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SEED BANK COMPOSITION OF A NORTHEASTERN U. S. TUSSOCK SWAMP

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Abstract: A seedling and sporeling emergence assay was conducted on 50 soil cores taken from within *Carex stricta* tussocks (*intra*-tussock) and from paired, adjacent *inter*-tussock areas in the Hawkins Conservation Area, South Hadley, Massachusetts, USA, to test the hypothesis that local heterogeneity in water levels alters seed bank composition and subsequent seedling emergence patterns. Soil cores were sliced into 2.5-cm-thick sections and split into flooded and drawn-down treatments. Germination of buried seeds and spores was assessed in these treatments under greenhouse conditions for 6 months. Eighteen species emerged from both treatments combined: 17 from *inter*-tussock samples and 12 from *intra*-tussock samples. Pooled across sample depths and watering treatments, more species of grasses, forbs (exclusive of *Impatiens capensis*), and woody plants germinated from *intra*-tussock samples, while more pteridophytes germinated from the *inter*-tussock samples. Emergence of pteridophytes, grasses, and forbs was associated significantly with sample depth. More pteridophytes germinated from samples close to the swamp surface, while grasses and forbs were most abundant in samples 10–20 cm below the surface. In the drawn-down treatment, pteridophyte and forb seedlings were more plentiful from *inter*-tussock samples. In contrast, more forb seedlings emerged from *intra*-tussock samples in the flooded treatment. This variation in forb emergence seems to reflect differences in species composition within and between tussocks. Twenty-two species occurred in the standing vegetation of the study area, but only nine of these also occurred in the seed bank. The composition of standing vegetation atop and between tussocks did not differ significantly. Grasses, which dominated the seed bank, were absent from standing vegetation. Grasses clearly represent a persistent population of seeds in the seed bank, while forbs are more transient within the seed bank. The depth-stratified species composition of the seed bank also suggests patterns of temporal succession in the aboveground vegetation of this New England tussock swamp.

Key Words: *Carex stricta,* Massachusetts, seed bank, tussock swamp

INTRODUCTION

Soil seed banks are key determinants of wetland community composition (e.g., van der Valk and Davis 1978, van der Valk 1981, McGraw 1987, Leck 1989, Vivian-Smith and Handel 1996, Weiher et. al. 1996). Although not as well-studied as their upland counterparts, wetland seed banks have been shown to play an important role in wetland regeneration and community persistence after disturbances (e.g., van der Valk 1981, Leck 1989, Ellison and Bedford 1995, Brown and Bedford 1997). Seeds of many wetland species germinate in response to dramatic changes in wetland hydrology, such as complete drawdowns or excessive flooding (e.g., Leck and Graveline 1979, van der Valk 1981, Galinato and van der Valk 1986, Leck 1989). Here, we report results of a study in which we examined the seed bank from a wet, red maple tussock swamp where local heterogeneity in water levels caused by the growth form of the dominant plant (the tussock-forming *Carex stricta*) may alter seedling emergence patterns and subsequent vegetation structure at very small scales. We document the distribution of buried seeds within and between tussocks and experimentally test the hypothesis that germination success and seedling composition depends on sample origin (within or between tussocks) and flooded or drawn-down conditions. We also contrast the composition of the seed bank with that of the standing vegetation.

Relative to other wetland types, wet tussock wetlands have received comparatively little attention in the ecological literature (e.g., Costello 1936, Roach 1983, Rejmánková and Rejmánek 1995, Johnson et al.

1996, Vivian-Smith 1997). Wet tussock swamps in the north-eastern and north-central United States and southern Canada are characterized by 0.5 to > 1.0 m-tall promontory structures ('tussocks') built up through growth and slow decomposition of *C. stricta.* Dried culms and old roots of *C. stricta* accumulate debris and create a peaty soil atop which grow the current year's tillers. Tussock crowns generally remain at or above the maximal water level in the swamp throughout the year. Growth of *Carex stricta* is slow; Costello (1936) estimated that individual tussocks may live for > 50 yrs. The presence of tussocks in a wetland creates a heterogeneous landscape, with light availability, soil oxygen content, soil moisture, and soil and air temperatures varying from the swamp surface between tussocks up to the tussock crown (Yapp 1909). For example, Costello (1936) reported that soil moisture of *C. stricta* tussocks ranged from 60 to 80% during the driest of summer days. As in other communities where micro-environmental gradients structure plant communities and alter species diversity (e.g., Tilman 1982, Keddy and Ellis 1984, Titus 1990), environmental gradients created by tussocks may locally alter vegetation pattern and associated seed banks (Roach 1983). In *Sphagnum* wetlands with the hummock-hollow topography, the comparatively small hummocks can alter floristic diversity at centimeter to meter scales (e.g., Watt 1947, Rydin 1986, Vivian-Smith 1997).

Here, we address four specific questions regarding germination and recruitment of buried seeds in a wet tussock swamp in western Massachusetts. First, does the total number of seeds in the seed bank on tussocks differ from the total number of seeds buried between tussocks? Second, are there significant differences in species composition within and between tussocks with respect to soil depth? Third, do germination frequencies of seeds from given depths within and between tussocks differ after soil samples have been allowed to dry completely? Fourth, what is the relationship between seed bank and current vegetation composition in this tussock swamp?

MATERIALS AND METHODS

Study Site

We studied the tussock swamp in the Hawkins Conservation Area, a small (< 2 ha) wetland located in South Hadley, Massachusetts, USA. Hawkins Conservation Area is located just north of a glacial drumlin and is most likely underlain by stratified drift or till. The wetland has been protected since 1977 but is now surrounded by residential buildings. There is no evidence of past logging or clearing at this site, and the dominant species at the site are *Carex stricta, Impatiens capensis,* and *Acer rubrum,* the last of which forms a closed canopy over the wetland. All samples were taken in 1996 from within a 50 × 50 m plot that included all tussocks within this wetland. Tussock density in the study plot is $0.15 \cdot m^{-2}$. Although the tussocks occur in the lowest and wettest section of Hawkins Conservation Area, within the study plot itself, the tussocks are randomly distributed in space. This plot remained wet (standing water < 5 cm) during the entire spring and summer of 1996.

In April 1996, we surveyed the 2500 m^2 plot using a Topcon AT-G2 Auto Level equipped with an optical micrometer. Two hundred-fifty tussocks were located and mapped and their elevation measured relative to surrounding ground level (± 1 mm). Tussock height ranged from 0.05 to 0.6 m ($\bar{x}$ = 0.15, SD = 0.11 m) above the swamp surface. This survey allowed us to identify each tussock for subsequent sampling of seed banks and standing vegetation.

Seed Bank Studies

In May 1996, following the last spring frost, 25-cm-long soil cores were extracted from 25 randomly-selected tussocks and from paired, adjacent areas between tussocks (< 10 cm distant from the base of the tussock). This sample date was prior to any emergence of pteridophytes, graminoids, or forbs and prior to dispersal of *Acer rubrum* samaras. Cores taken from the soil between tussocks (*inter*-tussock cores) were extracted using a 5-cm-diam, stainless-steel soil corer. Because tussocks are densely rhizomatous, we were unable to use the corer to take cores from within the tussocks (*intra*-tussock cores). Instead, we cut a 5-cm-thick wedge out of each tussock and then trimmed this wedge to a brick that was the height of the tussock and 5 × 5 cm in cross-section. All cores were returned to the laboratory, split lengthwise, and then each half cut into 2.5-cm-long sections. Each section represented a sample from a fixed depth (in 2.5-cm increments) within each core. The replicate halves at each depth were used to test the effects of flooded and drawn-down conditions on germination frequency and rates from each core.

For germination, each sample was homogenized and placed in 4 × 4 cm plastic cell inserts in standard greenhouse trays. The depth of the homogenized samples was approximately 3 cm. All samples were placed in a climate-controlled glasshouse. Air temperature was maintained at 25 °C and relative humidity maintained at 70%. No supplemental lighting was used, and on sunny days, photosynthetically active radiation (PAR) reached a maximum of $1{,}300\ \mu mol \cdot m^{-2} \cdot s^{-1}$. Samples in the *flooded* treatment were placed in trays lacking drainage holes and were watered daily to maintain saturation (water level at the top of the samples). Samples in the *drawn-down* treatment were first allowed to dry out completely (approximately 3 wks) and then placed in trays with drainage holes. Subsequently, these samples were watered daily but were not kept saturated.

Every day, from June through December 1996, we counted the number of seeds and spores germinated from each sample. As seedlings and sporelings became large enough to identify, they were removed from the flats. We note that this method of assessing the buried seed and spore pool normally underestimates the true seed bank population, as some seeds and spores remain dormant and do not germinate under the conditions used. However, this method provides a reasonable relative estimator of number of viable seeds, as well as potential population size and composition (McGraw 1987).

At the time of soil sampling in the field, we also measured soil temperature at 5-cm depths within the tussock using a Campbell soil moisture probe (Campbell Scientific, Logan, UT) attached to a Li-Cor data logger (Li-Cor Inc., Lincoln, NE).

Composition of Standing Vegetation

During June 1996, after the spring flush of seedling emergence, we identified and counted all plant species on 250 tussocks within the study plot and in adjacent areas of similar diameter (and random direction) between these tussocks. We did not find additional species in the study plot during regular visits to the site throughout the summer.

Statistical Analyses

All statistical analyses were conducted using Systat version 7.0 for Windows (SPSS, Inc., Chicago, IL). Seedling germination data were normalized using a generalized power transformation (Box and Cox 1964) prior to statistical analysis.

RESULTS

Seed Bank Analysis

Eighteen different species emerged across all treatments (Table 1). Fourteen species emerged both from cores taken between tussock and from cores taken from within tussocks. The composition of the emergents differed by TUSSOCK treatment ($P = 0.016$, Wilcoxon signed-rank test: *inter- vs. intra*-tussock). Because most species were uncommon (Table 1), we used ANOVA to analyze treatment-specific emergence patterns of species grouped into four vegetation classes: pteridophytes (including *Equisetum arvense*), grasses, forbs, and woody species (*Acer rubrum, Ulmus rubra,* and *Vitis riparia*). Pooled across depths (Table 1), more seedlings of grasses and woody species emerged from *intra*-tussock samples ($P < 0.001$ and $P = 0.035$, respectively), while more pteridophytes emerged from *inter*-tussock cores ($P < 0.001$). There were no significant differences in forb emergence frequency within or between tussocks ($P = 0.18$), which is most likely due to the high numbers of *Impatiens capensis* individuals in all samples. There was, in fact, no difference in the number of emergents of *Impatiens* among TUSSOCK treatments ($P = 0.37$), and removal of this species from the overall analysis led to a significant TUSSOCK effect (0.338 seedlings/sample (270/m^2) *within* tussocks *vs.* 0.192 seedlings/sample (196/m^2) *between* tussocks; $P = 0.017$). More than 90% of the *Impatiens* seedlings emerged from samples taken from 0–7.5 cm.

Table 1. Species germinated from the core samples. Values shown are total number of each species germinated from all *inter-* and *intra*-tussock samples (pooled across treatments and depths). Sample size = 25 cores for each TUSSOCK treatment group. Nomenclature follows Gleason and Cronquist (1991).

Species	*Inter-* tussock	*Intra-* tussock
Acer rubrum L.	0	5
Caltha palustris L.	32	1
Cardamine pratensis L.	6	2
Equisetum arvense L.	3	0
Eupatorium perfoliatum L.	19	7
Impatiens capensis Meerb.	68	50
Ludwigia palustris (L.) Elliott	4	0
Onoclea sensibilis L.	1	7
Pilea pumila (L.) A. Gray	0	1
Polygonum sagittatum L.	1	0
Rubus spp.	8	0
Solanum dulcamara L.	1	1
Solidago spp.*	11	4
Ulmus rubra Muhl.	0	5
Viola sp.	4	1
Vitis riparia Michx.	0	4
Poaceae**	417	60
unidentified pteridophyte species	51	68

* Includes *Solidago flexicaudus* L., *Solidago rugosa* Miller, and *Solidago* sp.

** Includes *Glyceria striata* (Lam.) A. Hitchc. and *Poa trivialis* L.

While the WATERING treatment (flooded *vs.* drawn-down) itself did not significantly affect emergence frequency of the four vegetation classes ($P > 0.1$, all cases), there was a significant TUSSOCK × WATERING treatment interaction in frequency of both pteridophyte and forb emergence ($P = 0.004$ and $P = 0.01$, respectively). Among samples in the drawn-down treat-

Table 2. Mean number of seedlings/sample (1 SD in parentheses) in each of the four vegetation classes (pteridophytes, grasses, forbs, woody species) that germinated from *inter-* and *intra*-tussock samples in the flooded and drawn-down treatments. To obtain means on a per m^2 basis, multiply the values by 800 (*intra*-tussock) or 1,020 (*inter*-tussock).

		Pteridophytes	Grasses	Forbs	Woody Plants
Inter-tussock	Flooded	0.6	0.6	0.5	0
		(0.98)	(1.08)	(0.76)	(0)
	Drawn-down	0.8	0.5	1.1	0
		(1.52)	(0.99)	(3.24)	(0)
Intra-tussock	Flooded	0.3	1.3	0.8	0.1
		(0.59)	(1.72)	(1.80)	(0.25)
	Drawn-down	0.02	2.0	0.4	0.1
		(0.14)	(1.94)	(0.72)	(0.24)

ment, significantly more pteridophytes emerged from *inter*-tussock samples than from *intra*-tussock samples. The tussock-specific difference in pteridophyte emergence frequency was less pronounced in the flooded samples (Table 2). In contrast, in the flooded treatment, more forbs emerged from *intra*-tussock samples than from *inter*-tussock samples, but the reverse was true in the drawn-down treatment (Table 2). While for pteridophytes, the significance of the TUSSOCK × WATERING interaction term reflects different numbers of individuals emerging in the four different treatments, for forbs, the significance of this term reflects different species composition of the four treatments (Table 3).

Analysis of covariance (ANCOVA) was used to examine the additional effect of depth on seedling emergence, and the interaction of sample depth with tussock. Pteridophyte, grass, and forb seedling emergence varied significantly with depth ($P = 0.01$, $P = 0.02$, and $P = 0.03$, respectively; Figure 1), and this pattern differed significantly between *intra-* and *inter*-tussock samples for grasses and forbs (TUSSOCK × DEPTH interaction term, $P = 0.006$ and $P = 0.002$, respectively; Figure 1) but not for pteridophytes (TUSSOCK × DEPTH interaction term, $P = 0.76$; Figure 1). There was no significant effect of sample depth on woody species emergence ($P = 0.46$; Figure 1). There were no interactive effects of DEPTH × WATERING treatment on emergence of any of the four vegetation classes ($P > 0.19$, all cases).

Soil temperature within tussocks (17.2 ± 1.2 °C) was significantly higher ($P < 0.001$, *t*-test, n = 50) than soil temperatures between tussocks (16.7 ± 1.0 °C).

Composition of Standing Vegetation

Twenty-two individual species were identified on both tussocks and in interstitial areas in the field (Table 4). Of these, 21 species were growing on living tussocks, and 18 species were growing between tussocks. *Impatiens capensis* was the most commonly found species, with 381 plants growing on tussocks and 439 plants growing interstitially. Of particular note were two 'upland' species, *Maianthemum canadense* and *Taraxacum officinale,* which were found growing only atop tussocks. Overall, however, there was no significant difference in vegetation composition growing on or between tussocks ($P = 0.62$, Mann-Whitney U Test).

Table 3. Forb species that emerged in the seed bank study, dependent on sample origin and watering treatment.

Inter-tussock		*Intra*-tussock	
Drawn-down	Flooded	Drawn-down	Flooded
Cardamine pratensis	*Caltha palustris*	*Caltha palustris*	*Caltha palustris*
Eupatorium perfoliatum	*Cardamine pratensis*	*Cardamine pratensis*	*Cardamine pratensis*
Impatiens capensis	*Eupatorium perfoliatum*	*Eupatorium perfoliatum*	*Eupatorium perfoliatum*
	Impatiens capensis	*Impatiens capensis*	*Impatiens capensis*
	Pilea pumila	*Ludwigia palustris*	*Ludwigia palustris*
	Solidago sp.	*Rubus* sp.	*Polygonum sagittatum*
	Solidago flexicaulus	*Solanum dulcamara*	*Solidago* sp.
	Viola sp.	*Solidago* sp.	*Solidago rugosa*
			Viola sp.

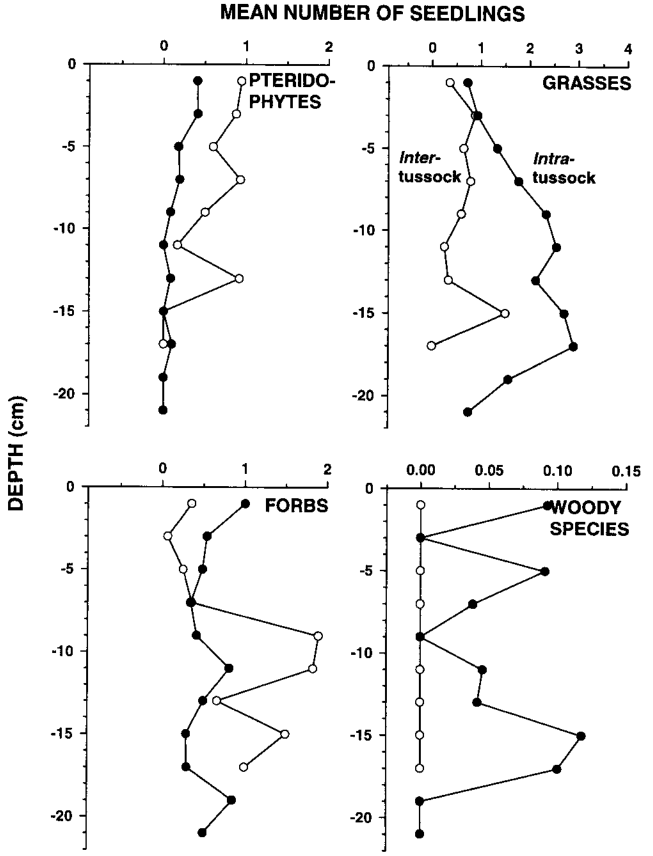

Figure 1. Seedling emergence as a function of depth from samples taken within and between tussocks (pooled across watering treatments). Values shown are mean number of seedlings (n = 25 samples per point; standard deviations omitted for clarity) in each of the four vegetation classes. Solid symbols represent *intra*-tussock samples, while open symbols represent *inter*-tussock samples.

Relationship Between the Seed Bank and Standing Vegetation

Only nine species were shared between the standing vegetation and the seed bank (compare Tables 1 and 4): *Acer rubrum, Cardamine pratensis, Equisetum arvense, Eupatorium perfoliatum, Impatiens capensis, Onoclea sensibilis, Solidago* sp., *Ulmus rubra,* and *Vitis riparia.* Overall, the similarity between the *inter*-tussock seed bank and the vegetation between tussocks was 29%, while the similarity between the *intra*-tussock seed bank and the vegetation atop tussocks was 17% (computed using Jaccard's index of similarity $J = c/(a + b - c)$, where c = the number of species in common, a = the number of species growing within the seed bank, and b = the number of species in the standing vegetation [Jaccard 1901]). Irrespective of tussock position, the similarity between the swamp seed bank and the standing vegetation was 23%.

Table 4. Composition of the standing vegetation in the study plot. Numbers given are the total number of individuals found on 250 tussocks and in 250 associated *inter*-tussock areas. All *intra*-tussock samples had *Carex stricta* tillers but were considered to be a single individual.

Species	*Inter*-tussock	*Intra*-tussock
Acer rubrum L.	5	12
Alnus sp.	4	5
Arctostaphylos uva-ursi (L.) Sprengel	9	4
Cardamine pratensis L.	49	17
Carex stricta Lam.	250	0
Crataegus sp.	2	0
Dryopteris cristata (L.) A. Gray	41	35
Equisetum arvense L.	87	44
Eupatorium perfoliatum L.	2	9
Galium sp.	126	88
Impatiens capensis Meerb.	439	381
Maianthemum canadense Desf.	0	4
Onoclea sensibilis L.	212	7
Osmunda cinnamonmea L.	55	175
Oxalis montana L.	0	12
Pinus strobus L.	2	9
Smilacina racemosa (L.) Desf.	3	8
Solidago sp.	61	129
Symplocarpus foetidus (L.) Nutt.	163	70
Taraxacum officinale Weber ex Wiggers	0	1
Toxicodendron radicans (L.) Kuntze	67	86
Typha latifolia L.	17	9
Ulmus rubra Muhl.	0	3
Vitis riparia Michx.	7	14

DISCUSSION

Most seed banks consist of two populations of seeds: transient seeds and persistent seeds (e.g., Roach 1983, Leck 1989). The transient population consists of those seeds that germinate during the first germination season following dispersal (such as *Impatiens capensis*; Leck 1979, Leck and Simpson 1987). Seeds in the transient seed bank comprise a relatively large component of the spring emergents and contribute significantly to short-term regeneration following small disturbances. Seeds that fail to germinate in the first germination season enter the persistent seed bank. All these seeds are not continuously dormant but may undergo annual cycles of dormancy (in fall and winter, for example) followed by nondormancy (in spring or summer). Even when these seeds are not dormant, they may fail to germinate because they require an additional environmental cue, such as light, that they do not receive (see Baskin and Baskin (1998) for a more detailed discussion of dormancy requirments). This persistent seed bank is the principal source for system recovery from large-scale disturbances (Roach 1983, Leck 1989). In tussock swamps, secondary succession and responses to small-scale disturbance normally depend on clonal expansion of extant vegetation and short-term recruitment of seedlings from surrounding species (Roach 1983). Seeds in the persistent seed bank rarely contribute to such short-term regeneration dynamics (Roach 1983).

Except for those of *Impatiens capensis,* most of the seeds that germinated in our seed bank trials appear to have come from the persistent seed bank. Although the strength of this inference is limited because our samples were collected before the spring emergence season, this conclusion is supported by our observation that the majority of seeds that emerged from the soil cores were of wetland species (as opposed to upland species that could have dispersed into our study area from surrounding habitats) different from those encountered in the standing vegetation (Tables 1 and 4) and showed pronounced variability with sampling depth (Figure 1). In particular, grasses dominated the seed bank (Table 1), especially at middle depths (Figure 1), but were absent from the standing vegetation (Table 4). Like Roach (1983), we found that forb species in this tussock swamp generally were more common closer to the surface, while grasses were buried deeper in the soil (Figure 1). This result is suggestive of temporal succession in the above-ground vegetation of this swamp. The data collected in this study thus likely represent a 'transect backwards in time' (*sensu* McGraw 1987), illustrating the history of the development of this swamp, and also may reflect potential vegetation composition of this swamp following a future, large-scale disturbance. Because wetland seed bank studies may only account for a small fraction (typically < 5%) of the intact seeds present in the soil (e.g., van der Valk and Rosburg 1997), our data represent a very conservative estimator of the diversity of seeds present in the soil and, consequently, a conservative estimator of the regenerative potential of this swamp.

While the topographic heterogeneity generated by the tussocks themselves appears to have little effect on the standing vegetation (Table 4), the seed bank within and between tussocks differs significantly (Tables 1–3, Figure 1). The observed differences likely result from (1) differential burial ability of seeds in the soft muds between tussocks and in the dense rhizomatous mass within the tussock; (2) loss of seeds from the tussock into surrounding *inter*-tussock areas by gravity-driven water flow; or (3) changes in long-term viability of buried seeds in the different habitats resulting from microclimatic differences within and between tussocks. We hypothesize that differential burial ability of seeds and loss of seeds from tussocks into surrounding *inter*-tussock areas becomes more important as tussocks age. Because of the slow accretion rate of tussocks themselves (< 1 cm per yr; Costello 1936), seeds found at lower depths likely were buried when there was much less topographic variability in the swamp than there is at present. While transport of seeds throughout the soil profile by earthworms and other soil invertebrates is theoretically possible, we did not find any earthworms in our cores, and we suspect that such vertical transport is uncommon in this system. Rather, differences in patterns of emergence from lower depths most likely reflect different patterns of loss of seeds from within tussocks *vs.* between tussocks. Lacking data on the ages of the tussocks in our study area, we are unable to evaluate this hypothesis more completely.

Soil temperature and oxygen availability are both higher within tussocks than in the muds between them, while soil moisture tends to fluctuate less within tussocks than between them (Yapp 1909, Costello 1936). Although we were unable to measure all of these variables across the same depth gradients from which we sampled seeds, we did find that soil temperatures in late May were significantly warmer (≈ 1 °C) at 5-cm depths within tussocks than between them. Together with inferred higher oxygen availability within elevated tussocks (cf. Yapp 1909, Costello 1936), these data suggest that decomposition rates are likely to be faster in the relatively warm, aerobic tussocks than they are in the relatively cool, anoxic *inter*-tussock muds. Spores of pteridophytes and seeds of forbs may either germinate rapidly from within tussocks or soon decompose there, leading to the observed relatively low number of pteridophytes and forb seedlings emerging from *intra*-tussock cores (Table 2, Figure 1). The generally smaller grass seeds are known to be long-lived in upland seed banks (e.g., Ellis 1991), and our data (Table 1, Figure 1) similarly suggest that grass seeds persist longer within tussocks, which represent 'islands' of uplands within the swamp. Although woody species also emerged only from *intra*-tussock cores, the very small number of woody seedlings makes it difficult to draw inferences regarding their absence from *inter*-tussock areas. However, we note that among standing vegetation, woody species (*Acer, Alnus, Pinus, Ulmus, Vitis*) dominate atop tussocks, which suggests that tussocks provide safe-sites for their establishment within this swamp.

We observed significant interactions between TUSSOCK and WATERING treatments only for pteridophytes and forbs. For pteridophytes, the direction of response relative to WATERING treatment was the same for both *inter*- and *intra*-tussock treatments (more seedlings of similar species from *inter*-tussock samples), only the magnitude of the response differed (Table 2). However, for forbs, the response to the WATERING treatment shifted between *inter*- and *intra*-tussock samples (Table 2): more forbs emerged from *intra*-tussock samples than from *inter*-tussock samples in the flooded samples, while the reverse occurred in the drawn-down samples (Table 2), and the species composition differed among the treatments as well (Table 3).

The data presented in this paper demonstrate significant variation in seedling emergence and composition that depends on sample origin with respect to tussocks and depth and on moisture available to buried seeds. The importance of the tussocks themselves should not be underestimated. They support standing vegetation and hold a seed bank different from that in the surrounding swamp, thereby increasing overall swamp species richness. Although there was little similarity between the standing vegetation and the emergents from the seed bank, soil seed banks likely reflect past vegetation history of this swamp and land-use changes in surrounding areas. As in other wetlands (van der Valk 1981, Leck 1989, Ellison and Bedford 1995, Brown and Bedford 1997), the seed bank would be the primary source of its regeneration and persistence following disturbance.

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