that has had an overriding influence on the Iowa landscape and has likely favored species with an output advantage of abundant seeds over species with far fewer seeds.

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Few plant species have widespread distributions and occur wherever there is suitable habitat. Instead, most are absent from an abundance of seemingly suitable sites. For some species the explanation is an evolutionary one of specialization, but for non-specialized species limited distribution is tied to limited colonizing ability (Harper et al. 1997). At a landscape scale, colonization is limited by lack of seeds or lack of suitable microsites for seedling survival (Eriksson and Ehrlén 1992, Matlack 1994).

Recently Westoby et al. (2002) identified the seed mass and seed output ratio as one important “dimension of variation” among plants because it is a predictor of dispersal capacity (seed output) and establishment success (seed mass). By identifying dimensions that are easily measured and result in consistent rankings among species, the goal is to synthesize disparate literature,

resulting in greater power to predict changes in species composition, particularly in light of global climate change and other human disturbances (Westoby et al. 2002).

Understanding the relationship between seed size and number, and the landscape-scale limits to distribution takes on added importance when considering the dramatic alterations humans are imposing on landscapes worldwide. Conversion of native habitat to agricultural and urban uses is resulting in a landscape dominated by human settlement, with increasingly isolated patches of remnant vegetation (Saunders et al. 1990, Pimental et al. 1992), and where, for species to persist in the landscape, local extirpation of populations must be countered by successful dispersal to and establishment in new patches (Westoby et al. 2002). At the same time, these remnants

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may be subject to timber harvesting, grazing, trampling and other human impacts that lead to loss of species and that may eliminate microsites needed by some species to re-establish (Robinson et al. 1994, Drayton and Primack 1996, Bratton and Meier 1998).

Limited seed dispersal has often been implicated in the limited colonization ability of some species, particularly in fragmented landscapes and in secondary woods. For example, Matlack (1994) identified a suite of species in the eastern United States that either did not migrate or migrated very slowly because they had ant or unspecialized seed dispersal syndromes. Similarly, in Poland species that lacked a means of long-distance dispersal showed limited ability to colonize isolated and secondary woods (Dzwonko and Loster 1988, 1992). These and other studies have focused on how different dispersal syndromes influence dispersal distance, but they don't include productivity, a key component of dispersibility, or address why forest species with similar dispersal syndromes may differ, often dramatically, in dispersal ability.

In this study I compared seven species that had ubiquitous distributions, that is, they generally occurred wherever there was suitable habitat, to seven species that had comparatively restricted distributions. Each common species was also paired with restricted species in the same genus or family, so that species relatedness could be used to factor out the potentially confounding effect of comparing species with different fruit and seed morphology, biology and dispersal mode (Mazer 1989, Harper et al. 1997, Silvertown and Dodd 1997). I tested the hypothesis that species with restricted distributions have a more limited capacity for dispersal compared to related common species, where dispersal capacity was inferred from seed number. Species producing fewer seeds will be less mobile across the landscape compared to a species with greater output (Rees 1995, Jakobsson and Eriksson 2000, Aarssen and Jordan 2001, Murray et al. 2002, Westoby et al. 2002) as long as other factors that influence colonization, such as dispersal vector and persistence in the seed bank, are held equal, which was achieved in my study by comparing related species that share more affinities with one another than with members of the other pairs (Thompson and Rabinowitz 1989, Westoby et al. 2002). The possibility that species are limited by lack of suitable microsites for seed germination, emergence and seedling survival, is being examined in a subsequent study.

Methods

Study area

The study was conducted in central Iowa, U.S.A. The overstory of upland forests in this region are dominated by *Quercus alba*, *Q. macrocarpa*, *Q. rubra* and

Q. velutina, *Carya ovata*, *Acer nigrum*, *Tilia americana* and *Prunus serotina* (van der Linden and Farrar 1993). The modern forest community originated after the retreat of the Wisconsin glaciation about 13,000 years ago, and in central Iowa, the early spruce dominated forests began to be replaced by the modern deciduous forest about 8,000–9,000 years ago (Pusateri et al. 1993). Until European settlement began in the mid-1800s, the vegetation was a mosaic of prairies, wetlands and woodlands, and was a transition zone between the eastern deciduous forest and the tallgrass prairie (Roosa 1981, Smith 1998). In central Iowa the landscape was dominated by prairie with extensive tracts of forest along rivers and streams and savanna or more open woods found in the uplands (Norris and Farrar 1999). However, since settlement, the state has been dramatically altered by conversion of forests and other native habitats to agricultural land, and Iowa has now lost more native habitat than nearly any other state in the U.S.A. Most woodlands in central Iowa are now highly fragmented into scattered and small remnants surrounded by crops and other alterations to the landscape, with some more extensive tracts of forest protected along the major rivers (Bernstein 1998). In addition, much of the forest in Iowa was historically grazed by cattle, a disturbance that, at least in the short term, shifts the vegetation of closed canopy forests towards an understory flora of habitat generalists and introduced species (Pettit et al. 1995, Mabry 2002).

Species choice

The first criterion used to select species was frequency data obtained from inventory of 103 20 × 20 m permanently marked plots placed in central Iowa, U.S.A., forests (C. Mabry, unpubl.). These plots were located in 21 upland forested sites distributed over 12 counties in central Iowa. The sites ranged from the highest quality, least disturbed forests remaining in Iowa, to forests that were currently or recently grazed by cattle. Using the frequency data from this inventory (number of plots where a species was present), I selected 14 species and assigned them as common or restricted based on their frequency (Table 1). Although *Viola pubescens* is only 19 percent less frequent than *V. sororia* in this data-set, the pairing was included because *V. pubescens* is considered rare to infrequent in its statewide distribution, and is strongly associated with relatively undisturbed woods, while *V. sororia* is a very widespread inhabitant of shady sites (Eilers and Roosa 1994, Mabry 2002).

There were two additional criteria for species selection. First was the ability to match a common and restricted species within the same genus or family. Inclusion of phylogeny has often been limited by lack of robust phylogenies for many major groups (Gaston

Table 1. Fourteen Midwestern, U.S.A. woodland herbaceous species in seven families analyzed for differences in seed number and size. Frequency is the number of plots each species occurred in (out of 103 plots); sites is the number woodland sites sampled; samples are the number of plants harvested per site.

Family and species	Frequency	Sites	Samples
Asteraceae			
<i>Solidago ulmifolia</i>	55	3	10
<i>Solidago flexicaulis</i>	31	3	10
Berberidaceae			
<i>Podophyllum peltatum</i>	59	3	10
<i>Caulophyllum thalictroides</i>	12	3	10
Cyperaceae			
<i>Carex blanda</i>	93	4	8
<i>Carex jamesii</i>	49	4	8
Liliaceae			
<i>Erythronium albidum</i>	69	4	10
<i>Uvularia grandiflora</i>	36	4	10
Poaceae			
<i>Festuca obtusa</i>	87	3	8
<i>Elymus villosus</i>	9	3	8
Ranunculaceae			
<i>Ranunculus abortivus</i>	90	4	10
<i>Ranunculus hispidus</i>	22	4	10
Violaceae			
<i>Viola sororia</i>	98	3	10
<i>Viola pubescens</i>	77	3	10

1994). However, when a phylogeny is not available, comparing congeneric or confamilial pairs of species is an acceptable substitute because we can be reasonably sure that these pairs share a more recent common ancestor than species from other genera or families (Silvertown and Dodd 1997). Although some species within each pair may differ in some significant ways, each pair shares far more affinities with one another than with the members of the other pairs, particularly in fruit and seed morphology, and in dispersal mode, factoring out of the analysis such potentially confounding traits.

Second, because this was a study using naturally-occurring populations, selection of species pairs was constrained by the requirement that they co-occur at a minimum of three sites (where site was a woodland spatially isolated from all other sites by a minimum of 15 kilometers), and that their populations be intermixed within sites and be of sufficient size to allow a minimum of eight individuals to be destructively harvested.

The species that differed in frequency, that could be paired within genus or family and that co-occurred in natural populations large enough to allow destructive harvest essentially limited the possible pairings to those that I included in the study. No species was included that has a capacity for long-distance dispersal by animals, a dispersal mode that would potentially mitigate the disadvantage of large seeds. I don't believe lack of this dispersal mode influenced the results because large-seeded fleshy fruited species do not necessarily disperse long distances (Jakobsson and Eriksson 2002). In general, long-distance dispersal by animals should

probably be treated separately because animals introduce a number of complicating factors; for example passage of seeds through some bird species results in seed destruction, while other bird species consume the fleshy parts only (Harper 1977). Differences in clonal growth were not considered important in this study because clonal growth would not be a factor promoting long-distance dispersal in this fragmented landscape, and is not always a factor in local dynamics (Fröberg and Eriksson 1997). Table 1 gives a complete list of species and families, frequency of occurrence, number of sites sampled, and number of individuals harvested within each site.

Sampling

Individuals were selected for harvest by randomly selecting 8–10 individuals from a population at each site. For species where fruits mature over time, the marked individuals were closely monitored so that fruits were not lost prior to the final harvest. When all fruits had matured, whole plants (roots, vegetative and reproductive structures) were harvested. Because some of the species included in the study are clonal, some harvested individuals could have been ramets from the same genet, a source of error not accounted for in this study design. In two instances it was necessary to modify the harvest strategy. In central Iowa, *Uvularia grandiflora* generally occurs in very small populations and destructive harvest would have essentially eliminated the populations. However, at one site the population consisted of thousands of individuals; at this site, a separate sub-sample of 25 individuals was harvested. Root mass of these plants was regressed on total plant mass to estimate the mass and allocation of the sample plants ($R^2=0.90$). Because *Podophyllum* is highly clonal and lacks a concentrated root system, root mass was not estimated for the *Podophyllum*–*Caulophyllum* comparison.

Upon harvest, vegetative and reproductive structures were separated, oven-dried at 55°C for a minimum of 48 h, and weighed. Total seed number per plant was the number of mature seeds; mean seed mass was the mean mass of individual mature seeds, and was used as a measure of seed size, and, except for the perigynia of the two *Carex* species, did not include accessory structures. Shoot mass was the above ground vegetative structures minus the accessory structures immediately supporting the fruits (of very minimal mass), and was also obtained in order to examine the potential relationship between plant size and the number and size of seeds. The data were analyzed using two-way ANOVA with type III (sequential sums of squares). Family was treated as a block, and restricted vs common status as the independent variable (applied to species); mean seed mass and mean seed number per plant were the dependent

variables. Family was considered a block because I wanted to control for variation among families but was not interested in this source of variation as an experimental question. To examine the importance of including taxonomic data, the ANOVA was also done without family as a block factor. The relationships between shoot mass (plant size), seed number and seed mass were analyzed using Pearson product moment correlation. To normalize distributions, mean seed number, seed mass, and vegetative mass data were log transformed before analysis. Analyses were carried out using Data Desk v.6 (Data Description, Inc. 1997).

Results

Restricted species produced on average nearly an order of magnitude fewer seeds compared to common species (94 vs 663 seeds). Mean seed mass of restricted species was also over an order of magnitude greater for restricted compared to common species (0.015 g vs 0.0003 g). Results of ANOVA showed that these differences were significant at $p \leq 0.05$ (Table 2). When taxonomic information (families treated as blocks) was not included in the analysis, the ability to detect differences between restricted and common species was reduced (Table 2). The observed differences were consistent across plant families. Restricted species in all seven families included in the study had larger seeds than the related common species, and restricted species in six of the seven families had fewer seeds compared to the related common species (Table 3, Fig. 1).

There was a strong negative correlation between seed size (mass) and number ($r = -0.817$, $p = 0.0004$).

Table 2. Analysis of variance for relationship between abundance status and two reproductive traits for woodland herbaceous species in the Midwestern, U.S.A. Status refers to common versus restricted. results with family are given followed by the analysis with family excluded.

	df	Mean square	Probability
Mean seed biomass			
status	1	1.466	0.0093
family	6	0.943	0.0082
error	6	0.103	
status	1	1.466	0.1200
error	12	0.523	
Mean total seed number			
status	1	0.902	0.0275
family	6	1.125	0.0058
error	6	0.108	
status	1	0.902	0.2497
error	12	0.616	
Total vegetative biomass			
status	1	0.163	0.2850
family	6	0.163	0.3549
error	6	0.119	
status	1	0.163	0.3025
error	12	0.141	

Common species averaged less total vegetative mass compared to restricted plants (vegetation mass 2.37 g vs 3.57 g), but this difference was not significant (Table 2), and neither seed number or mass was strongly correlated with aboveground vegetative mass ($r = 0.227$ and 0.138 for seed mass and number respectively). Similar results were obtained when root mass was included (data not presented). This suggests that greater seed number in common species could not be attributed to larger plant size, nor could greater seed size be attributed to larger plants among restricted species. The relationship between reproductive measures and vegetative mass can also be examined by first calculating seed number (output) per unit of above shoot mass (about ground canopy), then correlating it with seed mass (Henery and Westoby 2001); these measures were strongly negatively correlated ($r = -0.91$, $p \leq 0.0001$, Fig. 2). The inverse relationship between seed mass and number, and between seed mass and the number of seeds produced per unit of canopy both suggest some level of trade-off in these species between seed size and number.

Discussion

Restricted woodland herbaceous species in this study produced nearly an order of magnitude fewer seeds. They also produced over an order of magnitude heavier seeds compared to related common species. This supports the hypothesis that restricted species are limited by dispersal because a species producing comparatively few seeds has a lower chance of reaching an unoccupied patch compared to a similar species with higher seed production e.g. they have an output advantage (Rees

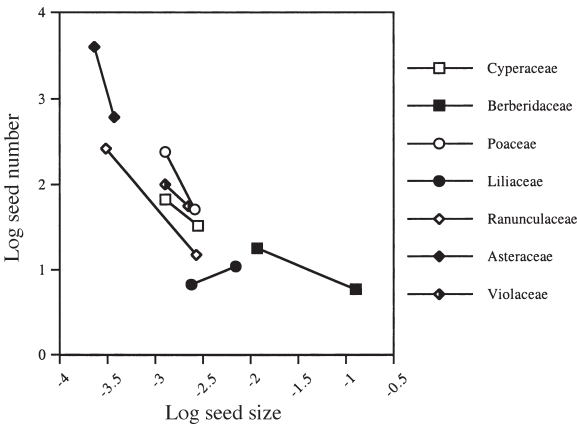


Fig. 1. Relationship between seed mass and seed number for seven pairs of Midwestern, U.S.A. forest understory species. Lines connect confamilial or congeneric groups of species. For each pair, the symbol on the left end of the line represents the common species, and the symbol on the right end the more restricted species.

Table 3. Mean values of two reproductive measures for restricted and common Midwest, U.S.A. woodland herbaceous species.

Family	Restricted species	Mean	Common species	Mean
Seed biomass				
Asteraceae	<i>Solidago flexicaulis</i>	0.0004	<i>Solidago ulmifolia</i>	0.0002
Berberidaceae	<i>Caulophyllum thalictroides</i>	0.127	<i>Podophyllum peltatum</i>	0.012
Cyperaceae	<i>Carex jamesii</i>	0.003	<i>Carex blanda</i>	0.0001
Liliaceae	<i>Uvularia grandiflora</i>	0.007	<i>Erythronium albidum</i>	0.002
Poaceae	<i>Elymus villosus</i>	0.003	<i>Festuca obtusa</i>	0.001
Ranunculaceae	<i>Ranunculus hispidus</i>	0.003	<i>Ranunculus abortivus</i>	0.0003
Violaceae	<i>Viola pubescens</i>	0.002	<i>Viola sororia</i>	0.001
Seed number/plant				
Asteraceae	<i>Solidago flexicaulis</i>	603	<i>Solidago ulmifolia</i>	3944
Berberidaceae	<i>Caulophyllum thalictroides</i>	6	<i>Podophyllum peltatum</i>	18
Cyperaceae	<i>Carex jamesii</i>	33	<i>Carex blanda</i>	68
Liliaceae	<i>Uvularia grandiflora</i>	11	<i>Erythronium albidum</i>	7
Poaceae	<i>Elymus villosus</i>	51	<i>Festuca obtusa</i>	236
Ranunculaceae	<i>Ranunculus hispidus</i>	15	<i>Ranunculus abortivus</i>	266
Violaceae	<i>Viola pubescens</i>	55	<i>Viola sororia</i>	100

1995, Jakobsson and Eriksson 2000, Aarssen and Jordan 2001, Murray et al. 2002, Westoby et al. 2002). Heavier seed mass may also reduce dispersibility (Wood and del Moral 1987, Ehrlén and Eriksson 2000, Dupré and Ehrlén 2002, Mauer et al. 2003, Verheyen et al. 2003), although in some instances this may not been the case (Brown 1992, Mauer et al. 2003). Because the ability to detect differences between restricted and common species was reduced when taxonomic data was not included in the analysis, the results also demonstrate the value of including taxonomic or phylogenetic information when comparing traits among species.

I also found that there was an inverse relationship between seed number and seed mass, and between seed mass and the number of seeds produced per unit of canopy. These patterns suggest that common species increased seed production by reducing seed size, and restricted species increased seed size by reducing seed number. These results also add support to the idea that

seed mass output forms an important dimension of variation across species that co-exist (Henery and Westoby 2001, Westoby 2002). Ecologically, this dimension is significant because it may help explain the co-existence in communities of species that emphasize different strategies: increased colonization potential through greater seed output on one hand, and increased probability of successful recruitment by producing larger seeds more resistant to hazards on the other (however, a spectrum of trade-offs or strategies are possible, Leishman et al. 2000).

Increased colonization potential arises from the “output advantage” of species with high seed production (achieved here by reducing seed size), because any one seed is more likely to reach a vacant patch compared to a species with lower seed output (Rees 1995, Jakobsson and Eriksson 2000, Aarssen and Jordan 2001, Murray et al. 2002, Westoby et al. 2002). In contrast, larger seeds have a lower probability of colonizing but are more likely to persist through hazards that include competition, defoliation, drought, shade, and burial under soil or litter (Winn 1985, Harper et al. 1970, Baker 1972, Westoby et al. 1997, 2002; reviewed by Leishman et al. 2000). Persistence under these conditions is associated with larger seedlings and greater nutrient reserve that can be deployed early in the life of the seedling to support carbon deficits (Westoby et al. 1997, Jakobsson and Eriksson, 2000, Westoby et al. 2002).

Although the strength of the relationship varies, inverse relationships between seed mass and number has also been found for other deciduous forest herbs (Dupré and Ehrlén (2002), sand dune annuals (Rees 1995), grassland plants (Jakobsson and Eriksson 2000), monocarpic weedy herbs (Aarssen and Jordon 2001), species occurring in a range of habitats (Shipley and Dion 1992) and six *Solidago* species (Werner and Platt 1976). On the other hand, Winn and Werner (1987) did not find strong trade-offs among these components of yield. In addition, Bruun (2001) pointed out that if larger seeded species have longer life spans than those

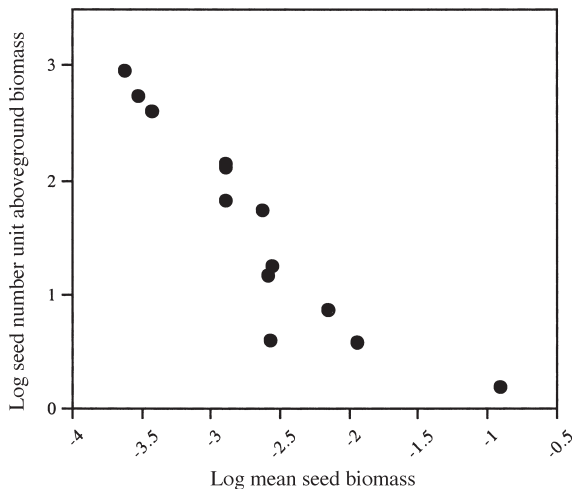


Fig. 2. Relationship between the numbers of seeds produced per unit of aboveground biomass and mean biomass of the seeds for fourteen Midwestern, U.S.A. forest understory species.

with smaller seeds, then life time reproductive effort of larger seeded species may in fact be greater, and a trade-off may not be observed if lifespan is considered. Furthermore, Bruun points out that even when seed mass is a good predictor of recruitment success, there may still be abundant unexplained variation, indicating other unidentified factors also influence recruitment success, potentially weakening the functional interpretation of trade-offs.

I am aware of only two other studies that quantified the relationship between seed mass and the number of seeds produced per unit of canopy (Aarssen and Jordan 2001, Henery and Westoby 2001). The results of both studies support the results found here, that for a given plant size seed mass and number cannot both be maximized. In addition, Henery and Westoby (2001) concluded that seed mass was the main driver of variation in seed output per unit canopy; the regression slope of the this relationship was -1.02 . For comparative purposes, the slope of this relationship in my study was -0.93 .

The potential trade-off between dispersal and recruitment offers an explanation for why there is a mix of seed numbers and sizes among this group of woodland perennial herbaceous species, but does not explain why species with a greater output of small seeds have a higher frequency of occurrence compared with species with fewer larger seeds, e.g. why there appears to be a greater advantage to output versus persistence. Family membership, life history, habitat and ecological factors may influence seed mass variation in angiosperms (Mazer 1989). I controlled for differences in family, and included species of only one life form and habitat type. Two ecological factors that are of overriding importance in the central Iowa landscape, cattle grazing and habitat fragmentation, very likely have promoted the greater abundance of species with relatively high output of small seeds.

Since settlement by Europeans 150 years ago, Iowa's forests have declined dramatically in both area and quality. Estimates of original cover range from 1.8 to 2.7 million ha, and reached a low of 0.65 million ha in 1974 (Jungst et al. 1998). Nearly 90 percent of the remaining forests have been grazed by cattle (Whitney 1994), although with varying intensity. However, between 1974 and 1992 the number of cattle in Iowa decreased by 41 percent and resulted in the abandonment of former woodland pastures. The United States Forest Service then reclassified these former pastured woodlands as forest (Jungst et al. 1998). By 1990 reclassification, along with secondary succession on abandoned agriculture land, accounted for an increased in Iowa forest area from its low of 0.65 ha to 0.81 million ha (Jungst et al. 1998), a trend that has continued (Brandrup, pers. comm.)

Grazing, reforestation and fragmentation may favor species with greater seed output by creating a plentitude of vacant patches or open sites. Both moderate and intensive cattle grazing result in elimination or decline in native species (DenUyl et al. 1938, Pettit et al. 1995, Mabry 2002). Once cattle have been removed former woodland pastures provide abundant open sites for re-colonization by woodland species. New woodlands formed by secondary succession also represent sites readily available for colonization. Because of their output advantage (above) common species have a greater probability of dispersing to these available sites. The fragmented landscape of Iowa has also likely promoted the distribution of species with relatively high reproductive output. For example, Dupré and Ehrlén (2002) found that species that produce fewer seeds were more negatively affected by isolation of deciduous forest patches in Sweden than more productive species, and numerous other studies have noted that spatially isolated woods tend to lack species with limited dispersal capacity compared to woods that are near seed sources (Peterken and Game 1984, Dzwonko and Loster 1992, Matlack 1994). Eriksson and Jakobsson (1998) have also suggested that the abundance of many species in fragmented landscapes is determined by dispersal rather than competitive ability.

Because of altered site conditions, Cattle grazing may also favor the successful establishment of small seeded species relative to those with larger seeds. A well-documented impact of cattle grazing is soil compaction, which decreases the size of both soil particles or aggregates and soil pores (Chandler 1940, Kucera 1952). Cattle grazing can also dramatically reduce the amount of leaf litter (DenUyl 1938). Re-colonization by smaller-seeded species may then be favored because compacted soil conditions make burial by larger seeded species more difficult (Mazer 1989), and because lack of ground cover favors small over large seeded species (Reader 1993).

The results of Jakobsson and Eriksson's (2002) work in Swedish forests offers some support to this interpretation. They found that abundance of forest species in two of three Swedish forests was positively related to seed size because larger seed size improved recruitment. However, in a third forest area, no relationship between seed size and abundance was found. They interpreted this as due to the more intensive management of the third forest, which may have decoupled the relationship between seed size and successful recruitment. Local site conditions, and an altered balance between factors promoting dispersal and persistence are plausible explanations for the greater frequency of small seeded species in this landscape; however, causal relationships between these factors were not investigated in this study. Other limitations at the establishment phase that could influence species distribution and

abundance include competition, facilitation, frugivory, seed predation, seedling herbivory, (Rust and Roth 1981, De Steven 1991, Gill and Marks 1991, George and Bazzaz 1999, Bruun 2001).

It would be useful for conservation efforts, our understanding of community assembly, and for predicting the effects of climate change and other human impacts if the relationship between seed size and abundance, and therefore dispersal, found in this study followed a general pattern. There is some evidence of a general tendency for seed output to be related to abundance. In a review of 54 studies and 94 traits, Murray et al. (2002) found that seed output was the only trait that was consistently related to species abundance patterns. In four of six studies, species with narrow geographical ranges produced fewer seeds (per unit measurement) than common species (Murray et al. 2002). In another study, Murray and Westoby (2000, cited in Murray et al. 2002) found that increased seed output also separated species that were locally abundant throughout their ranges from those that have sparse populations everywhere. General trends in other traits, including seed size, were not evident from the research he examined, however, and this is also reflected in literature I reviewed. For example, in her study of co-occurring prairie grasses in the Midwestern United States, Rabinowitz (1978) found that sparse grasses had lighter propagules compared to the common grasses, while Eriksson and Jakobsson (1998) found that abundance of Swedish grassland species was not directly related to seed size or number, but did find that more abundant species had smaller seed size deviation. As noted above, Jakobsson and Eriksson (2002) found that abundance forest understory species in two of three Swedish forests was positively related to seed size, which partially differs from what I found among this group of co-occurring woodland herbaceous species in the Midwest United States. Even within a very closely related group relationships between traits and abundance may vary. For example, Fiedler (1987) did not find consistent differences in seed weight among a common species of *Calochortus* lily compared to four congeneric rare species (seeds of the common species were lighter than two of the four rare species). Even though consistent or general relationships between seed traits and abundance may not emerge, the consistent pattern of differences across families in seed size and number found for the species in this study do suggest that within plant community types or regions more limited generalizations about factors limiting plant colonization may be possible.

In summary, my data show that within the woodland understory plant community in central Iowa U.S.A., restricted species produced far fewer but heavier seeds compared with closely related common species, suggesting that they are limited by dispersal. This pattern can

be understood as a trade-off in strategy favoring establishment versus one favoring dispersal, as well as a reflection of landscape history that has likely favored species with abundant dispersible seeds. Information from this study on seed number and size is also important for conservation and ecological restoration because the data suggests that common species are good colonizers and are likely to disperse to woodlands on their own, allowing limited resources available for restoration efforts to be focused the less common larger-seeded species (Dobson et al. 1997).

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