Germination and seedling growth of bog plants in relation to the recolonization of milled peatlands

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Abstract

Two controlled experiments were conducted to evaluate the potential for vascular plants to germinate and establish in milled peatlands and to assess whether easily measured plant traits can be used to predict their probable success. Study species included twenty species of perennial herbs, shrubs and trees occurring frequently in undisturbed bogs or abandoned milled bogs in Québec, Canada. First, a glasshouse experiment was performed to test the effect of burial under peat on germination and seedling emergence. Second, a growth chamber experiment was conducted to measure relative growth rate and other growth parameters of seedlings between 1 and 3 weeks of age. In the burial experiment, seedling emergence decreased exponentially with peat depth for most species examined. The slope of the exponential decline varied between species and was strongly correlated to seed mass. Seeds less than 0.1 mg in mass were most sensitive to burial. In the seedling growth experiments, *Betula* species had the highest absolute and relative growth rates, which may help to explain their prevalence in milled bogs. Relative growth rate (RGR) was not correlated with seed mass, however it was strongly correlated with leaf area ratio (LAR) and especially specific leaf area (SLA) of seedlings, except for species with seed mass less than 0.01 mg. Screening of species for seed mass and SLA should help predict their germination and establishment success or failure in milled peatlands and allow more directed interventions to favour the establishment of desirable species in milled bogs.

Introduction

Plants recolonizing severely disturbed sites are faced with numerous challenges. Seeds or other diaspores must disperse to the site. Once settled, they must break dormancy, germinate, and sequester sufficient resources to establish and grow. During the restoration of disturbed plant communities, desirable species are actively introduced, and environmental conditions are selectively ameliorated to promote their establishment and growth. Prediction of the responses of desirable and undesirable species to critical environmental conditions is consequently essential to the prescription of suitable restoration techniques. One

approach to this problem is the identification and screening of plant traits required for species to survive critical environmental filters (Keddy (1992, 1999)). A list of easily measured traits would be especially useful for the prediction of successful species at different stages through the recolonization process.

Milled bogs are examples of severely disturbed ecosystems that have been the subject of restoration attempts (Wheeler and Shaw 1995; Rochefort 2000). In North America, peat is usually extracted from bogs using the modern method of milling and vacuum collection (Crum (1988), pp. 182–188). Once abandoned, milled peat surfaces are large (up to 5 km²), flat and bare of vegetation. Poorly- to well-decom-

posed *Sphagnum* peat substrates usually remain (< 1 m thick), which are acid (pH 3 to 5) and nutrient-poor (Wind-Mulder et al. 1996). There is no seedbank (Salonen 1987), and natural recolonization after the cessation of extraction activities is very slow (Desrochers et al. 1998; Bérubé and Lavoie 2000). Dispersal is a major constraint to natural recolonization of milled bogs; species with good dispersal abilities are favoured (Curran and MacNaeidhe 1986; Salonen 1987; Salonen and Setälä 1992; Poschlod 1995). However, microclimatic and substrate conditions in milled bogs also appear to be harsh and limiting to the subsequent germination of seeds and seedling establishment (Salonen et al. 1992; Tuittila et al. 2000).

Seed burial in milled bogs appears to be a critical filter for some species that impedes the release of seed dormancy and germination. Seeds may be buried under water- or wind-deposited loose peat and litter, or burial may result from the instability of milled peat substrates (Campbell et al. 2002). Small-seeded species are in general more dependent on light for germination than large-seeded ones (Milberg et al. 2000), and the emergence of buried seeds has repeatedly been correlated with seed size (old field herbs: Reader (1993); emergent macrophytes: Jurik et al. (1994); arid woodland species: Jurado and Westoby (1992); rainforest trees: Vázquez-Yanes and Orozco-Segovia (1992)). However, the application of this relationship to bog species and the seed size limit for emergence under peat are not known.

Once emerged, seedlings in milled bogs will be subject to surface instability and strong winds (Campbell et al. 2002), hot and dry surface conditions in mid-summer (Price 1997; Price et al. 1998), needle ice which forms near the peat surface in spring and fall and damages roots (Quinty and Rochefort (2000); E. Groeneveld, Université Laval, pers. comm.), and low pH, nutrient-poor conditions (Salonen 1994; Wind-Mulder et al. 1996). Seedling mortality is consequently high (C. Lavoie, Université Laval, pers. comm.). Seedlings must rapidly attain sufficient size and extend roots to sequester nutrients and especially water to avoid summer drought and heat stress. Large root mass also improves seedling survival after needle ice damage (Roach and Marchand 1984). The size of a seedling at any particular time after germination depends on both seed size and its relative growth rate (RGR: growth in mass per unit mass; Causton and Venus (1981)). Larger seeds produce larger seedlings soon after germination, and large seed size alone increases early seedling survival in drought-prone or

nutrient-poor habitats (Leishman and Westoby 1994; Milberg and Lamont 1997). However, species with higher RGR eventually outperform others if suitable conditions for growth persist. Smaller-seeded species generally have greater RGR (Fenner 1983; Shipley and Peters 1990; Marañon and Grubb 1993; Swanborough and Westoby 1996). Easily measured sub-components of RGR, especially specific leaf area (SLA: leaf area per unit leaf mass) also predict RGR (Lambers and Poorter 1992; Reich et al. 1992; Saverimuttu and Westoby 1996; Hunt and Cornelissen 1997).

In this study, two controlled experiments were conducted to evaluate the germination and establishment potential of bog plants and to identify simple traits that predict their responses in milled bogs. A first experiment was conducted to: 1) determine the response of bog plants to burial by peat; 2) evaluate whether seed mass was a good indicator of burial response; and 3) determine the size limit of seeds sensitive to burial. A second experiment on the same species was conducted to: 4) measure relative growth rate and especially root performance of these bog plants; 5) evaluate how seed mass predicts growth parameters; and 6) if RGR can be predicted by easily measured sub-components of RGR.

Methods

Plant species

Study species were chosen as the most frequent vascular plants occurring in either natural bogs or abandoned milled bogs in Québec (Appendix 1). The former species are desirable species for restoration, while the latter species actually recolonize milled bogs but include undesirable species not usually found in undisturbed bogs (e.g., *Betula* species). In total, 21 species were chosen, including polycarpic perennial herbs, shrubs and trees. Fruiting bodies of all species except *Rubus chamaemorus* were collected in the summer and fall of 1997 and 1998 from milled and natural peatlands near Rivière-du-Loup (47°45′ N, 69°30′ W), Rivière-Ouelle (47°27′ N, 69°57′ W) and Québec City (46°47′ N, 71°03′ W). Fruiting bodies were always collected from multiple individuals at each site. Seeds were cleaned, dried at room temperature for 2 to 3 weeks then stored at 8 °C under dry, dark conditions until the start of stratification pre-treatments, as outlined below. *Rubus chamaemorus* fruits were collected in summer 1995

from Havre Saint-Pierre (50°16′ N, 63°35′ W) and frozen until 1997 when they were cleaned, dried, then stored as above. Single populations of seeds were used for each species, therefore intraspecific genetic variation was not considered in this study. Nomenclature follows Scoggan (1978), except for *Vaccinium oxycoccus* L.

A subsample of seeds of each species was taken to determine seed dry mass. Seed appendages were removed prior to weighing, except for small-seeded, winged species (*Drosera*, *Kalmia*, *Ledum* and *Rhododendron* spp.). Seeds were dried at 70 °C for 48 hours, then weighed to 0.01 mg precision. For large-seeded species, 20 seeds were weighed individually, while for smaller-seeded species, ten batches of 4, 20 or 100 seeds were weighed.

Experiment 1: seed burial and germination

The effects of burial on seedling emergence of study species was first evaluated in an experiment in spring 1998 from seed collected in 1997 and stratified, but germination for several species was poor or nil, apparently caused by a fungal infestation during stratification pre-treatment. The experiment was repeated in spring 1999 using mostly seeds collected in 1998 with modifications of pre-treatment conditions. Germination was acceptable for all species, except for *Carex limosa*, *C. stricta* and *Scirpus cespitosus* which had low seed viability. Consequently, the 1999 experiment is reported here for all species except for *C. limosa* and *S. cespitosus*, for which data from the 1998 experiment is presented, since both germinated well that year. *Carex stricta* did not germinate well in either year and is not reported.

All species received the following stratification pre-treatment. Seeds were placed in Petri dishes on filter paper, wetted with distilled water and allowed to imbibe for 24 hours. Excess water was removed and seeds were spread evenly. Petri dishes were sealed with parafilm, covered in foil and placed at 4 °C for 20 weeks until the beginning of the experiment. Seeds of *Carex oligosperma* and *Rubus chamaemorus* were treated differently since no germination was found in the 1998 experiment, although seeds were viable and scarified. Both species have hard, thick seed coats. Their seeds were first stratified in nylon bags in moist peat at 4 °C for 54 weeks prior to being removed and stratified as above in Petri dishes for 20 weeks.

Burial treatments were prepared in early May 1999 in the following manner. The substrate was a fibric *Sphagnum* peat, medium-brown in colour when moist (von Post scale 2; pH 3.8; Munsell colour 10YR 4/4). The peat was first passed dry through a 2.36 mm sieve, then wetted with distilled water. Square pots 8 cm wide and 9 cm deep with drainage holes were filled to 2 cm from the rim and levelled. Peat-filled pots were then refrigerated until seeds were sown. Seeds were counted in a room illuminated only by dim incandescent bulbs covered by a green gelatin lighting filter with a red to far red ratio (660: 730 nm) of 0.18, and efforts were made to limit their exposure to this light. Either 25 or 50 seeds were counted per pot, depending on the species, and evenly spread in each pot, except within 1 cm of their edge. Seed coats of *Carex oligosperma* and *Rubus chamaemorus* were scarified with a file. Seeds were buried under one of four depths of sifted peat: 0, 5, 10 or 15 mm, determined on a mass basis and corrected for peat subsidence during watering based on preliminary tests. Peat was added in 2 to 3 mm thick layers and wetted with a fine mist between layers to ensure full hydration of the peat. Seeded pots were refrigerated at 8 °C in the dark for 1–3 days prior to the experiment.

Pots were placed on a single table in a glasshouse and arranged in a random complete block design with five blocks. Blocks were rotated twice monthly. Pots were watered with a fine mist of deionized water (pH 4.9; conductivity: $\sim 5 \ \mu S \, cm^{-1}$) every 1 to 3 days from early May to mid-August to maintain the peat surface moist. From mid-August through September when seedling emergence was infrequent, the experiment was watered at 3 to 5 day intervals, and the peat surface dried out between waterings. Mean minimum and mean maximum air temperatures in the glasshouse ranged from 15 and 26 °C in May to 18 and 29 °C in July. Every 2 to 3 days and less frequently in August and September, emerged seeds were noted and carefully removed with forceps. After sowing, seed viability of each species was determined on a subsample of 100 stratified seeds. The viability of small-seeded species (< 1 mm diameter) were tested by cutting them open and examining for firm, healthy-looking tissues, while that of larger seeds was evaluated using the tetrazolium test (International Seed Testing Association 1985).

For *Carex limosa* and *Scirpus cespitosus*, the 1998 experiment was conducted in the same manner as in 1999, with the following differences. Seeds were collected in 1997 and stratified in nylon bags buried in

Table A1. The composition of the modified Rorison solution used in the seedling growth rate experiment as compared to means (and ranges) of water chemistry of milled and undisturbed bogs in eastern Canada (Wind-Mulder et al. 1996). Micronutrients in the Rorison solution (Fe, Mo, Mn, Zn, Cu and B) are not shown. Concentrations are in mg L^{-1}.

	pH	NH_4^+	NO_3^-	P [a]	K	Ca	Mg	S
Modified Rorison solution	3.6 [b]	11.2	0	6.2	15.6	4.0	4.8	12.8
Milled bogs	3.9	3.8	0.1	< 0.1	0.8	0.8	1.0	2.6
	(3.7–5.6)	(0.0–15.8)	(0.0–0.9)	(< 0.1–0.4)	(0.1–4.2)	(< 0.1–8.3)	(0.0–4.9)	(< 0.1–8.4)
Natural ombrotrophic bogs	3.8	1.1	< 0.1	< 0.1	0.3	0.8	0.7	0.9
	(3.7–4.0)	(< 0.1–2.8)	(< 0.1–< 0.1)	(< 0.1–0.2)	(0.2–0.4)	(0.2–4.6)	(0.3–3.1)	(0.2–3.2)

[a] Phosphorus in the modified Rorison solution is phosphate, while in bogs it is measured as total phosphorus.
[b] pH of solution after addition to peat-filled pots.

moist *Sphagnum* peat at 4 °C for 22 weeks. Fifty seeds of each species were sown and only three burial treatments were used, namely 0, 5 and 10 mm. The experiment began in early May, but lasted only 43 days until mid-June. Mean minimum and maximum air temperatures in the glasshouse were 16 and 27 °C in May and 15 and 26 °C in June. Seed viability was not determined.

Linear regressions were performed separately for each species on $\ln(x + 1)$ transformed final emergence percentages to determine the effect of burial depth. Once emergence for a species was zero across all replicates, subsequent depths were not included in the regression analyses. Correlation analyses were performed to determine how log mean seed mass of species is correlated to the slopes of these negative exponential models. Statistical analyses were conducted using the GLM and CORR procedures of SAS statistical software (SAS Institute (1996–1999)) and were considered significant at $P \leq 0.05$.

Experiment 2: seedling growth rates

For most species, 1998 seeds were placed under stratification for 25 weeks prior to the experiment, using the same technique as in experiment 1. For *Carex oligosperma* and *Rubus chamaemorus*, 1997 and 1995 seeds were used, respectively, which were first stratified in nylon bags in moist peat at 4 °C for 70 weeks prior to being removed and stratified as above. *Carex limosa* seeds were only collected in summer 1999 and stratified for 6 weeks prior to the experiment.

Square pots 6 cm wide and 155 mL in volume were filled with the same sieved *Sphagnum* peat used in the burial experiment and wetted with a nutrient solution (see below). Between 10 and > 100 seeds were sown per pot on the peat surface, then pots were refrigerated at 4 °C until the start of the experiment. Pots were placed in two growth chambers in a random complete block experimental design with 8 blocks (one pot for each harvest per species per block). Pots received 14 hours of daylight, minimum and maximum temperatures of 13 and 26 °C, and 242 μmol m^{-2} s^{-1} of PAR provided by 160 W cool white fluorescent tubes and 40 W incandescent bulbs. Pots were watered every 2 to 3 days with 50 mL of a nutrient solution, consisting of a 20% Rorison solution (Booth et al. 1993) with NH_4-N and only 5% of the calcium in the full Rorison solution. This solution had nutrient concentrations similar to maxima found in natural and milled bogs in eastern Canada, with slightly elevated levels of phosphorus (Table A1). Once germinated, seedlings were carefully thinned to one per pot.

Seedlings were harvested at 7 and 21 days after germination and were carefully removed from pots while immersed in water. Seedlings were scanned digitally using an image scanner at a resolution of 177 pixels cm^{-1}. Leaf area and maximum rooting depth were measured using Scion Image software (Scion Corporation 2000). Rooting depth was defined as the length of the longest root. Seedlings were weighed whole during the first harvest due to the small size of many species, but were separated into component parts (roots, shoot, leaves) at the second harvest and weighed. Mass was determined by drying plant parts at 70 °C for 48 hours, then weighing to 0.01 mg precision.

The following growth parameters were calculated based on means and variances at both harvests of seedling dry weight (W), leaf dry weight (L_W) and leaf area (L_A) (Causton and Venus (1981), p. 21–22 and 30–32): absolute growth rate (AGR, mg day^{-1}),

defined as dW/dt where t is time; relative growth rate (RGR, mg mg^{-1} day^{-1}), defined as (dW/dt)(1/W); unit leaf rate (ULR, μg mm^{-2} day^{-1}), defined as (dW/dt)(1/L_A); and overall leaf area ratio (LAR, mm^2 mg^{-1}), defined as L_A/W. RGR is the product of ULR and LAR. The two sub-components of LAR, specific leaf area (SLA, mm^2 mg^{-1}), defined as L_A/L_W, and leaf weight ratio (LWR, mg mg^{-1}), defined as L_W/W, were only calculated from the second harvest. Three other parameters were calculated to assess root performance based on mean values and variances of rooting depth (R_L) at both harvests: the absolute root penetration rate (ARPR, mm day^{-1}), defined as dR_L/dt; the root length ratio (RLR, mm mg^{-1}) defined as (R_L/W), and calculated in a manner analogous to the leaf area ratio; and the root length to leaf area ratio (R_L/L_A, mm mm^{-2}). This last ratio was calculated to provide an index of seedling desiccation tolerance (Hendrix et al. 1991). Root weight ratios were not calculated because of the extremely low root mass of many species, even at the second harvest. Correlation analyses between growth parameters and mass or RGR were performed with SAS statistical software (SAS Institute (1996–1999)). P values were adjusted to experiment-wise error rates using the stepwise Bonferroni adjustment with the MULTTEST procedure of SAS.

Results

Experiment 1: seed burial and germination

The timing of germination of unburied seeds varied substantially among species (Figure 1), with median germination times ranging from 6 days (*Picea mariana*) to 39 days (*Vaccinium angustifolium*). Buried seeds showed similar patterns as unburied seeds. They generally emerged 2 to 7 days later depending on the species and burial depth, except for *Vaccinium angustifolium* and *V. oxycoccus* which lagged by up to 26 and 14 days, respectively, with 15 mm burial (data not shown). For most species, seedling emergence declined with burial depth (Figure 2), and followed a exponential function of the form:

$$E = ae^{-B_E Z},$$

where E is the percent emergence of viable seeds, ln a is the intercept, B_E is the slope of emergence (mm^{-1}), and Z is the burial depth (mm). However,
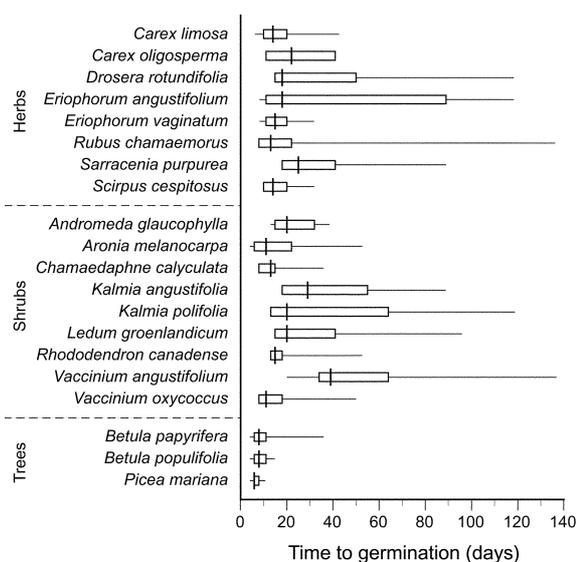
Figure 1. Germination timing of surface-sown seed of herbaceous, shrub and tree species. Horizontal lines show initial and final germination, boxes show 10% and 90% germination and the vertical line shows 50% germination.

four species of herbs, namely *Carex oligosperma*, *Eriophorum angustifolium*, *E. vaginatum*, and *Scirpus cespitosus*, did not show any significant effect of burial on germination, at least within the range of burial depths tested (0 to 15 mm). The slopes of seedling emergence differed significantly between remaining species ($F_{15,277}$ = 11.77, $P < 0.0001$). The strength of the decline of seedling emergence with burial varied dramatically among species and was most marked in small-seeded species (*Andromeda*, *Chamaedaphne*, *Drosera*, *Kalmia*, *Ledum* and *Rhododendron* spp.), which hardly germinated at just 5 mm depth. Seed mass was strongly correlated with the negative exponential slopes of log emergence (B_E) versus burial depth (Fig. 3a). Species with seeds lighter than approximately 0.1 mg were most affected by burial.

Experiment 2: seedling growth rates

Growth parameters could not be determined for *Carex stricta* due to poor germination and for *Kalmia angustifolia* that had small seedlings that were frequently too light to be weighed even at the second harvest. The remaining species showed wide variation in growth parameters (Appendix 2). Their absolute growth rate (AGR) ranged over almost three orders of magnitude and was positively correlated to log seed mass (Fig. 3b). However both species of *Betula*
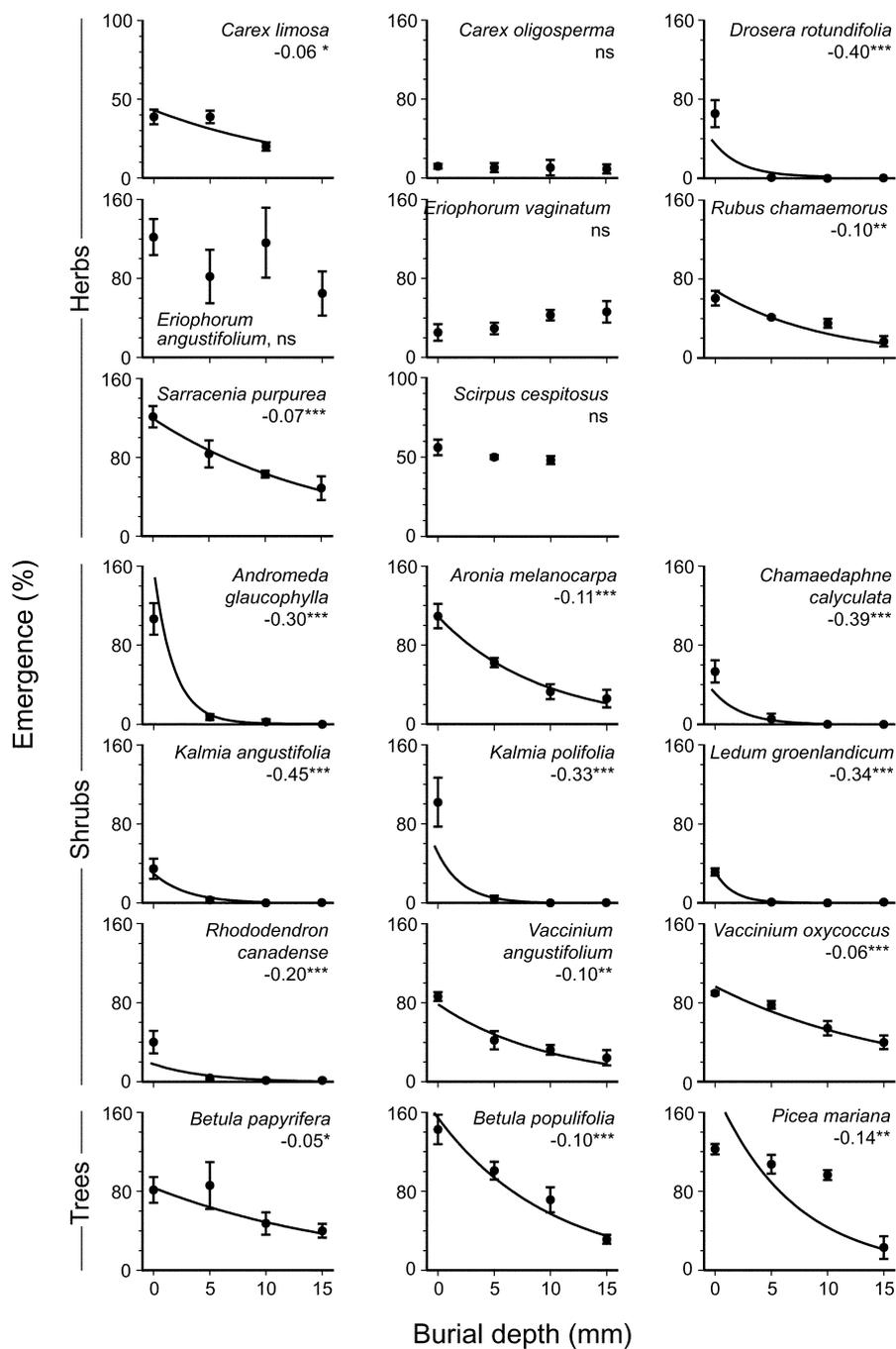
Figure 2. Seedling emergence of study species as functions of seed burial depth (mean ± SE). Emergence is expressed as percent of viable seed sown, corrected using separate seed viability tests, except for *Carex limosa* and *Scirpus cespitosus*, which are expressed as percent seed sown. Percent emergence occasionally have values in excess of 100% as a result of seed viability corrections. Curves are fitted to species with significant negative exponential functions between mean emergence and burial depth. Values of significant slopes are given below the species name. Significance of slopes: ns, not significant; * $P \leqslant 0.05$; ** $P \leqslant 0.01$; *** $P \leqslant 0.001$.

were outliers, with greater AGR than predicted by seed mass. Relative growth rate (RGR) across all spe-

cies was 0.131 ± 0.013 day^{-1} (mean ± SE), with *Betula* species and *Aronia melanocarpa* having the high-
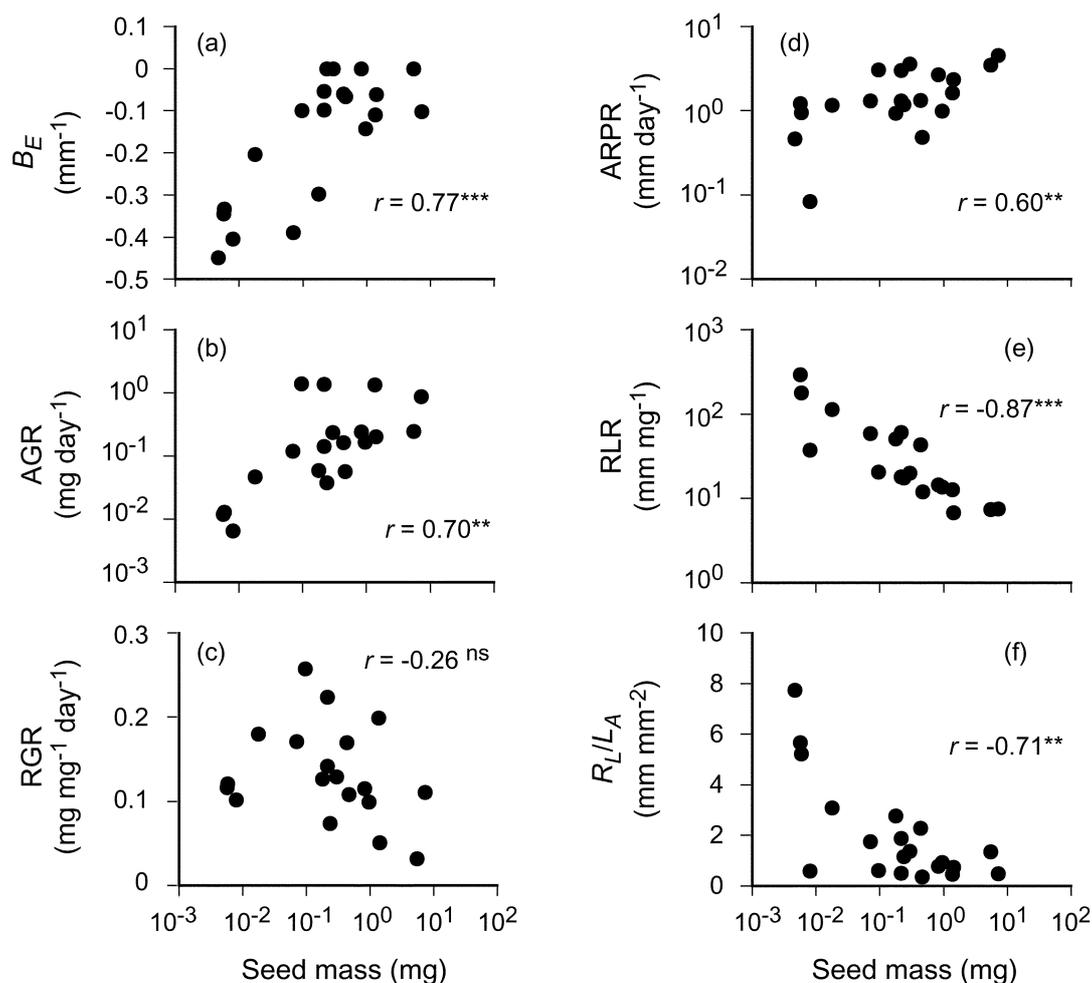
Figure 3. Correlations between log seed mass of bog plants and (a) the slope of the negative exponential functions of seed emergence versus burial (B_E), (b) seedling absolute growth rate (AGR, log scale), (c) seedling relative growth rate (RGR), (d) absolute rate of root penetration (ARPR, log scale), (e) overall root length ratio (RLR, log scale), and (f) the ratio of maximum root length to leaf area (R_L/L_A). Significance of correlations: ns, not significant; * $P \leqslant 0.05$; ** $P \leqslant 0.01$; *** $P \leqslant 0.001$. P values were adjusted using the stepwise Bonferroni procedure based on k = 6 tests.

est values and *Carex* species the lowest. However, log seed mass was not correlated with RGR of study species (Fig. 3c). None of the sub-components of RGR was correlated with RGR either (Figure 4). However, the three smallest-seeded species, *Drosera rotundifolia*, *Kalmia polifolia* and *Ledum groenlandicum*, were outliers, especially for correlations of RGR with LAR or SLA. These small-seeded species have especially high SLA. If these three species were excluded, RGR was strongly correlated with LAR and especially with SLA at day 21, but remained uncorrelated with ULR or LWR (Figure 4).

In terms of root performance, *Drosera rotundifolia* barely formed a root system while at the other ex-

treme, *Aronia melanocarpa*, *Betula* spp., *Carex* spp., *Eriophorum* spp. and *Rubus chamaemorus* had good root penetration with root lengths of 4 to 9 cm after three weeks (Appendix 2). Large-seeded species in general had greater ARPR (Fig. 3d). High root penetration was also associated with high absolute growth rates (log scales, $r = 0.74$, $P = 0.0003$). However, root length ratio (RLR) on log scale was strongly and negatively correlated with log seed mass (Fig. 3e), indicating that small-seeded species tended to produce much longer and thinner roots in relation to total seedling mass than larger-seeded species. This was especially true for ericaceous shrub species. Small-seeded species also tended to have much
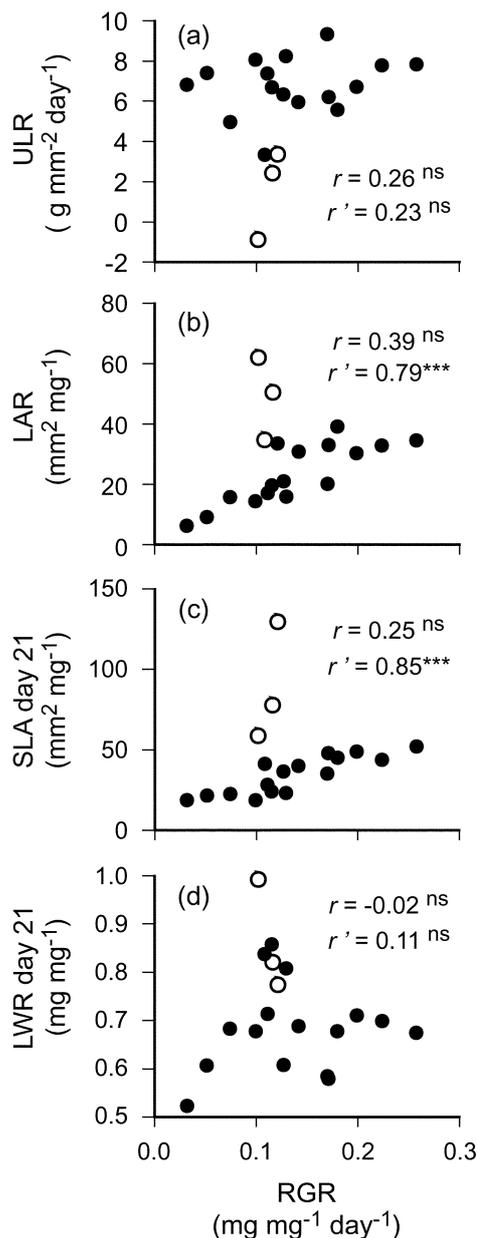
Figure 4. Correlations between relative growth rate (RGR) of bog plant seedlings and (a) unit leaf rate (ULR), (b) overall leaf area ratio (LAR), (c) specific leaf area at day 21 (SLA) and (d) leaf weight ratio at day 21 (LWR). Correlations coefficients are given for the entire data set (r) and without the three smallest-seeded species (r'), which are shown by hollow circles. Significance of correlations: ns, not significant; $* P \leq 0.05$; $** P \leq 0.01$; $*** P \leq 0.001$. P values were adjusted using the stepwise Bonferroni procedure based on k = 4 tests.

higher root length to leaf area ratios (Fig. 3f), especially species with seeds less than 0.1 mg, except for *Drosera rotundifolia* which was an outlier.

Discussion

Seed burial delays and reduces seedling emergence of most species. The slope of the negative exponential relationship between burial depth and emergence appears to be a useful measure to quantify the burial response. Light transmission through litter or soil follows a similar negative exponential function with depth, known as the Beer-Lambert extinction law (Facelli and Pickett 1991). But light transmittance is essentially nil beyond 2 mm of dark-coloured, fine-textured soils or litter (Kasperbauer and Hunt 1988; Mandoli et al. 1990; Benvenuti 1995), with strong declines in red to far red ratios (Bliss and Smith 1985; Mandoli et al. 1990). Although a light extinction curve for the peat used in the experiment was not measured, it was dark-coloured and relatively fine-textured, therefore light transmission should be nil by 5 mm depth. Since light can only act as a cue for germination within the first few millimetres of peat, other factors must cause the observed exponential declines of emergence at deeper burial depth, possibly inhibitory CO_2/O_2 ratios or the death of buried seed and seedlings (Baskin and Baskin (1998), p 149).

The burial response was strongly related to seed mass, as in other habitats (Jurado and Westoby 1992; Vázquez-Yanes and Orozco-Segovia 1992; Reader 1993; Jurik et al. 1994). Burial under peat is especially serious for species with seed mass less than approximately 0.1 mg. Buried seeds may subsequently move to the surface and germinate through processes such as freeze-thaw action or peat decomposition and subsidence, however the ability of study species to form seedbanks is poorly known (Moore and Wein 1977; Huopalainen et al. 2000). Species with viable seedbanks usually have small and compact seeds (Thompson et al. 1993), which should favour species such as *Andromeda glaucophylla* and *Chamaedaphne calyculata*.

The dormancy syndromes of study species are poorly known, making it difficult to assess their probable germination timing in the field. However, many germinate better after cold stratification (*Aronia*, *Betula*, *Kalmia*, *Picea mariana* and *Rhododendron* spp., Young and Young (1992); *Chamaedaphne calyculata*, Densmore (1997); *Drosera rotundifolia*, Crowder et al. (1990); *Rubus chamaemorus*, Taylor (1971); *Sarracenia purpurea*, Ellison (2001); *Vaccinium oxyccocus*, Jacquemart (1997)), therefore spring germination likely predominates. Whether in spring or fall, any window for germination and establishment in milled

bogs will be constrained by damaging needle ice events near the soil surface in spring and fall (E. Groeneveld, Université Laval, pers. com.) and by hot and dry surface conditions in mid-summer (Price 1997; Price et al. 1998), the importance of which varies between sites and years. Differences in germination timing among species suggest that species emerge at different times during these windows and consequently differ in age at which they are confronted with unfavourable conditions. For instance in spring, species with rapid germination (e.g., *Picea mariana*) would be more prone to needle ice damage while those with slow germination (e.g., *Vaccinium angustifolium*) may avoid needle ice but may only partially germinate before the onset of summer surface drought.

Once emerged, successful establishment of seedlings in milled bogs will depend primarily on their ability to rapidly attain sufficient size, especially their roots, during favourable growth windows. Survival thresholds of seedling size or root length are not known, and would likely vary between sites and years depending on microclimatic conditions. However, the relative survival ability of species can be judged by their absolute growth rate (AGR) and root penetration rate (ARPR). Large-seeded species generally had higher AGR and ARPR. On the short term, seed size is consequently of major importance in determining probable seedling survival. Large-seeded species will be able to extend long and robust roots deeper into the milled peat substrates and thereby avoid drought stress near the surface (Price 1997). Smaller-seeded species which have greater root length to leaf area ratios will be drought-tolerant (Hendrix et al. 1991; Marañon and Grubb 1993), but will be faced with greater drought stress near the surface in mid-summer than large-seeded species which can avoid surface drought by extending their roots to greater depth. Absolute growth rate is a function of both seed size and RGR. Given favourable conditions and sufficient time, large-seeded species will be surpassed by smaller-seeded species with higher RGR. Among study species, *Betula papyrifera, B. populifolia* and *Aronia melanocarpa* had the highest absolute growth over three weeks as a result of their high RGR and in spite of their smaller seed size. Actual RGR depends on the intrinsic maximal RGR of the species and on growing conditions. Species were supplied with nutrients at concentrations close to the maximum values observed in milled bogs, therefore RGR and related measures can be considered as maximum values encountered in these environments. However, nutrient concentrations in milled bogs are often up to an order of magnitude lower than in the nutrient solution used in this study. The growth of species with high maximum RGR is more strongly depressed by reduced resources than those with low maximum RGR, and RGR in fertile conditions is not correlated to that in infertile conditions (Shipley and Keddy 1988; van der Werf et al. 1993). Therefore, species with high RGR (e.g. *Aronia melanocarpa*, *Betula* spp., *Rhododendron canadense*, *Vaccinium oxycoccus*) may have greater reductions in growth under the average nutrient conditions found in milled bogs than those with low RGR (e.g. *Carex* spp., *Drosera rotundifolia, Picea mariana*, *Rubus chamaemorus*, *Sarracenia purpurea*, *Scirpus cespitosus*). However, nutrient concentrations in this study are similar to those used for infertile conditions in previous studies (Shipley and Keddy 1988; van der Werf et al. 1993), therefore reductions in RGR may not be severe.

No relationship was found between RGR and seed mass, in contrast to other studies (Fenner 1983; Shipley and Peters 1990; Marañon and Grubb 1993; Swanborough and Westoby 1996). However, this general relationship is relatively weak with lots of scatter (Shipley and Peters 1990) and depends on the species assemblage as well as growth conditions. LAR and especially SLA were the best indicators of RGR, consistent with other studies (Lambers and Poorter 1992; Reich et al. 1992; Saverimuttu and Westoby 1996; Hunt and Cornelissen 1997), except for small-seeded species. However, these studies and the present one were all conducted at lower light levels relative to full sunlight (this study: 242 vs 1500 μmol m^{-2} day^{-1}). Recent research has shown that at higher irradiance, ULR is correlated more strongly with RGR than SLA or LAR, (McKenna and Shipley 1999; Poorter (1999, 2001); Ryser and Wahl 2001). In the field, SLA may therefore be useful as a predictor of RGR only under slightly shaded conditions. Species with seeds less than 0.01 mg did not follow the correlation between SLA and RGR. These outliers may be a result of greater error associated with their measurement (Appendix 2). Alternatively, the larger SLA may reflect a strategy of these very small-seeded species to maximise light capture during early seedling growth. Increases in leaf water content is one strategy used by species to increase SLA without investing in leaf biomass (Shipley 1995).

A few simple traits therefore help to predict the probable germination and establishment performance

of species recolonizing milled bogs. Seed mass is a good indicator of burial response, early seedling growth and root performance, while SLA is a better indicator of RGR, at least under lower light conditions and except for very small-seeded species. No effort was made to separate possible phylogenetic constraints from these relationships, as attempted in other studies (Saverimuttu and Westoby 1996; Swanborough and Westoby 1996), therefore care should be taken in extrapolating these results to other species. However, these relationships were strong and in agreement with previous work, therefore seed mass and SLA should provide good indications of the germination and establishment potential of other species.

Seed mass and relative growth rate alone do not necessarily predict overall recolonization success in milled bogs. For instance, although high RGR helps to explain the prevalence of *Betula* species and *Aronia melanocarpa*, small-seeded species (*Kalmia angustifolia*, *Chamaedaphne calyculata* and *Ledum groenlandicum*) are frequent recolonizers in spite of being sensitive to burial and having low RGR (Appendix 1). Besides germination and establishment, actual recolonization also depends on differential dispersal, subsequent growth and reproduction of species (Salonen (1987, 1990); Salonen et al. 1992; Salonen and Setälä 1992). However, the screening of species for these traits permits judgements on probable success of naturally-dispersed or introduced species during germination and establishment phases. Furthermore, it allows for diagnoses of the causes of recolonization failure. In a restoration context, this is valuable information. Desirable species that are vulnerable during germination and establishment can be targeted and suitable restoration procedures can be implemented to aid in their establishment. Similar screening processes should aid in the restoration planning of other disturbed environments.

Appendix 1

Table A1. Selected plant species, their rank frequency in natural and milled bogs and their seed mass. Study species are the most common species in natural bogs (31 bogs surveyed, 76 species in total; L. Rochefort, unpublished data) or in abandoned milled bogs (11 bogs surveyed, 132 species in total; L. Rochefort and F. Quinty, unpublished data) located in Québec.

Species	Family	Rank frequency in natural bogs	Rank frequency in milled bogs	Seed mass [a] (mg)
Herbs				
Carex limosa	Cyperaceae	9	Absent	1.42 ± 0.10
Carex oligosperma	Cyperaceae	7	89	5.47 ± 0.13
Carex stricta	Cyperaceae	Absent	9	0. 40 ± 0. 06
Drosera rotundifolia	Droseraceae	6	64	0.008
Eriophorum angustifolium	Cyperaceae	46	10	0.30 ± 0.03
Eriophorum vaginatum	Cyperaceae	11	4	0.83 ± 0.05
Rubus chamaemorus	Rosaceae	13	7	7.30 ± 0.16
Sarracenia purpurea	Sarraceniaceae	12	115	0.47 ± 0.03
Scirpus cespitosus	Cyperaceae	14	Absent	0.238
Shrubs				
Andromeda glaucophylla	Ericaceae	8	81	0.179
Aronia melanocarpa	Rosaceae	27	11	1.37 ± 0.09
Chamaedaphne calyculata	Ericaceae	2	5	0.071
Kalmia angustifolium	Ericaceae	4	1	0.005
Kalmia polifolia	Ericaceae	3	31	0.006
Ledum groenlandicum	Ericaceae	5	2	0.006
Rhododendron canadense	Ericaceae	Absent	12	0.018
Vaccinium angustifolium	Ericaceae	21	3	0.216
Vaccinium oxycoccus	Ericaceae	1	21	0.436
Trees				
Betula papyrifera	Betulaceae	Absent	6	0.22 ± 0.02
Betula populifolia	Betulaceae	Absent	8	0.096
Picea mariana	Pinaceae	10	22	0.96 ± 0.10

[a] Large seeds were weighed individually (n = 20) and are shown with mean ± SE.

Appendix 2

Table A2. Growth parameters of bog plant species between 7 and 21 days age (mean ± SE).

Species	AGR [a] (mg day^{-1})	RGR (mg mg^{-1} day^{-1})	ULR (μg mm^{-2} day^{-1})	LAR (mm^2 mg^{-1})	SLA day 21 (mm^2 mg^{-1})	LWR day 21 (mg mg^{-1})
Herbs						
Carex limosa	0.20 ± 0.06	0.051 ± 0.016	7.40 ± 0.99	9.2 ± 2.0	22 ± 4	0.61 ± 0.09
Carex oligosperma	0.25 ± 0.10	0.032 ± 0.012	6.83 ± 1.53	6.4 ± 1.8	19 ± 3	0.52 ± 0.11
Drosera rotundifolia	0.01 ± 0.00	0.102 ± 0.036	−0.89 ± 2.09	62.0 ± 21.7	59 ± 8	0.99 ± 0.10
Eriophorum angustifolium	0.24 ± 0.03	0.129 ± 0.010	8.25 ± 0.72	15.9 ± 1.5	23 ± 1	0.81 ± 0.04
Eriophorum vaginatum	0.24 ± 0.04	0.115 ± 0.011	6.70 ± 0.63	19.7 ± 2.2	24 ± 2	0.86 ± 0.07
Rubus chamaemorus	0.88 ± 0.17	0.111 ± 0.013	7.37 ± 0.69	17.2 ± 1.6	29 ± 3	0.71 ± 0.06
Sarracenia purpurea	0.06 ± 0.01	0.108 ± 0.021	3.34 ± 0.48	34.7 ± 5.7	41 ± 3	0.84 ± 0.06
Scirpus cespitosus	0.04 ± 0.01	0.074 ± 0.010	4.96 ± 1.11	15.9 ± 2.3	23 ± 2	0.68 ± 0.04
Shrubs						
Andromeda glaucophylla	0.06 ± 0.01	0.127 ± 0.010	6.34 ± 0.71	21.0 ± 2.8	37 ± 4	0.61 ± 0.06
Aronia melanocarpa	1.33 ± 0.14	0.199 ± 0.013	6.71 ± 0.41	30.4 ± 2.6	49 ± 5	0.71 ± 0.05
Chamaedaphne calyculata	0.12 ± 0.02	0.171 ± 0.016	6.21 ± 0.57	33.1 ± 6.1	48 ± 4	0.58 ± 0.05
Kalmia angustifolia	–	–	–	–	–	–
Kalmia polifolia	0.01 ± 0.00	0.121 ± 0.031	3.35 ± 2.64	33.5 ± 8.6	130 ± 63	0.77 ± 0.42
Ledum groenlandicum	0.01 ± 0.00	0.116 ± 0.033	2.42 ± 1.40	50.5 ± 17.0	78 ± 16	0.82 ± 0.13
Rhododendron canadense	0.05 ± 0.01	0.180 ± 0.034	5.58 ± 1.16	39.1 ± 15.7	45 ± 6	0.68 ± 0.09
Vaccinium angustifolium	0.14 ± 0.03	0.141 ± 0.029	5.95 ± 0.77	30.8 ± 12.2	40 ± 6	0.69 ± 0.10
Vaccinium oxycoccus	0.16 ± 0.02	0.170 ± 0.015	9.33 ± 0.74	20.2 ± 2.0	35 ± 3	0.58 ± 0.05
Trees						
Betula papyrifera	1.36 ± 0.14	0.224 ± 0.016	7.78 ± 0.52	33.0 ± 5.2	44 ± 4	0.7 ± 0.04
Betula populifolia	1.40 ± 0.14	0.257 ± 0.013	7.83 ± 0.44	34.6 ± 3.9	52 ± 3	0.68 ± 0.03
Picea mariana	0.17 ± 0.02	0.099 ± 0.009	8.06 ± 0.52	14.4 ± 1.0	19 ± 1	0.68 ± 0.04

Species	R_L day 7 (mm)	R_L day 21 (mm)	ARPR (mm day^{-1})	RLR (mm mg^{-1})	R_L/L_A (mm mm^{-2})
Herbs					
Carex limosa	8 ± 2	41 ± 9	2.36 ± 0.62	7 ± 2	0.73 ± 0.14
Carex oligosperma	23 ± 4	72 ± 10	3.47 ± 0.76	7 ± 2	1.35 ± 0.21
Drosera rotundifolia	1 ± 0	2 ± 0	0.08 ± 0.02	37 ± 18	0.59 ± 0.10
Eriophorum angustifolium	14 ± 1	64 ± 4	3.61 ± 0.32	20 ± 2	1.37 ± 0.18
Eriophorum vaginatum	13 ± 1	50 ± 5	2.67 ± 0.35	15 ± 1	0.78 ± 0.07
Rubus chamaemorus	26 ± 3	89 ± 10	4.52 ± 0.77	8 ± 1	0.47 ± 0.05
Sarracenia purpurea	3 ± 1	10 ± 1	0.48 ± 0.07	12 ± 3	0.36 ± 0.06
Scirpus cespitosus	2 ± 1	19 ± 3	1.17 ± 0.21	17 ± 4	1.15 ± 0.25
Shrubs					
Andromeda glaucophylla	12 ± 1	25 ± 2	0.94 ± 0.16	51 ± 5	2.78 ± 0.50
Aronia melanocarpa	25 ± 1	48 ± 7	1.63 ± 0.54	13 ± 2	0.47 ± 0.08
Chamaedaphne calyculata	15 ± 1	33 ± 3	1.30 ± 0.25	59 ± 11	1.75 ± 0.23
Kalmia angustifolia	4 ± 0	11 ± 1	0.46 ± 0.09	–	7.74 ± 2.42
Kalmia polifolia	6 ± 1	19 ± 2	0.95 ± 0.17	179 ± 106	5.22 ± 0.92
Ledum groenlandicum	9 ± 1	26 ± 3	1.22 ± 0.21	296 ± 179	5.67 ± 0.73
Rhododendron canadense	7 ± 1	23 ± 3	1.17 ± 0.24	113 ± 51	3.08 ± 0.83
Vaccinium angustifolium	20 ± 4	38 ± 4	1.30 ± 0.41	61 ± 35	1.87 ± 0.28
Vaccinium oxycoccus	15 ± 2	33 ± 3	1.33 ± 0.23	43 ± 9	2.29 ± 0.51
Trees					
Betula papyrifera	24 ± 2	65 ± 9	2.99 ± 0.65	18 ± 5	0.51 ± 0.06
Betula populifolia	18 ± 1	61 ± 7	3.05 ± 0.47	20 ± 4	0.61 ± 0.07
Picea mariana	13 ± 2	27 ± 4	0.99 ± 0.31	14 ± 2	0.92 ± 0.12

[a] Column abbreviations: AGR, absolute growth rate; RGR, relative growth rate; ULR, unit leaf rate; LAR, leaf area ratio; SLA, specific leaf area; LWR, leaf weight ratio; R_L, root length: ARPR, absolute root penetration rate; RLR, root length ratio; and R_L/L_A, root length to leaf area ratio.

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