Seed addition experiments are more likely to increase recruitment in larger-seeded species

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Colonisation theory predicts that large-seeded species are more likely to show increased seedling recruitment in response to seed addition than are small-seeded species. This is both because their seedlings tend to have better survivorship potential, and because their background density of germinating seedlings tends to be lower. We tested this hypothesis by combining data from a recent review of seed addition studies with seed mass data. Logistic regressions showed positive relationships between seed mass and propensity to increase seedling establishment in response to seed addition in experiments in which establishment success was assessed within 6 months or a year, but not in experiments in which establishment success was assessed more than a year after seed addition. When data for all time periods were combined, a generalised linear model including terms for seed mass, time and an interaction term showed a significant positive relationship between seed mass and species response to seed addition. Thus, knowing a species' seed mass significantly increased our ability to predict its response to seed supplementation.

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Many experiments have been conducted to determine whether plant species show increases in seedling recruitment in response to seed supplementation. A recent review by Turnbull et al. (2000) synthesised information from these studies, and showed that approximately 50% of all plant species investigated showed increased seedling recruitment in response to seed addition. The present paper extends Turnbull et al. (2000) by determining whether the likelihood of a species showing an increase in seedling establishment in response to seed addition can be predicted from the species' seed mass.

Seed mass is an extremely important trait in the establishment strategy of a plant species. The number of seeds a plant can produce for a given amount of energy devoted to reproduction is inversely related to the mass of the seeds produced (Smith and Fretwell 1974, Jakobsson and Eriksson 2000, Henery and Westoby 2001). The greater seed output of small-seeded species (for a given amount of biomass) means that they reach a greater proportion of potential establishment sites than do large-seeded species. The lower seed output of the larger-seeded species is thought to be compensated for during seedling establishment, as seedlings from large seeds are generally better at tolerating stresses such as drought, defoliation, shade and competition with other plants (reviewed in Leishman et al. 2000).

Habitat colonisation by plants is often modelled by dividing the available space into a number of patches. Theoretical traditions of this kind were collectively christened the 'sessile dynamics framework' by Fagerstrom and Westoby (1997). They include colonisation– extinction models (Levins 1969, Tilman 1994), lottery models (Sale 1977, Chesson and Warner 1981), and seed-size/number trade-off models (Geritz 1995, Rees and Westoby 1997). Seeds are dispersed across the patches in this theoretical space, such that any patch may be reached by zero, one, or more seeds. The

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colonisation success of a species in these models depends on the number of patches reached by seeds, and the proportion of seeds that successfully establish in the patches they reach. Thus, one might expect smallseeded species to be more constrained by patch availability (they can only colonise suitable patches not reached by a larger-seeded species), and large-seeded species to be more constrained by seed availability. On this reasoning, large-seeded species would be expected to show a greater increase in seedling establishment following seed supplementation than small-seeded species (Turnbull et al. 1999).

In this paper, we combine data from the review by Turnbull et al. (2000) with seed mass data to test the hypothesis that large-seeded species are more likely to show enhancement of seedling establishment following seed supplementation than small-seeded species.

Methods

Data from seed addition experiments were taken from Turnbull et al. (2000), plus Zobel et al. (2000); the only paper published between 1999 and the time of writing that met the criteria set out in Turnbull et al. 2000). These papers gave information regarding the outcome of seed addition experiments for 98 species. Seed mass data were found for as many of these species as possible. Where possible, these data were taken from the reference detailing the seed addition experiments in question. In other cases, data were gathered from published lists of seed mass (U.S. Department of Agriculture 1974, Mazer 1989, Thompson et al. 1997, Eriksson and Jakobsson 1998). Seed mass data could not be located for 14 of the 98 species, so these were excluded from the dataset. This left a total of 84 species for which seed mass and response to seed addition were both known (Appendix 1).

Following Turnbull et al. (2000), we divided experiments into those that assessed establishment success (1) within 6 months of seed addition, (2) 6-12 months after seed addition and (3) more than 12 months after seed addition.

The data used in this study (and in the original study) are binary – that is, the species are either recorded as showing a significant increase in seedling establishment in response to seed addition or not. Information regarding the relative magnitude of the increase in seedling establishment in response to a given amount of seed addition might have enabled us to investigate more sophisticated hypotheses regarding the nature of the relationship between seed mass and species response to seed addition. However, the data required to calculate an effect size more accurately were not often readily available. Therefore, such analyses lie beyond the scope of this paper.

Statistics

Seed mass was log₁₀ transformed before analyses. The probability that a species showed increased recruitment in response to seed addition was modelled as a function of log₁₀ seed mass using logistic regression (Sokal and Rohlf 1995). Logistic regression takes a binary dependent variable (in this case response to seed addition), and generates a probability function in relation to a continuous independent variable (in this case log seed mass). For some species, experiments had been done by different researchers or in different environments. For these species we weighted the data points, such that each species contributed a weight of one across however many different experiments had been done. Data for Quercus robur were excluded from the analyses, as this species had a seed mass over two orders of magnitude greater than any other species, and therefore had a disproportionately large effect on the results.

Results

When data from all experiments were combined, a logistic regression including terms for seed mass, time and an interaction between seed mass and time was highly significant (P = 0.002; n = 186). The contribution of seed mass to this model was positive. Thus, on average, large-seeded species were more likely to show increased seedling establishment in response to seed addition. However, the interaction between time and seed mass was a significant term in this model (P =0.009). When data from studies in which seedling establishment was assessed more than a year after seeds had been added were excluded from the analysis, neither the interaction between time and seed mass (P = 0.727), nor time itself (P = 0.390) were significant terms in the model. Thus, experiments where outcomes were assessed after more than 12 months did not show the same response to seed mass as experiments in which seedling establishment was assessed within a year. For this reason, we present the results of the three time periods separately, as well as in combination.

There was a positive relationship between seed mass and the likelihood of increased seedling establishment in response to seed addition in cases in which seedling abundance was assessed within 6 months of seed addition (P = 0.0026; n = 34; Fig. 1A). For these cases, the probability of a positive response to seed addition rose from about 0.15 for seeds of 0.1 mg, to 0.6 for seeds of 1 mg, to 0.9 for seeds of 10 mg. There was a similar positive relationship between seed mass and likelihood of increased seedling establishment in response to seed addition across the 40 species in which seedling abundance was assessed 6–12 months after seed addition (P = 0.019; Fig. 1B). However, in the 44 species where seedling establishment was assessed more than 12 months after seed addition, there was no significant relationship between seed mass and the chance of increased seedling establishment (P = 0.55; Fig. 1C).

The most striking difference between the results of experiments in which seedling establishment was assessed after more than 12 months and those in which seedling establishment was assessed within 12 months is the greater proportion of large-seeded species that did not show a significant increase in seedling establishment in the studies in which establishment was not assessed until more than a year had elapsed since seed addition.

Discussion

The most important finding of this work was that the logistic regression including terms for seed mass, time and an interaction between seed mass and time showed a significant positive relationship between seed mass



Fig. 1. Establishment success following addition of extra seed (A) within 6 months of seed addition (B) 6-12 months after seed addition and (C) more than 12 months after seed addition. Note that whilst weighting was used in the statistical analyses, all points are represented equally in the scatterplots. The line shows the curve fitted using logistic regression. Means are indicated by vertical lines.

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and the probability that a species shows increased seedling establishment in response to seed addition.

When the three time periods were considered separately, the predicted positive relationship was found for species whose response to seed addition was measured within 6 months, or within a year - but not for those in which seedling establishment was assessed more than a year after seed addition. The results for species in which seedling establishment was assessed within a year were entirely in line with current theory (see introduction). Why then, might this relationship have been absent from species in which seedling establishment was assessed more than a year after seed addition? Possible reasons fall into two categories: (1) species responses to seed addition might change over time, or (2) there might have been some difference between the species or the ecosystems in which experimenters chose to assess seedling establishment within a year, and those in which more than a year was allowed to elapse before seedling establishment was assessed.

In order to investigate the hypothesis that differences in results between the different time periods were caused by changes in species responses over time rather than by incidental differences between the studies or species, we asked whether species responses to seed addition were consistent in instances in which the same species had been studied over different time periods. Only thirteen species in which seedling establishment success had been assessed more than a year after seed addition had also had seedling establishment success assessed within a year of seed addition. Of these thirteen species, eleven remained consistent across all time periods observed. The two species that did register a change in response shifted from significant increases in seedling establishment within 6 months to non-significant changes in 12 months. Although there was no majority tendency for species responses to attenuate over time, it is not possible to be certain that this proportion of changes could not have altered the overall result.

We considered two main reasons why species might change their response to seed addition over time: (1) the temporary nature of the advantage of large-seededness and (2) competition between and within species.

The temporary nature of the advantage of large-seededness

It has been shown many times that large-seeded species are only at an advantage during establishment during the time when reserves are being deployed from cotyledons. Once cotyledon reserves have been committed, there is no longer any advantage for the larger-seeded species (Westoby et al. 1996). Nevertheless, one might expect the advantage gained earlier in development to persist, unless the small-seeded species actively outperform the larger-seeded species later on. Consequently, the fact that the advantage is temporary seems an unlikely explanation for unexpected results in the longer-term studies.

Competition within and between species

As seedlings grow larger, the number of seedlings that can be sustained in a given area necessarily decreases. As density increases, so will inter- and intra-specific competition, and some seedlings must die as a result of these interactions. As the number of seedlings that can survive in a given area decreases over time, the chance that an increase in seedling establishment in response to seed addition will register as significant may decrease. This mechanism could diminish the proportion of significant responses, and if it acted differentially according to seed mass, could obviate over time the relationship between seed mass and probability of observing a significant response. However, the overall proportion of species in which seedling establishment increased in response to seed addition was 53% in studies that examined establishment within 6 months, 52% where establishment was assessed 6 months to a year after seed addition, and 54% where establishment was assessed a year or more after seed addition. Thus, it seems unlikely that this mechanism can account for the unexpected results of the longer-term studies. In addition, the fact that the proportion of species showing increases in seedling establishment in response to seed addition remains relatively constant suggests that the difference between long-term and short-term studies might be due to something other than changes in species responses over time.

Differences between shorter-term and longer-term studies

Researchers might have decided to assess seedling establishment over different time periods because of differences in the natural history of their study systems. We were able to investigate some features of the species and studies in which seedling establishment was assessed more than a year after seed addition, in order to see whether any of these features might explain the different result found.

The dataset for species in which establishment was assessed more than 12 months after seed addition had an unusually high number of species from woodland habitats. This contributed to the generally higher seed mass observed in studies lasting a year or longer, as species from woodland habitats had significantly larger (P < 0.001) seeds than species from other habitats. However, the logistic regression remained non-significant when woodland species were excluded from analysis (P = 0.64).

Tilman (1997) contributed a high proportion of the species in which establishment was assessed more than 12 months after seed addition. In Tilman's study, seeds of different species were added to the same plots. In other words, this was the only study in which between-species rather than within-species competition was emphasised. We wondered if this or some other aspect of this study might have contributed to the unexpected result for studies in which seedling establishment was not assessed for at least a year after seed addition. However, the logistic regression remained non-significant (P = 0.76) when these data were excluded.

In short, we did not find any trait of species or study that explained the different results observed in the longer time periods. Still, we were able to test only a few hypotheses, and many more possibilities remain untested. We should also note that in dividing the 44 species for which we have data in this time period into smaller groups, we necessarily decrease our power to detect significant relationships.

The most important finding of this work was that the overall model including seed mass, time and an interaction term produced a significant positive relationship between seed mass and species response to seed addition. Thus, large-seeded species are more likely to show increased seedling establishment in response to seed addition than small-seeded species. When the three time periods were considered separately, the predicted positive relationship was found for species whose response to seed addition was measured within 6 months, or within a year - but not for those in which seedling establishment was assessed more than a year after seed addition. We are not able to explain the unexpected result observed in the longer-term studies at present. However, these studies account for only a third of our data. It remains the case that the overall model including seed mass, time and an interaction term produced a significant positive relationship between seed mass and species response to seed addition. Thus, knowing the seed mass of a species significantly increases our ability to predict the likely response of this species to seed supplementation.

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Appendix 1. List of species included in analysis. All data are from Turnbull et al. (2000), except those species from Zobel et al. (2000). Zeros represent instances in which seedling establishment did not increase in response to seed addition; ones represent instances in which significant increases in seedling establishment were observed following seed addition. Seed mass data are from: 1, the same source as seed addition data; 2, Thompson et al. (1997); 3, Eriksson and Jakobsson (1998); 4, U.S. Department of Agriculture (1974); 5, Mazer (1989).

Species	Family	Seed mass (mg)	Seed mass data source	<6 months	6–12 months	>12 months	Reference
Achillea millefolium	Asteraceae	0.16	2	0	0		Johnston (1992)
Actaea spicata	Ranunculaceae	5.9	1			1	Eriksson and Ehrlén (1992)
Agrostis capillaris	Poaceae	0.06	2	0	0		Johnston (1992)
Ambrosia artemisifolia	Asteraceae	4.02	1			0	Tilman (1997)
Amorpha canescens	Fabaceae	2.260	1			0	Tilman (1997)
Andropogon gerardi	Poaceae	2.89	1			0	Tilman (1997)
Anthoxanthum odoratum	Poaceae	0.523	1		1		Peart (1989)
Anthoxanthum odoratum	Poaceae	0.523	1	0	0		Johnston (1992)
Anthoxanthum odoratum	Poaceae	0.523	1	Õ	-		Johnston (1992)
Asclepias svriaca	Ascleniadaceae	4 780	1	Ū		0	Tilman (1997)
Asclepias tuberosa	Asclepiadaceae	5 270	1			Ő	Tilman (1997)
Aster azureus	Asteraceae	0.17	1			Ő	Tilman (1997)
Aster aricoides	Asteraceae	0.060	1			0	Tilman (1997)
Retula allegheniensis	Betulaceae	1.008	1		1	0	Ribbens et al. (1994)
Boutaloua curtinandula	Poncene	1.000	1		1	1	Tilman (1007)
Campanula rotundifolia	Campanulaceae	4.10	3		1	1	$\mathbf{Z}_{\text{obel et al}} (1997)$
Cansella huma nastoria	Brassiaaaaaa	0.040	2	0	1		\mathbf{P}_{pos} (1080)
Capsella bursa-pastoris	Brassicaceae	0.11	2	0	0		Labratan (1002)
Capsella dursa-pastoris	Brassicaceae	0.11	2	0	0		$\frac{10992}{1000}$
Cardamine pratensis	Drassicaceae	0.0	2	0			Labratan (1989)
Caraamine pratensis	Brassicaceae	0.0	2	1	0		Johnston (1992) 7_{abal} at al. (2000)
Carex flacca	Cyperaceae	0.57	2	1	0	1	Zobel et al. (2000)
Carlina vulgaris	Asteraceae	1.53	2	1	1	1	Greig-Smith and Sagar (1981)
Centaurea jacea	Asteraceae	1.064	3	0	1		Zobel et al. (2000)
Cerastium fontanum	Caryophyllaceae	0.16	2	0	0		Johnston (1992)
Cirsium palustre	Asteraceae	2	2	0	0		Shea (1994)
Cirsium vulgare	Asteraceae	2.64	2	1	1		Klinkhamer et al. (1988)
Convallaria majalis	Liliaceae	17	1			1	Eriksson and Ehrlén (1992)
Crepis capillaris	Asteraceae	0.21	2	0	0		Johnston (1992)
Cynoglossum officinale	Boraginaceae	27.027	5	1	1		Klinkhamer et al. (1988)
Dactylis glomerata	Poaceae	0.51	2		1		Zobel et al. (2000)
Daucus carota	Apiaceae	1.04	1	1	1	1	Gross and Werner (1982)
Daucus carota	Apiaceae	1.04	1	1	1	1	Gross and Werner (1982)
Deschampsia hociformis	Poaceae	0.29	1		0		Peart (1989)
Desmodium canadense	Fabaceae	4.71	1			1	Tilman (1997)
Festuca rubra	Poaceae	0.79	2	0	0		Johnston (1992)
Festuca rubra	Poaceae	0.79	2	1			Johnston (1992)
Festuca rubra	Poaceae	0.79	2		1		Zobel et al. (2000)
Filipendula vulgaris	Rosaceae	0.518	3		1		Zobel et al. (2000)
Frangula alnus	Rhamnaceae	17.9	1			0	Eriksson and Ehrlén (1992)
Holcus lanatus	Poaceae	0.318	1		1		Peart (1989)
Holcus lanatus	Poaceae	0.318	1	0	0		Johnston (1992)
Hypericum perforatum	Hypericaceae	0.037	3		1		Zobel et al. (2000)
Lathvrus montanus	Fabaceae	15	1			1	Eriksson and Ehrlén (1992)
Lespedeza capitata	Fabaceae	2.420	1			1	Tilman (1997)

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Appendix 1 (Continued).

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Species	Family	Seed mass (mg)	Seed mass data source	<6 months	6–12 months	>12 months	Reference
Liatris aspera	Asteraceae	2.4	1			1	Tilman (1997)
Linnaea borealis	Caprifoliaceae	1.2	1			1	Eriksson and Ehrlén (1992)
Linum catharticum	Linaceae	0.15	2	1			Kelly (1989)
Linum catharticum	Linaceae	0.15	2		1		Zobel et al. (2000)
Lotus corniculatus	Fabaceae	1.67	2	1	1		Johnston (1992)
Maianthemum biflorum	Liliaceae	9.1	1			1	Eriksson and Ehrlén (1992)
Medicago lupulina	Fabaceae	2.01	2		1		Zobel et al. (2000)
Monarda fistulosa	Lamiaceae	0.33	1			1	Tilman (1997)
Oenothera biennis	Onagraceae	0.200	1	1	1	1	Gross and Werner (1982)
Oenothera biennis	Onagraceae	0.200	1	0	0	0	Gross and Werner (1982)
Oenothera biennis	Onagraceae	0.410	1			1	Tilman (1997)
Panicum capillare	Poaceae	0.200	1			0	Tilman (1997)
Paris quadrifolia	Trilliaceae	4.6	1			0	Eriksson and Ehrlén (1992)
Plantago lanceolata	Plantaginaceae	1.9	2	1	0		Sagar and Harper (1960)
Plantago lanceolata	Plantaginaceae	1.9	2	0	0		Sagar and Harper (1961)
Plantago lanceolata	Plantaginaceae	1.9	2	0	0		Sagar and Harper (1960)
Plantago lanceolata	Plantaginaceae	1.9	2	0	0		Sagar and Harper (1961)
Plantago lanceolata	Plantaginaceae	1.9	2	0	0		Sagar and Harper (1961)
Plantago lanceolata	Plantaginaceae	1.9	2	0	0		Johnston (1992)
Plantago lanceolata	Plantaginaceae	1.9	2		1		Zobel et al. (2000)
Plantago maior	Plantaginaceae	0.24	2	0	0		Sagar and Harper (1961)
Plantago major	Plantaginaceae	0.24	2	1	0		Sagar and Harper (1961)
Plantago major	Plantaginaceae	0.24	2	1	0	0	Hawthorne and Cavers (1976)
Plantago media	Plantaginaceae	0.283	3	1	0		Sagar and Harper (1961)
Plantago media	Plantaginaceae	0.283	3	0	0		Sagar and Harper (1961)
Plantago media	Plantaginaceae	0.283	3	1	0		Sagar and Harper (1961)
Poa annua	Poaceae	0.26	2	0	0		Johnston (1992)
Polvgonum convolvulus	Polygonaceae	5.07	1			1	Tilman (1997)
Potentilla arguta	Rosaceae	0.12	1			0	Tilman (1997)
Ouercus robur	Fagaceae	3489.1700	4	0	0	0	Crawley and Long (1995)
Raphanus raphanistrum	Brassicaceae	4.471	5	1			Rees (1989)
Ribes alpinum	Grossulariaceae	4.8	1			0	Eriksson and Ehrlén (1992)
Rosa arkansana	Rosaceae	14.6	1			Ō	Tilman (1997)
Rubus saxatilis	Rosaceae	10.3	1			0	Eriksson and Ehrlén (1992)
Rudbeckia serotina	Asteraceae	0.15	1			1	Tilman (1997)
Rumex acetosa	Polygonaceae	0.74	2	0	0		Johnston (1992)
Rumex acetosella	Polygonaceae	0.4	2		0		Putwain et al. (1968)
Rumex acetosella	Polygonaceae	0.4	2	1	1		Johnston (1992)
Rumex acetosella	Polygonaceae	0.4	2	0	-		Johnston (1992)
Rumex crispus var littoreus	Polygonaceae	1 33	2	1		1	Cavers and Harper (1967)
Rumex crispus var littoreus	Polygonaceae	1.33	$\overline{2}$	ī		ī	Cavers and Harper (1967)
Rumex crispus var littoreus	Polygonaceae	1.33	2	1		1	Cavers and Harper (1967)
Rumex crispus var littoreus	Polygonaceae	1.33	$\overline{\overline{2}}$	1		Ō	Cavers and Harper (1967)
Rumex crispus var trigranulatus	Polygonaceae	1 33	2	1		1	Cavers and Harper (1967)
Rumex crispus var trigranulatus	Polygonaceae	1 33	$\overline{2}$	i		i	Cavers and Harper (1967)
Rumex crispus var trigranulatus	Polygonaceae	1 33	2	i		i	Cavers and Harper (1967)
Rumex crispus var trigranulatus	Polygonaceae	1.33	$\overline{2}$	0		0	Cavers and Harper (1967)

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Appendix	1	(Continued).

Species	Family	Seed mass (mg)	Seed mass data source	<6 months	6–12 months	>12 months	Reference
Rumex obtusifolius	Polygonaceae	1.1	2	1		1	Cavers and Harper (1967)
Rumex obtusifolius	Polygonaceae	1.1	2	1		1	Cavers and Harper (1967)
Rumex obtusifolius	Polygonaceae	1.1	2	1		1	Cavers and Harper (1967)
Rumex obtusifolius	Polygonaceae	1.1	2	0		0	Cavers and Harper (1967)
Rytidosperma pilosum	Poaceae	1.079	1		0		Peart (1989)
Schizachyrium scoparium	Poaceae	1.8	1			0	Tilman (1997)
Senecio jacobaea	Asteraceae	0.41	1		0		Crawley and Nachapong (1985)
Senecio jacobaea	Asteraceae	0.41	1	0	0		Johnston (1992)
Sinapsis arvensis	Brassicaceae	1.15	2	1			Rees (1989)
Solidago nemoralis	Asteraceae	0.060	1			0	Tilman (1997)
Sorbus aucuparia	Rosaceae	3.5	1			1	Eriksson and Ehrlén (1992)
Sorghastrum nutans	Poaceae	2.280	1			0	Tilman (1997)
Stellaria graminea	Caryophyllaceae	0.273	3	0	0		Johnston (1992)
Stellaria lutensis	Caryophyllaceae	4.56	1			0	Tilman (1997)
Stipa spartea	Poaceae	14.8	1			0	Tilman (1997)
Tragopogon dubius	Asteraceae	6.84	1	1	1	1	Gross and Werner (1982)
Tragopogon dubius	Asteraceae	6.84	1	1	1	1	Gross and Werner (1982)
Trientalis europaea	Primulaceae	0.6	1			1	Eriksson and Ehrlén (1992)
Trifolium repens	Fabaceae	0.56	2	1	0		Barrett and Silander (1992)
Trifolium repens	Fabaceae	0.56	2	1	1		Barrett and Silander (1992)
Trifolium repens	Fabaceae	0.56	2	0	0		Johnston (1992)
Tripleurospermum inodorum	Asteraceae	0.29	2	0			Johnston (1992)
Tsuga canadensis	Pinaceae	2.4256	4		1		Ribbens et al. (1994)
Vaccinium myrtillus	Ericaceae	0.4	1			0	Eriksson and Ehrlén (1992)
Vaccinium vitis-idaea	Ericaceae	0.3	1			0	Eriksson and Ehrlén (1992)
Verbascum thaspus	Scrophulariaceae	0.067	1	0	0		Gross (1980)
Verbascum thaspus	Scrophulariaceae	0.064	1	1	1	1	Gross and Werner (1982)
Verbascum thaspus	Scrophulariaceae	0.064	1	1	0	0	Gross and Werner (1982)
Veronica chamaedrys	Scrophulariaceae	0.18	2	0	0		Johnston (1992)
Viburnum opulus	Caprifoliaceae	30.5	1			0	Eriksson and Ehrlén (1992)
Vulpia bromoides	Poaceae	1.429	1		1		Peart (1989)