

Species-level versus community-level patterns of mycorrhizal dependence on phosphorus: an example of Simpson's paradox

V. J. ALLISON*† and D. E. GOLDBERG

Department of Ecology and Evolutionary Biology, University of Michigan, 830 N. University, Ann Arbor, MI 48109-1048, USA

Summary

1. Ecological studies commonly assume that it is possible to extrapolate from a response shown by a fixed set of species to the response when the species composition is allowed to change. However, as described by Simpson's paradox, this is not necessarily a reasonable expectation.
2. The impact of Simpson's paradox on an ecological question was tested using a meta-analysis of data on plant responses to arbuscular mycorrhizas. Although species-level response commonly declines as phosphorus availability increases, we hypothesized that the community-level response could either decline or remain constant.
3. As expected, mycorrhizal response of individual species declined significantly as P supply increased. The response averaged across multiple species was negative but not robust, so we cannot distinguish clearly between the hypotheses.
4. It is impossible to assume that community-level responses to environmental gradients are the same as those found at species level. We recommend that experimental tests of hypotheses should allow species identity to change with the environment.

Key-words: Community composition, environmental gradients, scale

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Introduction

Much research in ecology addresses how the intensity or nature of processes changes along environmental gradients. However, environmental gradients often involve changes in species composition as well, potentially confounding direct effects of the environmental change with effects due to the change in species composition. For example, Peltzer, Wilson & Gerry (1998) criticized many experiments testing how competition changes along productivity gradients because they do not distinguish between changes in the standing crop of neighbours, and the accompanying change in species composition. A related, and potentially more serious problem, is the tendency to generalize from the magnitude of response to some factor by a fixed set of species, to the response shown when species composition is allowed to change.

Attempts to extrapolate from processes that affect a fixed set of species are flawed due to a statistical

phenomenon known as Simpson's paradox. According to Simpson's paradox, it is impossible to determine the response of the whole based on the response of subgroups (Simpson 1951). This issue has been almost entirely ignored in the ecological literature, although its importance has been noted in questions of productivity–diversity relationships, where relationships are affected by spatial scale (Scheiner *et al.* 2000). The same holds for scaling from species to community-level responses. The response to an environmental gradient averaged over individuals of the same species will not necessarily show the same trend as response to the same gradient averaged over individuals of many species. In this paper, we illustrate the problem of Simpson's paradox, using arbuscular mycorrhizas as an example. We present two alternative hypotheses of how species responsiveness to mycorrhizas changes with phosphorus (P) availability, and distinguish between them using a meta-analysis.

Arbuscular mycorrhizal fungi (AM) are thought to increase plant nutrient uptake, largely by increasing the absorptive surface area at a lower cost to the plant than roots (Jakobsen, Abbott & Robson 1992; Marschner & Dell 1994; O'Keefe & Sylvia 1991; Schwiger, Robson & Barrow 1995). Although beneficial when plant growth is limited by nutrients, the symbiosis

*Author to whom correspondence should be addressed.

E-mail: vallison@anl.gov

†Current address: Bldg 203, E133, Environmental Research Division, Argonne National Laboratory, Argonne, IL 60439, USA.

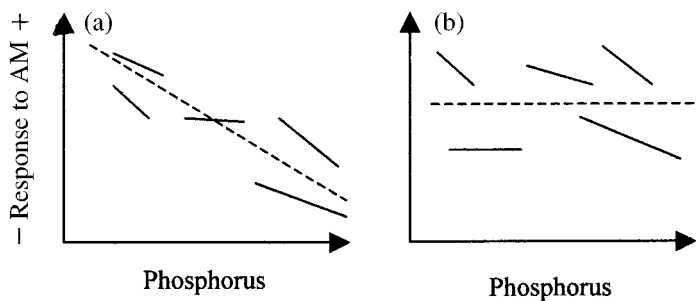


Fig. 1. Two hypothesized relationships between response of plants to arbuscular mycorrhizal colonization (AM) and P availability. The first (a) is based on the premise that if AM are important in determining growth under nutrient-limited conditions, on average, species will be less responsive to AM as P availability increases, and nutrient stress gives way to light stress. For any individual species (bold lines), response to AM is stronger at P-poor sites, and average response to AM averaged across all species (dashed line) declines similarly. The second hypothesis (b) proposes that each species undergoes an independent change in the type of resource-limiting growth as P availability changes. Each species shows a stronger positive response to AM in the lowest fertility areas in which it establishes, with response declining as P availability increases (bold lines). However, averaging over all the species found at a site (dashed line), the degree to which species respond to AM does not decline with productivity. As a result of change in species composition along the gradient, at any point there will be at least some species that respond strongly to AM.

is expensive to maintain. Hence, when light rather than nutrient availability limits growth, the cost of maintaining the symbiosis may outweigh the benefit obtained from it (Graham & Eissenstat 1994; Marschner & Dell 1994). Declining growth response to AM as P availability increases has been noted within a number of plant species (e.g. Boerner 1986; Cooper 1975; Mendoza & Pagani 1997). This leads to the assumption that plant species found in P-rich sites are less likely than those found elsewhere to depend on AM. This, in turn, suggests that the importance of AM in structuring communities is likely to be greater at P-poor sites.

However, this is not necessarily true. Our lack of broad-scale empirical studies makes it impossible to distinguish between two alternative hypotheses of how species' responsiveness to AM changes with P availability. The first is based on the premise that, if AM are important in determining growth under nutrient-limited conditions, on average, species will be less responsive to AM as P availability increases and nutrient stress gives way to light stress (Fig. 1a). For any individual species (Fig. 1a, bold lines), response to AM is stronger at P-poor sites, and the average response to AM averaged across all species (Fig. 1a, dashed line) declines similarly. The second hypothesis proposes that each species undergoes an independent change in the type of resource-limiting growth as P availability changes. At the lowest level of P availability at which a particular species can establish, growth will primarily be nutrient-limited and, as P availability increases, so will the relative importance of light competition. If this is the case, each species will show a stronger response to AM in the lowest fertility areas in which it establishes, with response declining as P availability increases (Fig. 1b, bold lines). However,

averaging over all the species found at a site (Fig. 1b, dashed line), the degree to which species respond to AM will not necessarily decline with productivity. As a result of change in species composition along the gradient, at any point along the gradient there will be at least some species that respond strongly to AM.

Ideally, distinguishing between these two hypotheses in the field requires manipulation of the AM status of communities along a gradient of P availability. This manipulation could be done with fungicide. If community response to fungicide was stronger at low than high P availability, it would support the first hypothesis. If community-level response to fungicide was as strong at high as low P availability, it would support the second. However, there is no fungicide specific to AM fungi. As a result, it is impossible to conclude that changes in response of the community to fungicide are due solely to changes in AM dependence.

Although it is not currently possible to distinguish between these two hypotheses using a direct experimental approach, existing data on species response to AM can be used. If the degree to which species respond to AM declines with increasing P availability, AM response of species typically found at P-poor sites will be greater, on average, than those found at P-rich sites (Fig. 1a, dashed line). Alternatively, species found at P-rich sites may be, on average, as responsive to AM as those found at P-poor sites (Fig. 1b, dashed line). In this paper we use previously published data on AM response to distinguish between these two hypotheses.

Methods

To obtain sources, we searched *Biosis* between 1985 and November 1999 (when the literature search was conducted), using the keywords 'mycorrhiza' and 'growth'. In addition, we added references from our files. Although not the most systematic approach, this increased the period from which references were drawn. In addition, it increased the number of ecological studies relative to agricultural ones. From this list, we excluded research on the effects of metals and other toxins, and on non-arbuscular mycorrhizal symbioses. We also excluded research that used units of P which could not be converted to mg P kg^{-1} soil; which did not give a biomass measure of AM response; or where no non-mycorrhizal control was established. We rejected studies that had P availability greater than 30 mg kg^{-1} , as the few studies performed at high P levels could bias the community trend. Other than for these reasons, no study was excluded on the grounds of perceived quality, as such subjective decisions have been shown by Englund, Sarnelle & Cooper (1999) to potentially bias results.

From these articles we recorded the species; P level; and biomass with and without AM. In addition, we recorded sample size. Because measures of variance were rarely reported, sample size was used to weight the analysis, with studies with many replicates given

more weight than those with few replicates. Although replicate number is not usually a good indicator of variability in ecological experiments, in this study it was a reasonable surrogate because of the similarity in experimental design among studies.

Response to AM was calculated as log mycorrhizal response ratio (lnMR). This metric is advantageous because it is symmetrical about zero, and its statistical properties are well known (Hedges, Gurevitch & Curtis 1999). It is calculated as:

$$\ln\text{MR} = \ln(\text{biomass with AM} / \text{biomass without AM}) \quad \text{eqn 1}$$

In some papers, a percentage response index (MRI) has already been calculated. This response ratio is calculated as:

$$\text{MRI} = [(\text{biomass with AM} - \text{biomass without AM}) / \text{biomass with AM}] \quad \text{eqn 2}$$

In these cases it was possible to convert from the response ratio to ln(MR), as:

$$\ln(\text{MR}) = -\ln(\text{MRI} - 1) \quad \text{eqn 3}$$

To determine average within-species AM response, we first determined the slope of the relationship between available soil P (as reported in the original source) and response measured as ln(MR). We used standard least-squares regressions, and calculated this slope for each species that had been grown over a range of P levels. Of these, one species was excluded as it had a fourfold steeper slope than any other species. The average slope and a 95% confidence interval about this slope ($n = 46$) were then calculated using bootstrapping in METAWIN (Rosenberg, Adams & Gurevitch 1997).

To determine how AM response averaged over many species changed with P availability, biomass response to AM was regressed against P availability (again, as reported in the original source), with each species represented by a single point. When a study assessed AM response over a range of P levels, only response at P level in unmanipulated soil was included in the regression. This excluded higher P levels resulting from fertilizer addition, and lower levels due to addition of sand. Response in unmanipulated soil, rather than the average response, was used to eliminate the potential for differences in treatment to influence AM response. Multiple points for a single species from a single study could not be included for several reasons, including lack of independence, and the potential for the negative response found within a species to impose a negative trend on the regression across species. Because both the dependent (lnMR) and independent (P-level) variables were measured with error, a reduced major-axis regression was used rather than a standard least-squares regression. This was calculated as a constrained nonlinear regression, as described by

Table 1. Species-level biomass response to AM along P gradients. Data are the mean and confidence interval of slopes of within-species least-squares regressions of P level against AM response

	<i>N</i>	Slope	95% CI lower	95% CI upper
Within-species	47	-0.030	-0.048	-0.012

Data sources: Anderson, Hetrick & Wilson (1994); Artunes & Cardoso (1991); Ba & Guissou (1996); Brandon & Shelton (1997); Dabas & Kaushik (1998); Haugen & Smith (1993); Henkel, Smith & Christensen (1989); Hetrick, Kitt & Wilson (1987); Johnson (1998); Khan *et al.* 1988; Lin & Fox (1992); Olsen & Habte (1995); Paula & Siqueira (1987); Raju *et al.* (1990); Schubert & Hayman (1986); Siqueira *et al.* (1998); Thingstrup *et al.* (1998).

Nichols (1996). Although the P levels used may not be precisely representative of the conditions to which each species is adapted, it would require consistent patterns in the direction of deviation relative to P availability to influence testing of the hypothesis. Because of the potential for large data sets to influence the analysis, the regression was performed a second time excluding individual data sets that contributed more than 5% to the original sample. In addition, because different methods of P extraction differ in efficiency of extraction, this reduced data set was further subdivided into studies that used the Olsen and Bray extractions, and regressions were repeated for these subsets. Least-squares regressions were performed in SYSTAT 9 (SPSS 1998), while reduced major-axis regressions were performed in SPSS 10.0 (SPSS 2000).

Results

For species-level responses, we first measured the slope of the relationship between biomass response to AM and P level for a single species at a time, then calculated a mean value of these slopes. Slopes were significantly negative on average (Table 1), indicating that, within species, plants respond more positively to AM when P availability is low.

For community-level responses, we calculated biomass response to AM only in unmanipulated soil for each species, and then regressed P level against response to AM across species. In this case, there was a weak but significant negative relationship between P level and AM response (Fig. 2, Table 2). When the two large data sets were removed, there was no significant relationship (Table 2). Further subdivision of this reduced data set into studies that used the Olsen and Bray extractions also found no significant relationship (Table 2).

Discussion

For individuals of a single species, declining response to AM fungi as P availability increases has frequently

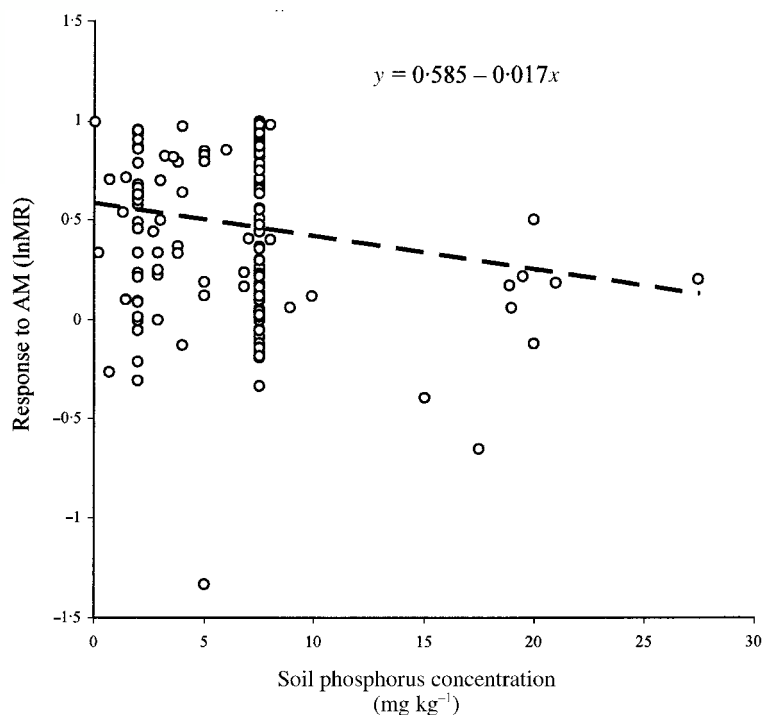


Fig. 2. Relationship between biomass response to AM and soil P concentration at the lowest level to which each species was exposed (full data set). For statistics, see Table 2; for data sources, see Appendix.

Table 2. Change in biomass response to AM with P level when averaged across many species, analysed with a reduced major-axis regression

	<i>N</i>	Slope	95% CI lower	95% CI upper
All studies	170	-0.017	-0.032	-0.003
Reduced data set	46	-0.019	-0.045	0.006
Olsen extraction	17	-0.016	-0.043	0.011
Bray extraction	11	-0.005	-0.141	0.132

All studies that met the criteria described under Methods are included in the full data set; individual data sets that contribute > 5% to the original sample are excluded from the reduced data set. The reduced data set is further subdivided into those that use the Olsen or Bray method of P extraction. For data sources, see Appendix.

been demonstrated, and is confirmed by our meta-analysis (Table 1). This finding leads to the assumption that species found in P-rich sites are less likely to depend on AM than species found at low-P sites. For example, Moyersoen, Alexander & Fitter (1998) found that growth of seedlings of *Oubanguia alata* was enhanced more by AM at low than high P availability, and suggested that AM should, in general, promote seedling growth more in the least fertile parts of the forest. However, as pointed out in Simpson's paradox, it is impossible to assume that the trend observed in the whole (across species) is the same as that observed in subgroups (within species). We hypothesized that along a gradient of P availability where species composition was allowed to change, the mycorrhizal response of the entire community could either decline (Fig. 1a), or not change (Fig. 1b).

The results of this study suggest the first hypothesis may be correct: biomass response to AM is more

strongly positive in species found at low than high P levels (Table 2; Fig. 2). However, this relationship breaks down when the reduced data sets are used (Table 2), suggesting the relationship is not robust. The decline in response to AM as P level increases is weak and extremely variable, and even in relatively P-rich sites there are some species that respond positively to the presence of AM fungi.

There are a number of weaknesses with any meta-analysis. In this case, perhaps the most important is differences in methods of P extraction. Methods differ in their efficiency of extraction, and this could contribute noise to the data set. However, when data sets are separated by extraction method, there is no significant relationship between response to AM and P levels (Table 2). A further caveat in attempting to extend these results to natural communities is that this approach ignores the potential for mycorrhizas to influence community composition by influencing interspecific interactions. For these reasons, and others, this study should not be viewed as an answer to the question of how the importance of AM changes with P availability. However, it makes an important point relevant to all ecological studies that address how processes are influenced by environmental gradients – any experimental approach taken must allow species composition to change. Almost all experimental tests hold species identity constant, and thus do not adequately test how processes change along environmental gradients, because trends shown in a subgroup of species are not necessarily the same as those shown by the whole community. Future studies should use species representative of natural communities at different points along environmental gradients, rather than using a subset of species and allowing just the environment to change.

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Appendix

Data sources and plant species used for analyses presented in Table 2

Source	Plant species	Source	Plant species
Abdel-Fattah (1997)	<i>Glycine max</i>	Wilson & Hartnett (1998)	<i>Sorghastrum nutans</i>
Allsopp & Stock (1992)	<i>Otholobium hirtum</i>		<i>Sporobolus airoides</i>
An <i>et al.</i> (1993)	<i>Aspalathus linearis</i>		<i>Sporobolus heterolepsis</i>
Anderson <i>et al.</i> (1994)	<i>Malus micromalus</i>		<i>Tridens flavus</i>
	<i>Andropogon gerardii</i>		<i>Tripsacum dactyloides</i>
	<i>Schizachyrium scoparium</i>		<i>Digitaria sanguinalis</i>
Armstrong <i>et al.</i> (1992)	<i>Aristida armata</i>		<i>Setaria glauca</i>
	<i>Cenchrus ciliaris</i>		<i>Setaria viridis</i>
	<i>Digitaria ammophilla</i>		<i>Agropyron cristatum</i>
	<i>Tyridolepis mitchelliana</i>		<i>Agropyron elongatum</i>
Azcom <i>et al.</i> (1988)	<i>Medicago sativa</i>		<i>Agropyron smithii</i>
Baon <i>et al.</i> (1994)	<i>Hordeum vulgare</i>		<i>Agrostis stolonifera</i>
Brandon & Shelton (1997)	<i>Leucaena leucocephala</i>		<i>Bromus inermis</i>
Cuenca <i>et al.</i> (1990)	<i>Cacao</i>		<i>Dichanthelium clandestinum</i>
Daba & Kaushik (1998)	<i>Acacia nilotica</i>		<i>Dactylis glomerata</i>
	<i>Dalbergia sissoo</i>		<i>Elymus canadensis</i>
Guisso <i>et al.</i> 1998	<i>Parkia biglobosa</i>		<i>Elymus cinereus</i>
	<i>Tamarindus indica</i>		<i>Festuca arundinacea</i>
	<i>Zizyphus mauritiana</i>		<i>Hordeum jubatum</i>
Haas <i>et al.</i> (1987)	<i>Capsicum annum</i>		<i>Koeleria pyramidata</i>
Haugen & Smith (1993)	<i>Anacardium occidentale</i>		<i>Lolium perenne</i>
Hayman & Tavares (1985)	<i>Fragaria vesca</i>		<i>Poa pratensis</i>
Henkel <i>et al.</i> (1989)	<i>Andropogon smithii</i>		<i>Bromus japonicus</i>
Hetrick <i>et al.</i> (1987)	<i>Zea mays</i>		<i>Bromus tectorum</i>
	<i>Sorghum vulgare</i>		<i>Hordeum pusillum</i>
	<i>Andropogon gerardii</i>		<i>Achillea millefolium</i>
Jakobsen (1987)	<i>Pisum sativum</i>		<i>Artemisia ludoviciana</i>
Johnson (1998)	<i>Salsola kali</i>		<i>Aster ericoides</i>
	<i>Panicum virgatum</i>		<i>Aster laevis</i>
Lin & Fox (1992)	<i>Musa paradisiaca</i>		<i>Aster sericeus</i>
Moor & Zobel (1998)	<i>Hypericum perforatum</i>		<i>Echinacea angustifolia</i>
Muthukumar & Udaiyan (1995)	<i>Tephrosia purpurea</i>		<i>Helianthus maximiliani</i>
Olsen & Habte (1995)	<i>Cajanus cajan</i>		<i>Hieracium longipilum</i>

Appendix Continued

Source	Plant species	Source	Plant species
Omar (1998)	<i>Triticum aestivum</i>	Wilson & Hartnett (1998)	<i>Kuhnia eupatorioides</i>
Osonubi <i>et al.</i> (1992)	<i>Acacia albida</i>		<i>Liatris aspera</i>
	<i>Acacia nilotica</i>		<i>Ratibida columnifera</i>
Parada & Liner (1996)	<i>Dendranthema grandiflora</i>		<i>Ratibida pinnata</i>
Raju <i>et al.</i> (1990)	<i>Sorghum bicolor</i>		<i>Rudbeckia hirta</i>
Roldan <i>et al.</i> (1992)	<i>Hedysarum confertum</i>		<i>Senecio plattensis</i>
	<i>Hedysarum spinosissimum</i>		<i>Solidago canadensis</i>
Schubert & Hayman (1986)	<i>Allium cepa</i>		<i>Solidago nemoralis</i>
Siqueira <i>et al.</i> (1998)	<i>Trema micrantha</i>		<i>Solidago rigida</i>
	<i>Schinus terebinthifolius</i>		<i>Vernonia fasciculata</i>
	<i>Stenolobium stans</i>		<i>Amorpha canescens</i>
	<i>Senna multijuga</i>		<i>Astragalus crassicaerpus</i>
	<i>Luehea grandiflora</i>		<i>Baptisia australis</i>
	<i>Jacaranda mimosaefolia</i>		<i>Baptisia bracteata</i>
	<i>Hovenia dulcis</i>		<i>Baptista lactea</i>
	<i>Senna macranthera</i>		<i>Cassia chamaecrista</i>
	<i>Senna spectabilis</i>		<i>Dalea purpurea</i>
	<i>Anadenanthera falcata</i>		<i>Dalea candida</i>
	<i>Cassia grandis</i>		<i>Desmanthus illinoensis</i>
	<i>Albizia lebeck</i>		<i>Desmodium illinoense</i>
	<i>Schizolobium parahyba</i>		<i>Desmodium sessilifolium</i>
	<i>Syzygium jambolanum</i>		<i>Lespedeza capitata</i>
	<i>Caesalpinia ferrea</i>		<i>Lespedeza cuneata</i>
	<i>Caesalpinia peltophoroides</i>		<i>Lotus corniculatus</i>
	<i>Ormosia arborea</i>		<i>Mimosa biuncifera</i>
	<i>Tipuana tipu</i>		<i>Psoralea esculenta</i>
	<i>Sapindus saponaria</i>		<i>Allium canadense</i>
	<i>Aspidosperma parvifolium</i>		<i>Allium stellatum</i>
	<i>Cedrella fissilis</i>		<i>Asclepias tuberosa</i>
	<i>Platycyamus regnellii</i>		<i>Asclepias verticillata</i>
	<i>Hymenaea courbaril</i>		<i>Euphorbia corollata</i>
	<i>Talauma ovata</i>		<i>Geum triflorum</i>
	<i>Bauhinia sp.</i>		<i>Oenothera speciosa</i>
	<i>Peltophorum dubium</i>		<i>Oxalis stricta</i>
	<i>Ceiba speciosa</i>		<i>Plantago lanceolata</i>
	<i>Copaifera langsdorffii</i>		<i>Rumex crispus</i>
Skalova & Vosatka (1998)	<i>Festuca rubra</i>		<i>Salvia azurea</i>
Thingstrup <i>et al.</i> (1998)	<i>Linum usitatissimum</i>		<i>Verbena hastata</i>
	<i>Brassica napus</i>		<i>Verbena stricta</i>
Vejsadova <i>et al.</i> (1992)	<i>Glycine max</i>		<i>Yucca glauca</i>
Weber <i>et al.</i> (1993)	<i>Cicer arietinum</i>		<i>Amaranthus spinosus</i>
Wilson & Hartnett (1998)	<i>Andropogon bladhii</i>		<i>Capsella bursa-pastoris</i>
	<i>Andropogon gerardii</i>		<i>Cassia chamaecrista</i>
	<i>Andropogon scoparius</i>		<i>Cirsium vulgare</i>
	<i>Andropogon virginicus</i>		<i>Erigeron annuus</i>
	<i>Bouteloua curtipendula</i>		<i>Erigeron strigosus</i>
	<i>Bouteloua gracilis</i>		<i>Daucus carota</i>
	<i>Buchloe dactyloides</i>		<i>Helianthus annuus</i>
	<i>Cynodon dactylon</i>		<i>Linum sulcatum</i>
	<i>Eragrostis curvula</i>		<i>Oenothera biennis</i>
	<i>Eragrostis spectabilis</i>		<i>Polygonum lapathifolium</i>
	<i>Panicum virgatum</i>		<i>Viola rafinesquii</i>