

THE RELATIONSHIP BETWEEN RELATIVE GROWTH RATE AND SENSITIVITY TO NUTRIENT STRESS IN TWENTY-EIGHT SPECIES OF EMERGENT MACROPHYTES

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SUMMARY

(1) Stress sensitivity is defined as the decrease in the relative growth rate of a species relative to a decline in resource supply. This definition is used to test the hypothesis of a trade-off between maximum relative growth rates and sensitivity to stress.

(2) The data used to test this hypothesis were collected from twenty-eight species of emergent macrophytes, occurring in north-eastern North America. Seedlings of these species were grown from seed in washed sand in a glasshouse in two nutrient conditions: full strength Hoagland's solution and one-tenth strength Hoagland's solution. Relative growth rates were determined from seedlings aged ten to thirty days old.

(3) There was no correlation between relative growth rate in the full strength Hoagland's solution and relative growth rate in the one-tenth Hoagland's solution ($r=0.29$, $P>0.1$).

(4) This resulted in a strong positive correlation between relative growth rate of these species in full strength Hoagland's solution and their sensitivity to decreasing nutrient supply (stress) ($r=0.80$, $P<0.001$), indicating that those species whose relative growth rate was highest in the more fertile conditions had their relative growth rate most depressed in the less fertile conditions.

(5) This relationship held even on a proportional basis, such that the proportional decrease in relative growth rate was correlated with sensitivity to nutrient stress ($r=0.55$, $P<0.01$).

INTRODUCTION

Species that typically occur in 'fertile' environments tend to have higher maximal relative growth rates than those that typically occur in 'infertile' habitats (e.g. Clarkson 1967; Grime & Hunt 1975; Grime 1979; Boston 1986; Chapin 1980, 1986). From such observations, Grime (1974, 1977, 1979) and others have hypothesized that such a correlation has a causal basis: species with high maximal relative growth rates do not occupy infertile habitats because their physiologies are more sensitive to suboptimal soil nutrient concentrations and so their relative growth rates decrease more rapidly as fertility of the environment decreases. This assumed trade-off is an important component of Grime's (1974, 1977, 1979) C-S-R model of plant strategies.

Relative growth rate is an important variable because it measures the rate of return of new tissue for a given investment in existing tissue. Continuing with the economic analogy, sensitivity to stress is a measure of the amount of 'perceived risk' involved in a particular investment when conditions deviate from the optimum. Note that this definition differs from that used by some authors (e.g. Larcher 1980) who define stress to be 'exposure to extraordinarily unfavorable conditions'. Grime's hypothesis, translated into an economic context, is that those investment strategies (genotypes) which have the

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greatest rate of return under optimal conditions are also the most susceptible to risk when environments deviate from the optimum. If this is correct, it can provide an important general principle for predicting (at least qualitatively) the response of species to suboptimal resource levels.

There are some published studies in which relative growth rates have been measured in environments differing in soil nutrient concentrations (Chapin 1980 and references therein), and the relationship described above has been found to occur. However, there are no studies in which a large number of species have been grown under comparable conditions in environments in which the relative degree of soil fertility can be quantified. Therefore, the extent of the generality of the proposed relationship between relative growth rates and sensitivity to nutrient concentrations is not known.

This paper tests Grime's (1974, 1977, 1979) claim of a general trade-off between the capacity for a high potential relative growth rate when growing in optimal growth conditions and the degree of reduction of relative growth rate in suboptimal environments ('stress tolerance'). This is done by comparing the seedling relative growth rates of twenty-eight species of emergent macrophytes at two points on a gradient of nutrient concentrations when all other resources (light, water, carbon dioxide) are not systematically varied. The terms 'stress' and 'sensitivity' in this paper require definition, as the concept of 'stress' and 'stress-tolerance' has been controversial (Harper 1982). This controversy has arisen, at least in part, from the lack of quantifiable measure of these terms.

An operational measure of stress and sensitivity to stress

Levitt (1980) has proposed definitions of stress and resistance to stress that removes any connotations of anthropomorphism, and is based on the engineering notion of these terms. His approach is followed in this paper, while acknowledging that the engineering analogy is not exact when applied to plants; it was also followed by Hunt & Nicholls (1986), although their assumption that stress and strain are necessarily equivalent is not made here.

Engineering concepts of stress and strain

In engineering, stress is the amount of external force applied to an object. Strain is a measure of the amount by which the object yields to a given force. An index of stress tolerance, the modulus, is the ratio of stress:strain.

Ecological concepts of stress and strain

If a species is grown along a gradient of increasing concentrations or intensities of a resource its relative growth rate will display suboptimal, optimal and supraoptimal responses, although under natural conditions supraoptimal (toxic) levels of a resource are relatively rare, except perhaps for micro-elements like iron or copper in very acidic or reducing environments. The stressfulness of an environment relative to a genotype is the magnitude of deviation of levels of the limiting resource from the optimal concentration. Thus, suboptimal resource levels are analogous to an external force in engineering. The analogue of the engineering concept of (elastic) strain is the decrease in relative growth rate of a species in a given environment from its maximum relative growth rate. Finally, the ratio of strain:stress is a measure of the susceptibility of a species to a given stress (Fig. 1). This is the inverse of the modulus and ranges from zero (completely insensitive to stress) to infinity (extremely sensitive to stress).

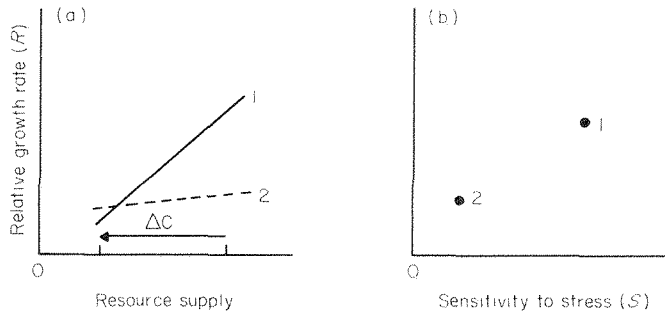


FIG. 1. (a) Hypothetical relationship between relative growth rate (R) and resource supply for species 1 and 2. Here, stress (ΔC) is equivalent for both species as they both reach maximal R at the same resource supply. (b) The resulting relationship between relative growth rate and sensitivity to stress for these two species. Species 1 is more sensitive to stress because, for an equivalent decrease in resource supply from the optimum, it shows a greater decrease in relative growth rate (ΔR).

METHODS

Relative growth rate

The per gram rate of biomass production (relative growth rate, symbolized by R_{ij} with units of $g(g\ time)^{-1}$) of a species i in environment j is defined in eqn (1), where y_{ijt} is the dry weight biomass (g) of an individual of species i in environment j at time t . This is strictly the instantaneous rate at which each gram of existing biomass at time t is producing new grams of biomass, and is analogous to the intrinsic rate of natural increase (r) in population biology (Pianka 1970). In this paper, R_{ij} is the slope of a linear regression of the natural logarithm of dry weight biomass on time. Because only two harvests were taken, this is an average value, not an instantaneous value.

$$R_{ij} = \frac{d \ln y_{ijt}}{dt} = \frac{1}{y_{ijt}} \frac{dy_{ijt}}{dt} \quad (1)$$

Sensitivity to stress

Using the concepts developed earlier, stress can be measured as the decrease in concentration of resource levels from the optimal levels (ΔC). Strain is measured as the decrease in relative growth rate from its optimum (ΔR_i). Stress sensitivity (S_{ij}) is the ratio of strain to stress and is measured in units of $g(\text{time } \Delta C)^{-1}$; sensitivity is proportional to strain in this experiment, because time and change in nutrient concentrations were the same for all species. A value of zero means that relative growth rate is not affected by a decrease in resource levels and the species is therefore very tolerant (not sensitive) of the stress.

$$S_{ij} = \frac{\hat{R}_i - R_{ij}}{\hat{C}_i - C_j} \quad (2)$$

where \hat{R}_i = maximum relative growth rate of i and \hat{C}_i = resource level at which \hat{R}_i occurs.

Sensitivity to stress can also be defined on a proportional basis (eqn (3)), and this may even be more relevant ecologically:

$$PS_{ij} = \frac{1}{\hat{R}_i} S_{ij} \quad (3)$$

Statistical tests

If proportional or absolute stress sensitivity increases with maximum relative growth rate then there must be a positive correlation between R_{ij} under optimal growth conditions and S_{ij} or PS_{ij} under stressed conditions. If there is no relationship, or if there is a negative relationship, then we can reject the hypothesized trade-off. However, testing for such a correlation is complicated by the fact that S_{ij} is defined in terms of R_{ij} . An alternative method would be to concentrate on the relationship between relative growth rates in the full strength and dilute nutrient environments (Fig. 2). If all species experience the nutrient stress in the same way then the slope of a reduced major axis regression (Sokal & Rohlf 1981) of the two sets of relative growth rate values would be unity (Fig. 2a). It is also possible that species with the highest relative growth rates in fertile conditions are the least affected by reduced nutrient levels, in which case the slope would be greater than unity (Fig. 2b). Therefore, it is sufficient to test the null hypothesis that the slope of the reduced major axis is unity against the one-tailed alternative that it is less than unity (of course, it can even be zero or negative). If there is no significant correlation between the two sets of relative growth rates then the null hypothesis can be rejected right away. Given such evidence, the significance of a positive correlation between R_{ij} in full strength Hoagland's solution and S_{ij} or PS_{ij} when nutrient concentrations are decreased can safely be tested.

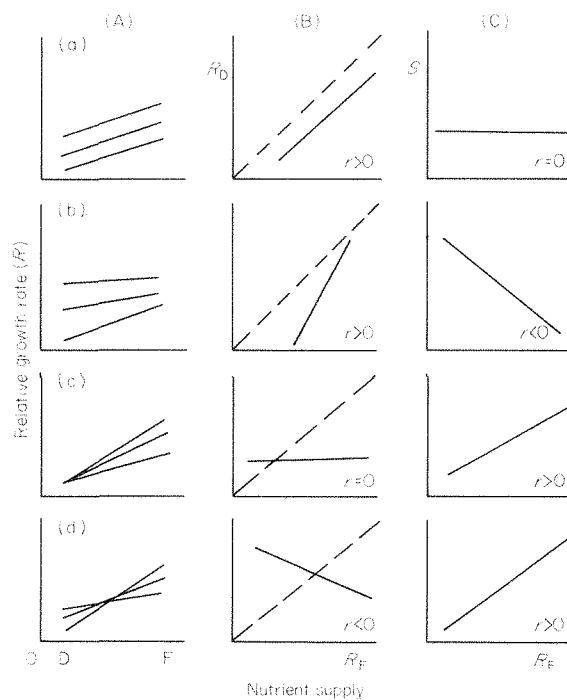


FIG. 2. (A) Four possible responses ((a) (b) (c) and (d)) of species' relative growth rate to decreases in resource supply. (B) Resulting relationships between relative growth rate in suboptimal environments (R_D) and in optimal environments (R_F). (C) The resulting relationships between sensitivity to stress (S) and maximal relative growth rates.

Experimental procedure

A gradient of nutrient concentration was established using a modified Hoagland's solution. Two different concentrations were used: a full-strength solution and one-tenth of this concentration. The nutrient concentrations are listed in Appendix 1.

Twenty-eight species of emergent macrophytes (listed in Appendix 2) were used in the experiment. These species occur on freshwater shorelines in north-eastern North America. There were two harvests, each with five replicates per species, for the two nutrient concentrations. Pots, each containing one individual, were arranged on the glasshouse bench in a randomized design of pairs of pots, one for each nutrient concentration. Each pot was 10.5 cm in diameter, 7.5 cm high, and contained 500 cm³ of washed sand. This volume is sufficient to allow even plants such as sunflower seedlings to grow for up to sixty days without becoming pot-bound (Grime & Hunt 1975). A lid, having a 2.5 cm hole in its centre, was placed on each pot. Once each week 50 cm³ of the appropriate nutrient solution was added to each pot. Each day sufficient water was added to the pots to keep the sand wet, but not so much that water would drain out of the bottom.

The glasshouse was maintained at approximately 25 °C throughout the experiment with temperatures occasionally varying from 15 to 30 °C. The experiment ran from mid-May until early July 1987. Seeds of the appropriate species were placed in the pots and the first seedling to emerge was used; all others were removed. The date of germination was recorded and the plant was then harvested at one of the two harvest dates: ten or thirty days after germination. These dates were chosen because most species studied by Grime & Hunt (1975) reached their highest relative growth rates between these dates.

Harvested plants were carefully cleaned to remove any sand from the roots, dried to a constant weight at 60 °C, and weighed to within 10 µg.

There is no evidence that full strength Hoagland's solution in a glasshouse represents ideal growth conditions for any or all of these species, although such conditions are probably a reasonable approximation to such a state for most species. In fact, subsequent observations have shown that this concentration is suboptimal for at least one species, *Lythrum salicaria*. Therefore, the R values quoted should be interpreted only as approximations of the R_{\max} values.

Taxonomic authorities are as in Fernald (1950), except where otherwise indicated.

RESULTS

Figure 3 shows the relationship between R_{ij} at full strength Hoagland's solution (symbolized as R_{iF} for 'full strength') and R_{ij} at one-tenth full strength (symbolized as R_{iD} for 'diluted'). There was no correlation between these two variables ($r=0.29$, $0.20 > P > 0.10$). As explained in the methods section and shown in Fig. 2, this resulted in a highly significant correlation between R_{iF} and S_{iD} ($r=0.80$, $P < 0.001$), indicating that those species having the highest relative growth rates in the fertile environment were most severely affected by a reduction in nutrient concentrations (Fig. 4). There was also a significant positive correlation between R_{iF} and PS_{iD} ($r=0.54$, $P < 0.01$), showing that even on a proportional basis those species having the highest growth rates in fertile environments were most sensitive to suboptimal nutrient concentrations (Fig. 5).

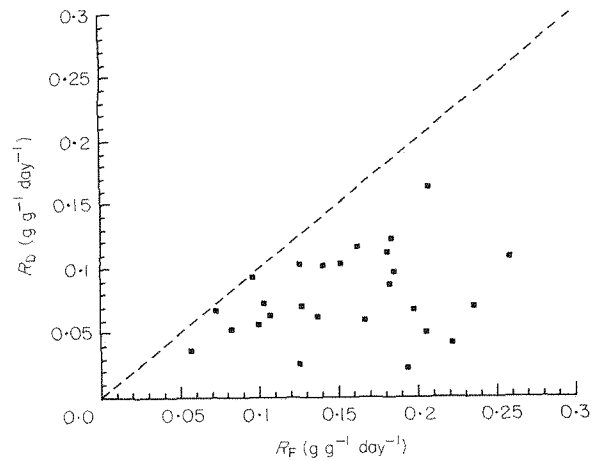


FIG. 3. Experimentally determined relationship between relative growth rates of twenty-eight emergent macrophytes in a glasshouse in the full-strength Hoagland's solution (R_F) and in the dilute solution (R_D); there is no significant correlation ($r=0.29$, $P>0.2$). The dashed line represents equivalent relative growth rates in the two nutrient solutions.

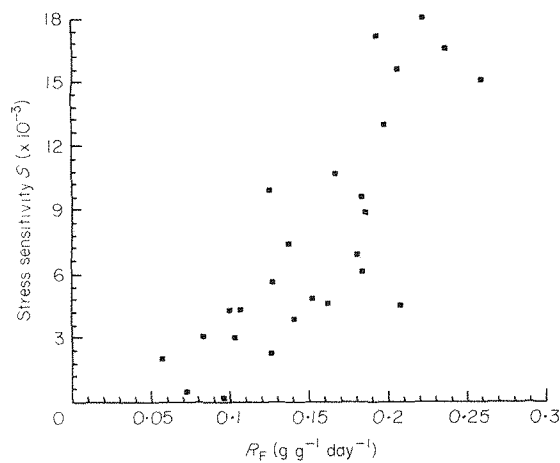


FIG. 4. Experimentally determined relationship between relative growth rates of twenty-eight emergent macrophytes in a glass-house in the full-strength Hoagland's solution (R_F) and sensitivity to stress; there is a significant correlation ($r=0.80$, $P<0.001$) due to an autocorrelation.

DISCUSSION

Conceptual models in community ecology which appear to provide simple and unifying explanations for disparate phenomena are useful for generating and focusing research. On the other hand, if such models cannot be translated into well-defined falsifiable hypotheses then they may channel valuable time and effort into unproductive and unresolvable controversy (Keddy 1987; Shipley & Keddy 1987b). Grime's (1974, 1977,

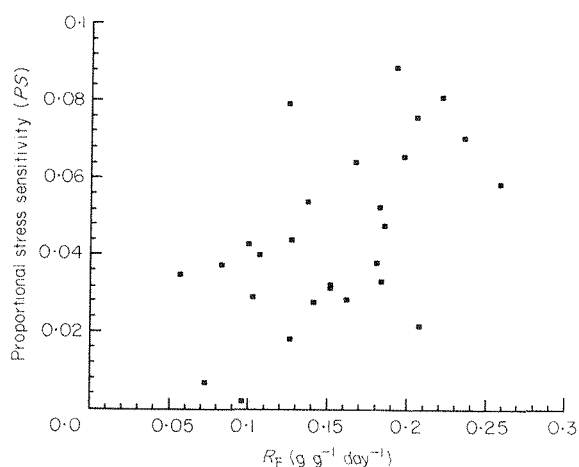


FIG. 5. Experimentally determined relationships between relative growth rates of twenty-eight emergent macrophytes in a glasshouse in the full-strength Hoagland's solution (R_F) and proportional sensitivity to stress; there is a significant correlation ($r=0.55$, $P<0.01$) due to an autocorrelation.

1979) C-S-R concept appears to be potentially useful, and this paper represents an attempt to translate one part of it into an operationally defined statement concerning the relationship between **R** and **S**.

The results summarized in Figs 4 and 5 are in qualitative agreement with the one aspect of the C-S-R model addressed in this paper. Those species that had the highest relative growth rates in the fertile conditions provided by full-strength Hoagland's solution had their relative growth rates most severely depressed in the infertile conditions of a one-tenth strength Hoagland's solution.

To study the effects of low light conditions, Fenner (1978) grew seedlings of six species of ruderals and six species of 'closed turf' species in 2.5-cm gaps in fertile soil under three different treatments: bare soil, short turf (1 cm high) and tall turf (up to 8 cm high) of *Festuca rubra*. Using his data on the relative growth rates of the twelve species in the three treatments, it was found that although the small-seeded ruderals had higher relative growth rates in the bare soil, this advantage was lost in the treatments involving an established canopy. There was no correlation between the relative growth rates in the bare soil and those in either the short-turf treatment ($r = -0.03$) or in the tall-turf treatment ($r = 0.18$). This is the same pattern as observed in this paper in relation to nutrient stress. Grime & Jeffrey (1965), in their study of the effects of shading, found that the relative growth rates of their species actually switched ranks when grown in open versus shaded conditions. The trade-off may therefore be quite general over many different forms of stress, although many more studies are needed to be confident of this.

Three caveats should be made concerning this study. First, although the replicates represented more than one population for each species, all seed was collected from a local area of the Ottawa River; therefore the measured variation in relative growth rates does not represent the total variation inherent in each species. Hunt (1984) has summarized data showing that variation between species in relative growth rates are about five times greater than variation between populations, genets and ramets of a single species. Therefore, the present results are not weakened by underestimating within-species

variation. It would be interesting to determine if the same relationship between R_{ij} and S_{ij} holds for different ecotypes of the same species, using a similar experimental approach.

Second, as stated earlier, the reported relative growth rates should not be interpreted as potential maxima for the species, as it is not known to what extent the chosen nutrient, light and temperature conditions represent optimal growth conditions. Indeed, species are likely to differ in their optimal growth conditions, so that such a screening programme can only approximate such conditions. However, there are recognizable ranges of intensity for most environmental factors where most species fare best physiologically (Fitter & Hay 1983); therefore, the range of optima between species is likely to be much less than the range of nutrient concentrations provided in the experiment, and so the general conclusion is still valid.

Third, although the general relationship between R and S was quite strong, there were exceptions. This may have been due to the artificial nature of the supply of nutrients as there was a flush of the same intensity and at the same time each week. Both theoretical (Sibly & Grime 1986) and experimental (Crick & Grime 1987) studies provide evidence that species show systematic differences in response to the temporal and spatial variance of nutrient supply, as well as to the absolute quantity of the nutrients. Of course, an adequate general test of this hypothesis would require a more sophisticated experimental design, but may be worth the added effort if the complexities of species' responses to temporally and spatially varying resource supply can be correlated with particular morphological or physiological traits.

The mechanistic explanation for the results reported in this paper are less clear. Shipley (1987a) measured the relative growth rates of twenty-five emergent macrophytes growing in nutrient enriched soil in a glasshouse, and found that R was negatively correlated with seed size: large-seeded species had lower R values than did small-seeded species. Fenner (1983) reported the same relationship. It is therefore possible that species in this experiment with low R values had low S values because the seedlings had higher initial nutrient reserves and were less dependent of external nutrient supplies. Alternatively, Chapin (1980) has reviewed evidence that stress-tolerant species have higher internal nutrient reserves in all phases of their life cycle because nutrients that are harvested by the plant are not allocated as quickly to meristems, resulting in lower per gram growth rates and higher tissue nutrient concentrations. There is no direct evidence to resolve these possibilities, but no correlation was found between R_{iF} and seed size in this study ($r = -0.21$, $P > 0.2$, seed weights log transformed for linearity), suggesting that the latter explanation is more likely.

The results of this study support the contention that there is a trade-off between relative growth rate and sensitivity to stress. If further work, examining a broad range of species and stresses, continues to confirm this generalization then general ecological characteristics of plant species may be confidently inferred from specific plant attributes. In the future this may allow us to predict, rather than simply explain, the ecology of species and communities.

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APPENDIX 1

Composition of stock solutions used to make up full-strength Hoagland's solution: the one-tenth Hoagland's solution was made up by adding one part of full-strength solution to nine parts of water. Note that the combined stock for minor elements was always prepared immediately before use from separate stocks of each minor element to prevent precipitation.

Stock solution composition (g dm ⁻³)	Full strength solution (cm ³ made to 1.0 dm ³ with distilled water)	
KNO ₃	101.10	5.0
Ca(NO ₃) ₂ ·4H ₂ O	236.16	2.0
MgSO ₄ ·7H ₂ O	246.5	5.0
KH ₂ PO ₄	136.00	1.0
Minor element (volume of stock)		1.0
Minor element stock composition (g dm ⁻³)	Combined stock (cm ³ made to 1.0 dm ³ with distilled water)	
H ₃ BO ₃	2.86	2.86
MnCl ₂ ·4H ₂ O	18.1	10.0
ZnSO ₄ ·7H ₂ O	22.0	1.0
MoO ₃	0.7	10.0
CuSO ₄ ·5H ₂ O	1.25	6.4

APPENDIX 2

Relative growth rates (R) ± standard error, of twenty-eight emergent macrophytes grown in Hoagland's solution (full strength or diluted × 10). Numbers of replicates given in parentheses. Seed dry weights ± standard error are given with all appendages (plumes, wings) removed (n = 5 replicates of 50 seeds).

Species	R g g ⁻¹ day ⁻¹		Seed weight (μg)
	Hoagland's	1/10 Hoagland's	
<i>Acorus calamus</i>	0.15 ± 0.02 (9)	0.10 ± 0.02 (9)	91 ± 17
<i>Bidens cernua</i>	0.18 ± 0.01 (10)	0.09 ± 0.02 (10)	104 ± 27
<i>B. frondosa</i>	0.20 ± 0.01 (10)	0.07 ± 0.01 (10)	175 ± 16
<i>Carex crinita</i>	0.18 ± 0.01 (10)	0.12 ± 0.02 (10)	63 ± 1
<i>Cyperus aristatus</i>	0.14 ± 0.06 (8)	0.10 ± 0.03 (10)	4 ± 1
<i>C. rivularis</i>	0.19 ± 0.02 (10)	0.10 ± 0.02 (10)	15 ± 3
<i>Dulichium arundinaceum</i>	0.06 ± 0.02 (9)	0.04 ± 0.02 (9)	53 ± 11
<i>Eleocharis erythropoda</i>	0.18 ± 0.02 (10)	0.11 ± 0.01 (10)	31 ± 5
<i>E. obtusa</i>	0.13 ± 0.05 (9)	0.03 ± 0.01 (8)	16 ± 8
<i>E. smallii</i>	0.18 ± 0.02 (10)	0.11 ± 0.01 (9)	145 ± 18
<i>Eupatorium perfoliatum</i>	0.24 ± 0.02 (10)	0.07 ± 0.01 (10)	10 ± 2
<i>Glyceria canadensis</i>	0.14 ± 0.02 (10)	0.06 ± 0.01 (10)	46 ± 5
<i>Hypericum majus*</i>	0.19 ± 0.03 (8)	0.02 ± 0.04 (10)	1
<i>Iris versicolor</i>	0.10 ± 0.02 (9)	0.09 ± 0.01 (10)	1364 ± 529
<i>Juncus filiformis*</i>	0.10 ± 0.01 (6)	0.06 ± 0.02 (7)	2
<i>Leersia oryzoides</i>	0.21 ± 0.01 (10)	0.05 ± 0.02 (8)	92 ± 18
<i>Lythrum salicaria</i>	0.22 ± 0.04 (9)	0.04 ± 0.02 (10)	5 ± 1
<i>Myrica gale</i>	0.07 ± 0.02 (10)	0.07 ± 0.01 (10)	143 ± 18
<i>Rhynchospora fusca</i>	0.11 ± 0.02 (10)	0.06 ± 0.01 (10)	42 ± 2
<i>Scirpus acutus</i>	0.21 ± 0.02 (10)	0.16 ± 0.02 (10)	161 ± 33
<i>S. americanus</i>	0.08 ± 0.05 (5)	0.05 ± 0.02 (7)	263 ± 45
<i>S. validus</i>	0.16 ± 0.03 (10)	0.12 ± 0.03 (10)	98 ± 7
<i>Stium suave</i>	0.26 ± 0.03 (7)	0.11 ± 0.03 (8)	110 ± 3
<i>Spartina pectinata</i>	0.17 ± 0.01 (10)	0.06 ± 0.01 (10)	161 ± 38
<i>Triadenum fraseri</i>	0.10 ± 0.02 (10)	0.07 ± 0.02 (10)	10 ± 2
<i>Typha angustifolia</i>	0.15 ± 0.03 (10)	0.10 ± 0.03 (9)	4 ± 1
<i>T. latifolia</i>	0.13 ± 0.03 (6)	0.10 ± 0.03 (8)	9 ± 1
<i>Xanthium strumarium</i>	0.13 ± 0.02 (10)	0.07 ± 0.01 (10)	2648 ± 846

* Seed weights too small to compute standard deviation.