A test of three juvenile plant competitive response strategies

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Abstract

Questions: 1. Are there competitive response strategies for light in juvenile plants? 2. If so, do plant traits (e.g. seed weight, relative growth rate, height and biomass) correlate with the strategies?

Location: Controlled greenhouse study using perennial vegetation typical of wet meadows in Northeast Ohio, USA.

Methods: We used two light manipulations in a greenhouse to screen ten replicates of 19 plant species for three proposed competitive response strategies ('*escape*', '*forage*', '*persist*'). We measured the time it took a seedling to die and the maximum height achieved when grown in the dark to assess two strategies, *persist* and *escape*. The biomass of seedlings when grown under a controlled, low-intensity, shifting light source was measured to test a third strategy, *forage*.

Results: We found significant variation across species in the measurements used to assess each strategy. The species ranking for each strategy was not concordant across strategies. Traits were found that correlated with the *escape* strategy (seed weight, height and biomass) and *persist* strategy (time to reach maximum height). No traits were found that correlate with the *forage* strategy.

Conclusions: There appear to be trade-offs by plants in the three strategies tested in this study. Species which had the best performance on one strategy typically scored poorly on the other strategies. However, many species fall in the middle range, ranking similarly across the '*persist*', '*escape*', and '*forage*' strategies.

Keywords: Light limitation; Plant competition; Trait screening; Wetland plant.

Abbreviations: CR = Competitive response, RGR = Relative growth rate.

Nomenclature: Gleason & Cronquist (1991); Anon. (1997).

Introduction

Plants can reproduce both vegetatively and sexually. Vegetative growth by clonal plants results in horizontal colonization and can occur even when clonal plants encounter low resource patches through translocation of stored acquired resources (Harper 1977; Birch & Hutchings 1994; Brewer et al. 1998). Seeds, however, potentially allow plants to diffuse through space and time via dispersal mechanisms and the seed bank (Fenner & Thompson 2004). Under the appropriate conditions a dispersed seed can germinate and establish at a 'safe site' temporally and spatially distant from its parent (Harper 1977; Strykstra et al. 2002). Such a safe site may occur among adult vegetation, but a seedling (i.e. juvenile plant) has a limited ability to acquire adequate resources from its environment and must rely on its seed stores until it develops roots for below-ground acquisition of water and nutrients, and leaves to intercept light for photosynthesis (Aarssen & Keogh 2002). The manner in which a juvenile plant utilizes stored resources and is able to acquire external resources will determine its establishment success.

A seedling experiences asymmetrical competition when establishing among mature vegetation, meaning that the competitive influence of the adult plant on the juvenile plant is much greater than the reverse (Keddy & Shipley 1989). Asymmetrical competition is understudied despite being the highest level of competition a plant might face (Aarssen & Keogh 2002). This unbalanced competitive interaction has led to the consideration of competition under two separate processes: (1) competitive effect, the negative effect one individual has on its neighbour; and (2) competitive response (CR), the ability to avoid suppression from its neighbours (Goldberg 1990, 1996). It has been suggested that all plants at all life stages simultaneously experience different levels of both competitive effect and response (Goldberg 1990, 1996; Howard & Goldberg 2001), but a seedling establishing among mature plants should exhibit little competitive

effect and a large CR (Keddy et al. 1998). These effects may be greater in highly productive systems where competition for light occurs, and less so in low productivity systems (Gerry & Wilson 1995).

Studies have found numerous correlates for competitive effect, such as relative growth rate (RGR) and functional groups (Goldberg 1996; Gaudet & Keddy 1988, 1995). Studies of CR are mixed in regard to the relationship between CR, RGR and functional groups, though most studies find no relationship (Keddy et al. 1998; Goldberg & Landa 1991). The lack of general correlates for CR makes predicting CR difficult. A potential resolution to this problem may be through a conceptual model developed by Keddy et al. (1998), which we will refer to as the competitive response (CR) strategy model.

Keddy et al. (1998) tested the CR of 48 wetland plant species. Using a comparative screening method, they placed each of the test species as juvenile plants under the canopies of seven mature sward species in outdoor mesocosms. Each of the 48 species was also grown without the sward species for calculation of CR.

After assessing plant biomass, they found no correlation between CR and competitive effect, or RGR. However, they found a wide range of CR values that, to them, suggested a set of possible strategic trade-offs. Keddy et al. (1998) proposed a conceptual model (the CR strategy model) that included three strategies to explain the variation of CR of juvenile plants growing under a canopy: (1) *persist*; (2) *escape*; (3) *forage*. The *persist* strategy is considered a sit-and-wait approach. Plants employing this strategy are thought to be able to wait for available resources due to their slow growth rate, but will eventually die if respiration exceeds the photosynthetic rate and stored resources are depleted. The *escape* strategy, they suggest, is where a plant grows rapidly in an attempt to break the surrounding canopy. *Escape* strategists should be characterized by higher RGR and higher achievable maximum heights using only seed energy reserve. The *forage* strategy is thought to be an opportunistic one, in which the plant is able to respond to patchy resources, as they are available. They proposed that *forager*s would be characterized by the ability to respond to patches and the speed at which they do so. *Persist*, *escape* and *forage* strategies are roughly comparable to, respectively, stress-tolerator, ruderal, and competitor plant strategy types for established plants (Grime 1977). However, because juvenile and adult characteristics are not correlated (Shipley et al. 1989; Grime et al. 1999) the two models are independent. The CR concepts are also comparable to recruitment strategies of tree seedlings. Tree seedling species establishment is sometimes placed on a dichotomous scale ranging from pioneer species to shade-tolerators, which are similar to *escaper*s and *persister*s (e.g. Agyeman et al. 1999). All

three strategies from the CR strategy model can be tested across species using laboratory manipulations.

We used comparative screening methods in the greenhouse to measure the performance of 19 species as a test of the CR strategy model. Comparative screening allows for the study of patterns that will be more generally applicable across species. This is done by applying identical treatments to a wide range of species (Grime & Hunt 1975; Grime 2001; Gaudet & Keddy 1988). Manipulations were provided by altering light availability rather than by placing juvenile plants into direct competition with adult plants. The objective of the study was to test the CR strategy model and place each test species into one of the three strategy types. To test the model our measurements for each strategy must be independent of one another and show variation across species along the axis of variation for each strategy type.

Methods and Analysis

A total of 19 perennial species covering a range of life history and morphological traits were selected for this experiment (Table 1), representing a wide range of form (e.g. grass or forb) and function (e.g. relative growth rate). The species selected are all typical of wet meadows and can be expected to be found occurring naturally in the same community. Seeds came from a commercial source, Ernst Seed Company, Meadville PA, or were collected in the field. Seeds from Ernst were a combination of field-collected and cultivated plants that were bulk processed so that there was genetic variability. Field collected seeds were taken from multiple individuals, and from at least three sites, which were then combined by species.

Ten replicates of each species were randomly located under two treatment conditions in a greenhouse. Tests of each strategy were adapted from the methods proposed by Keddy et al. (1998). Species were grown in a dark treatment to test both the *escape* and *persist* strategy. A shifting low-light treatment was used to measure the *forage* strategy. Ten replicates of each species were also grown under full light.

All plants were grown in sand in 225-mL containers sitting in a 250-mL cup filled with water. The container had holes in the bottom, was lined with landscape fabric to prevent loss of sand, and the height of the cup was such that the maximum water level was 7 mm below the sand surface. 25 mL of $2 \times$ Rorison's solution was added prior to sowing (Nitrogen: 112 mg/L, Phosphorus: 31 mg/L, Potassium 78 mg/L) (Hendry & Grime 1993). Seeds were germinated under natural light conditions on wet sand in Petri dishes. As soon as radicle emergence was observed, the seed was placed into the centre of the container just below the sand surface and randomly located under the

Table 1. List of study species. [a] = Gleason & Cronquist (1991); [b] = US Fish and Wildlife Service (1997); g = grass; f = forb; w = woody; y = yes; n = no.

Species	Abbreviation	Family	Life form	Wetland classification [b]
Agrostis stolonifera[a]	ASTO	Poaceae	g	FACW
Andropogon gerardii[a]	AGER	Poaceae	g	FAC-
Asclepias incarnata[a]	AINC	Asclepiadaceae	f	OBL
Bromus altissimus[a]	BALT	Poaceae	g	
Carex crinita[a]	CCRI	Cyperaceae	g	OBL
Carex lurida[a]	CLUR	Cyperaceae	g	OBL
Carex tribuloides[a]	CTRI	Cyperaceae	g	FACW+
Carex vulpinoidea[a]	CVUL	Cyperaceae	g	OBL
Cephalanthus occidentalis[a]	COCC	Rubiaceae	w	OBL
Desmanthus illinoensis[a]	DILL	Mimosaceae	f	FAC
Echinacea purpurea[a]	EPUR	Asteraceae	f	
Echinochloa crusgalli[a]	ECRU	Poaceae	g	FACU
Elymus virginicus[a]	EVIR	Poaceae	g	FACW-
Glyceria occidentalis[b]	GOCC	Poaceae	g	OBL
Liatris spicata[a]	LSPI	Asteraceae	f	FAC+
Lythrum salicaria[a]	LSAL	Lythraceae	f	FACW+
Phalaris arundinacea[a]	PARU	Poaceae	g	FACW
Rudbeckia hirta[a]	RHIR	Asteraceae	f	FACU-
Scirpus expansus[a]	SEXP	Cyperaceae	g	OBL

controlled light treatment. Individuals and species varied in the timing of germination. Consequently, not all individuals or species were tested simultaneously. However, individuals of the same species were tested within a few days of each other. Constant greenhouse conditions were maintained throughout the testing. Temperature was maintained with an air conditioner between 20 °C and 25 °C. Humidity was consistently between 35% and 45%.

In the dark manipulation, used to test the *persist* and *escape* strategies, seedlings were positioned under a plastic canopy that excluded all light from entering. A fan and duct circulated ambient greenhouse air through the light-exclosure. Plants were arrayed in ten randomized blocks, each of which contained one replicate of each species. Water was added to the cups every four days to maintain water levels. The height of each plant was measured every second day until the plant died, the time of which was also recorded. The plant was determined to be dead when the tissue turned brown or when the plant was no longer able to remain upright. During measurements and watering, care was taken to ensure that as little light as possible entered the exclosure; all room lighting was turned off and the plastic cover was left in place as much as possible. Plants may have been exposed to up to 10 min of very low-light levels (< 0.20 µmol.s^{-1}.m^{-2}) every two days. The entire plant, above and below-ground parts, was removed from the pot as soon as it was determined to be dead. Plants were then dried at 65 °C for at least 48 h and weighed.

In the foraging treatment, the plant was grown inside a covered tube (10 cm diameter and 20 cm tall) with a 15 mm hole drilled in the tube 5 cm from the top. The light source in the greenhouse was four 1000 W lights (16 h light / 8 h dark) distributed equally over the plant array. The mean light level in the tubes was 0.40 µmol.s^{-1}.m^{-2}. The plants were watered every four days to maintain water levels. After 14 days, plants received an additional dose of Rorison's solution to ensure they were not nutrient limited. The height of all plants was measured every second day and the covered tubes were rotated 90° to change the direction of the light source. All species displayed shoot emergence at the time of the first measurement. The entire plant was harvested after 20 days, dried for at least 48 h at 65 °C and the entire plant (roots and shoots) weighed.

Ten replicates of all 19 species were grown under the full light from the growth lights (98 µmol.s^{-1}.m^{-2}, 16 h light / 8 h dark, natural light was excluded by blacking out windows) in order to calculate CR. The height of the plants was measured every second day. After 20 days the plants were harvested, dried for 48 h at 65 °C and the entire plant weighed. Additionally, ten randomly-selected seeds of each species were dried for 48 h at 65 °C and individually weighed using an electro-balance (Cahn Model 25).

The measures used to assess each strategy were time to death, maximum-height^2/day and plant weight/seed weight for the *persist, escape* and *forage* strategies respectively. One-way, fixed-effect ANOVAs, factored by species, were used to check for variation among species on each of the strategy measures. Data was checked for homogeneity and normality. A *post-hoc* Tukey HSD was used to find differences among species. Pair-wise Spearman's ρ was calculated to verify independence of the three strategies from one another across species. All analyses were done using JMP 5.1 (Anon. 2003).

Simple linear regressions were done to examine the

Table 2. Mean standard measurements for all species. Plant height and weight were measured after 20 d of growth. Seeds and plants were dried for at least 48 h at 65 ºC before weighing. Standard errors are in parentheses. RGR values come from [a] = Shipley & Parent (1991); [b] = Levang-Brilz & Biondini (2002); [c] = Taub (2002).

Species	Mean plant height (mm)	Mean plant weight (mg)	Mean seed weight (mg)	RGR
Agrostis stolonifera	116.89 (8.14)	8.37 (2.25)	0.07 (0.01)	0.28[a]
Andropogon gerardii	79.62 (22.42)	10.88 (2.24)	3.23 (0.27)	0.1[b]
Asclepias incarnata	146.99 (6.48)	100.05 (10.09)	6.43 (0.42)	0.2[a]
Bromus altissimus	187.10 (18.30)	30.63 (6.82)	4.85 (0.27)	
Carex crinita	79.11 (9.72)	11.99 (2.55)	0.86 (0.07)	0.19[a]
Carex lurida	73.72 (4.52)	18.99 (3.58)	1.54 (0.17)	
Carex tribuloides	116.84 (10.55)	8.44 (1.52)	0.13 (0.01)	
Carex vulpinoidea	187.63 (10.91)	19.71 (3.06)	0.25 (0.01)	
Cephalanthus occidentalis	33.68 (9.87)	10.04 (2.82)	5.85 (0.41)	
Desmanthus illinoensis	146.58 (11.31)	63.83 (10.25)	6.76 (0.28)	
Echinacea purpurea	50.43 (3.38)	24.90 (3.71)	4.42 (0.45)	
Echinochloa crusgalli	473.11 (13.83)	221.13 (15.65)	4.02 (0.13)	0.29[a]
Elymus virginicus	76.50 (29.41)	8.65 (3.13)	3.45 (0.43)	0.130[c]
Glyceria occidentalis	194.13 (18.53)	23.66 (11.9)	2.36 (0.07)	
Liatris spicata	58.13 (13.53)	9.86 (2.43)	3.24 (0.17)	
Lythrum salicaria	42.36 (6.77)	32.96 (7.84)	0.08 (0.01)	0.27[a]
Phalaris arundinacea	189.37 (26.46)	37.31 (9.86)	0.92 (0.08)	0.258[c]
Rudbeckia hirta	19.38 (8.52)	6.22 (3.58)	2.70 (0.35)	0.12[b]
Scirpus expansus	9.65 (3.20)	0.52 (0.20)	0.12 (0.01)	

relationships between the strategy measures (dependent variables) and empirical characters of the plant species used (independent variables) (see Table 2). Additional tests were performed in the analysis of the *escape* strategy. We chose to use height^2/time as the metric. By multiplying rate by height, we emphasize the requirement of growing above the canopy. If height was used alone, the bolting aspects of the strategy would be neglected because a plant could grow tall but over a very long time. Likewise, using growth rate alone would be inaccurate because a plant could grow extremely rapidly to a small height. Therefore, height^2/time was the best representation of the conceptual idea of the *escape* strategy: fast growth, to a critical canopy height. A Pearson correlation coefficient was calculated to examine the relationship between the three potential metrics of *escape*: maximum height, growth rate and height^2/time. All three showed significant variation across species and were highly correlated with one another (not shown).

CR (R_m) for each species was calculated as in Keddy et al. (1998): $R_m = 100 \, (x_1 - x_2) / x_1$, where x_1 is the weight of the target plant grown under full light conditions; and x_2 is the weight of the target plant grown in low light (*forage* strategy test conditions). CR, and other variables, were compared against published relative growth rates (RGR) for some species (Table 2).

Results

Persist strategy

The duration a plant was able to live without light was variable across species (Fig. 1, ANOVA: *F*-ratio =15.5; *df* =18; *P* < 0.001). The longest-lived species were able to survive for approximately 30 days while some species died 10 days after germination.

Smaller-seeded species tended to survive longer than larger-seeded species; however, this relationship was only marginally significant (Table 3). Species that took longer to reach their maximum height survived longer than species that reached their maximum height relatively faster (Table 3). These findings indicate that slow-growing species generally survived longer.

There was no relationship between the plant's biomass or height and its ability to survive (Table 3). No species acquired biomass above that of the initial seed weight when grown in the dark. Similarly, there was no relationship between the time to death and the height of the plants that were grown under full light (Table 3).

Escape strategy

The measurement of *escape* showed variation amongst species (Fig. 2, ANOVA: *F*-ratio =22.2; *df* =18; *P* < 0.001). Larger-seeded species were faster growers than smaller species (Table 3). However, this relationship appears to be driven by the three species with the highest mm^2/day values. The ability to bolt was highly correlated
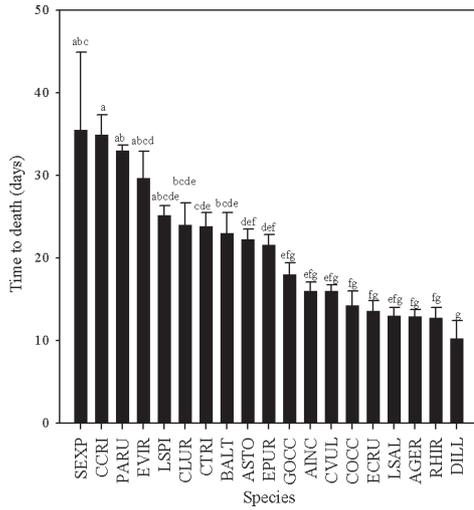
Fig. 1. Mean time to death for plants grown in the dark. Letters represent groups of species that are not significantly different from one another (Tukey HSD). Error bars represent standard error. Species are represented by their abbreviations (Table 1).

Table 3. Regressions of strategies against plant traits. Significant results ($P < 0.05$) bold. Traits refer to species means. Light biomass and light height refer to full light conditions for 20 d. RGR is obtained from published sources. Time to max. height is the length of time it took each species to grow to its maximum height when grown in the dark. Experimental height refers to the height of each species when grown under the foraging manipulation. Max. 2-day growth refers to the largest change in height over a 2-day measurement interval. Dark height refers to dark conditions. Competitive response R_m was calculated according to Keddy (1988); see Text. For each regression $n = 19$, except for RGR where $n = 9$.

Trait	Strategy	Correlation coefficient	P
Seed weight (dry)	*Persist*	–0.406	0.084
	Escape	**0.534**	**0.019**
	Forage	–0.190	0.436
Light biomass	*Persist*	–0.348	0.145
	Escape	**0.873**	**0.0001**
	Forage	–0.121	0.623
RGR	*Persist*	0.068	0.862
	Escape	0.299	0.435
	Forage	0.464	0.209
Height under foraging treatment	*Forage*	–0.187	0.444
Max. 2-day growth in the dark	***Escape***	**0.944**	**0.0001**
	Persist	–0.435	0.6861
Light height	*Persist*	–0.198	0.417
	Escape	**0.789**	**0.0001**
	Forage	–0.016	0.947
Time to max. height in the dark	***Persist***	**0.769**	**0.0001**
	Escape	–0.020	0.935
Dark height	*Persist*	0.015	0.862
	Escape	0.913	0.435
Competitive response	*Persist*	0.009	0.971
	Escape	0.137	0.576
	Forage	0.066	0.789

with the biomass of the species when grown in the light and the maximum growth over a two-day interval (Table 3).

The time to maximum height was not correlated with the ability to *escape* (Table 3). The five best *escaper*s showed a negative relationship with the time to maximum height, as expected, but the trend was not apparent in the 14 remaining species.
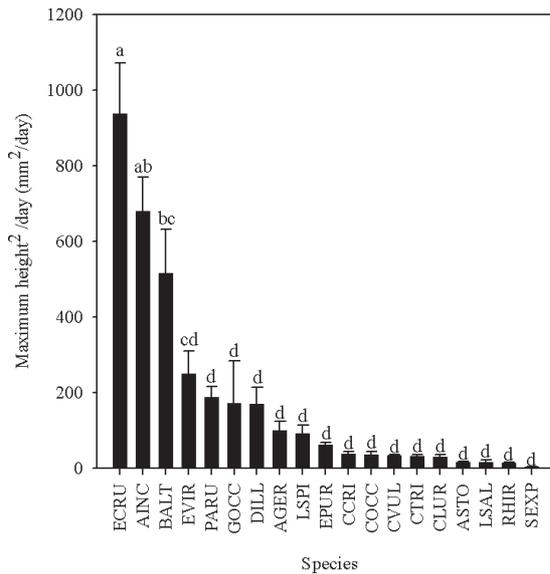

Fig. 2. *Escape* value (maximum height²/days) for each species when grown in the dark. Letters represent groups of species that are not significantly different from one another (Tukey HSD). Error bars represent standard error. Species are represented by their abbreviations (Table 1).
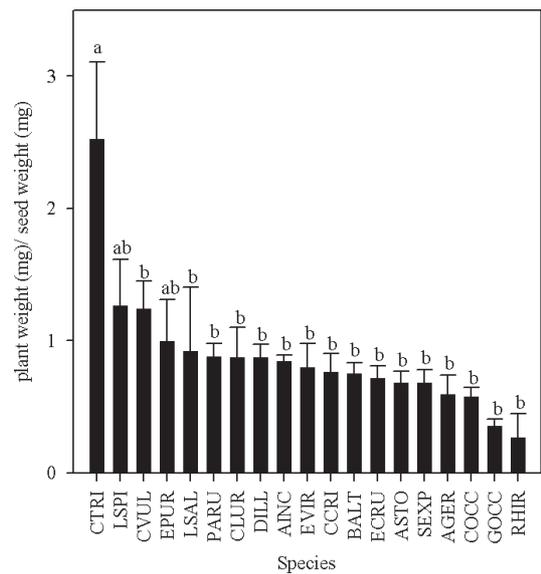

Fig. 3. Mean plant weight/seed weight for each study species when grown in low-light conditions with a shifting light source. Letters represent groups of species that are not significantly different from one another. Error bars represent standard error. Species are represented by their abbreviations (Table 1).

Forage strategy

Variation was observed across the measure of foraging ability for all species (Fig. 3, ANOVA: F-ratio = 34.0; df =18; $P < 0.001$). Three species gained biomass under the shifting light environment, while the other species lost biomass compared to their seed biomass. No plant traits were identified as predictors of the *forage* strategy.

Relationships between strategies and CR

Pairwise Spearman ρ values indicate that the measures for the three strategies were not concordant with each other: $\rho = –0.016, p = 0.95$ (*forage* by *escape*); $\rho = –0.004, p = 0.99$ (*persist* by *escape*); $\rho = 0.233, p = 0.34$ (*persist* by *forage*). In each pairwise comparison between the strategies we have rejected the null hypothesis that the strategies are concordant with each other. The CR values measured in this study unexpectedly correlate with published RGR values for nine species ($r^2 = 0.49, p = 0.037$). However, this relationship appears to be driven by two species with low RGR values.

Discussion

To establish the legitimacy of juvenile plant CR strategies for light the indices created for the three strategies must be shown to (1) comprise a broad range of values across species and (2) be independent of each other. We found that species vary in response for each of the strategies; species' rankings for each strategy were not concordant across strategies – if a species ranks high on one strategy it does not rank high on another. Thus trade-offs may exist between strategies. We did not find negative correlations between our tests for strategy traits because we were testing between three potential strategies – i.e. a poor *persister* may be either a good *escaper* or a good *forager* or some combination of the two. Therefore, our results support the CR strategy model.

There is a quantitative difference between a plant's competitive effect and CR, and there is evidence to suggest that these two competitive traits are not concordant (Keddy et al. 1998; Goldberg & Landa 1991). We found a wide variation in CR, while different CR strategies are evident at the juvenile stage. So, conventional traits such as growth rate and height are not the only factors that determine a plant's success at establishing. The ability to *persist* and *forage* may play a strong role in determining establishment success. We have shown that there is a detectable pattern in how different species respond to shading. For *escape* and *persist* strategies, it is possible to predict a species' response based on plant traits. The *escape* strategy is predicted by seed size,

height and biomass, while the *persist* strategy is predicted by the time to reach maximum height. For the *forage* strategy our design may have limited the interpretability of results; no predictors were found.

Persist strategy

Persist species take longer to reach their maximum height and must be allocating their energy reserves in small portions compared to species that display *escape* or *forage* strategies. Seed size is proportional to seed energy stores (Fenner 1983) but it is not necessarily the case that species capable of persisting have greater energy stores. In this study, seeds of long-lived species tended to be smaller than those of shorter-lived species. The small-seeded species may possess a mechanism by which they slowly allocate their energy. In tropical trees, with seeds of similar size, it has been shown that the most shade-tolerant species, without photosynthetic cotyledons, rely on their seed resources longer than light dependent species, with photosynthetic cotyledons (Kitajima 2002).

There is no relationship between the maximum height of a species and its persistence ability. *Persist* species should not need to allocate as much growth to height as *escape* species. However, a few grasses were relatively long-lived and had high maximum heights. These same grasses were also in the median range of seed weight and therefore may have had enough resources for the observed growth and regulate their use of energy over a longer time. In addition, species that reached a low maximum height were not necessarily long-lived. In a study of adult dune species' ability to survive simulated burial, by growth in complete darkness, plants showed no correlation between size or morphology and survival (Sykes & Wilson 1990). Although the Sykes & Wilson study dealt with adult plants, our situation is analogous in that the plants are restricted to utilization of only their stored resources. The ability to survive may be determined more by energy regulation, than by the amount of energy available.

The ability to *persist* appears to be an important trait in this predominantly wetland derived species set. Wetlands are frequently highly productive environments (Whittaker & Likens 1975), but are also subject to disturbance (Keddy 2000). The *persist* strategy would be advantageous when wetlands are dominated by large competitive species. Any disturbance that removed the dominant species would create opportunity for a *persist* strategist.

Escape strategy

Escape species were larger-seeded species. Presumably, these species have the necessary resources immediately available to them in their seed reserve to grow

tall to acquire light (Fenner 1978; Gross 1984). Poor *escape* species, with smaller seeds, lack these resources and therefore must acquire them in order to grow. When grown in light, good *escape* species had significantly higher biomass after 20 days than did poor *escape* species. These species have intrinsically higher growth rates, but the time to reach maximum height was not a predictor of *escape* response. However, for the five best *escape* strategists there appears to be a strong trend for higher *escape* values with lower time to maximum height (not tested). These five species also had among the largest seeds. This finding coincides with a large set of theory that suggests a trade-off between small seeds with high dispersal ability and large seeds with high competitive ability (Coomes & Grubb 2003).

Independently published RGR values were not a significant predictor of *escape* ability; this is surprising, given that fast growing species were significantly better *escaper*s. This may be due to the reduced number and selection of species with published relative growth rates. It may also be because plant development in the dark is different from development in the light even at the cellular and sub-cellular levels (von Arnim & Deng 1996). The growth of plants under the dark conditions may be independent of RGR measures obtained in light. It should also be noted that CR was correlated with RGR. This was unexpected due to the large amount of uncertainty in this relationship (Keddy et al. 1998; Goldberg & Landa 1991). Again, the reduced sample in this regression may be part of the explanation, and the relationship appears to be driven by two species. RGR did not correlate with either of the other two.

Forage strategy

The measurement of *forage* ability shows a range of values across species. However, there is an indication that light levels were too low for most species, because for most species there was no biomass accumulation. A slightly higher light level may have revealed greater variation in response. Consequently, results from the foraging test should be interpreted with caution. Nonetheless, three species were able to respond indicating their ability to forage and accumulate biomass at low-light levels. Foraging has been observed in plants (Campbell & Grime 1989; Birch & Hutchings 1994; Day et al. 2003) and thus it should be investigated more thoroughly with respect to CR. It has even been shown that some species increase biomass production, above what is achieved under full light, when light is patchily available (Wijesinghe & Hutchings 1996).

Conclusions

The apparent trade-off between *escape* and *persist* is clear. *Escape* strategists are likely to allocate the majority of their resources for immediate growth, while *persist* species use the majority of their resources for maintenance until the opportunity (i.e. resource availability) for growth arises. The trade-off between these two strategies and the *forage* strategy is less obvious. Due to their rapid growth rate, *foragers* can exploit patchy resource environments. Consequently, they direct the majority of their energy to growth, like an *escaper*. What is the fate of a *forager* that no longer has access to resources? It seems likely that *foragers* search until resource supply is exhausted, which for some large-seeded species may be a relatively lengthy time, thus positioning the strategy similarly to *persist*. Yet, the *forager* is unlike the *escaper* because it is not unidirectionally apical in its search nor is its growth necessarily constant. This variability in the *forage* strategy may therefore have contributed to the difficulty in testing it and finding correlates. CR did not correlate with the *escape*, *forage* or *persist* strategies. This was expected because performance on any one of the strategies could contribute to successful response.

Our study has important implications for restoration, conservation, and invasion ecology. We have identified a trait, response to shading, which could allow an ecosystem manager to be more selective as to which species are allowed to establish within an ecosystem. For example, *L. salicaria* is a troublesome invader of wetlands across North America (Thompson et al. 1987; but see Farnsworth & Ellis 2001). Our study demonstrates that the encouragement of tall, dense vegetation would limit the ability of *L. salicaria* to invade, but may still allow native species (e.g. *S. expansus*) to colonize and establish. It may also be possible for a land manager seeding an ecosystem to select plants that have a higher probability of being successful based on the existing vegetation.

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