Germination and establishment of forest sedges (*Carex*, Cyperaceae): tests for home-site advantage and effects of leaf litter[1]

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We investigated aspects of germination and seedling establishment that might influence the distribution and diversity of *Carex* species growing in the forest understory. We tested the ability of *Carex communis* and *C. platyphylla* to germinate and establish at plots where adult individuals of one of these two species, or one of two other *Carex* species (*C. backii* and *C. plantaginea*), occurred in an old-growth forest in southern Québec, Canada. We also tested for effects of leaf litter on germination and establishment of these sedges. From a series of experiments in the field and in a lath house, we found no evidence of home-site advantage with respect to germination or seedling establishment. Leaf litter had a negative effect on germination and establishment. The results emphasize the importance of dispersal and colonization events in determining local diversity and distribution of *Carex* species in upland forests. High frequency of occurrence of *C. communis* at our study site may result from relatively wide dispersal provided by ants, and a suite of traits associated with ant dispersal in some understory *Carex* species.

Key words: ant dispersal; *Carex*; Cyperaceae; forest herbs; leaf litter; sedges; seed germination; species diversity.

Differences or similarities among plant species in their requirements for successful germination and establishment have important implications for the maintenance of species diversity. On the one hand, under the assumption that community composition is at equilibrium (Tilman, 1982), diversity may be maintained if regeneration requirements vary among species such that each species is either a better competitor in, or more tolerant of, a distinct set of micro-environmental conditions within a heterogeneous habitat (Grubb, 1977). Alternatively, similar requirements for regeneration may be shared by many species within a given habitat, with diversity maintained by the stochasticity of dispersal and colonization events, and with local community composition in a continuous state of flux, or non-equilibrium (Chesson and Case, 1986; van der Maarel and Sykes, 1993; Hubbell et al., 1999). Given these competing views, it is important to determine the degree to which the local distributions of co-occurring species are limited by their requirements for germination and successful seedling establishment. Comparative studies of closely related species may be particularly informative because potentially confounding evolutionary differences in traits affecting regeneration are minimized (Harvey and Pagel, 1991; Sultan et al., 1998).

Patterns of germination and establishment can also be interpreted in relation to the overall characteristics of different habitats. For seeds of herbaceous plants in the understory of temperate deciduous forests, the physical barrier imposed by tree leaf litter often inhibits germination and establishment (Sydes and Grime, 1981a, b; Beatty and Sholes, 1988; Facelli and Pickett, 1991; Eriksson, 1995). Although leaf litter covers almost all of the forest floor after canopy trees shed their leaves in autumn, redistribution and decomposition create spatial variation in the degree of litter cover in spring and early summer. Seedling establishment is also known to be dependent on seasonally changing light and temperature conditions (Baskin and Baskin, 1998), on the availability of mineral nutrients (Vasseur and Gagnon, 1994), and on disturbance events, such as the creation of canopy gaps (Collins, Dunne, and Pickett, 1985; Whigham, O'Neill, and Cipollini, 1993; Valerde and Silvertown, 1997). Seeds of many forest herbs are dormant during summer and require a period of cold temperatures to break dormancy, thus maximizing the likelihood of germinating in spring when conditions for seedling establishment are generally favorable (Baskin and Baskin, 1998). In addition, a requirement for light and fluctuating temperatures in some species is thought to function in the detection of gaps or areas free of leaf litter (Baskin and Baskin, 1998; Schütz, 1998).

In a companion study (Vellend, Lechowicz, and Waterway, 2000), we demonstrated distinct differences among the environmental distributions of four *Carex* species in a 1200-ha old-growth northern deciduous forest at Mont St. Hilaire, Québec, Canada (45°32′ N, 73°8′ W), where >50 *Carex* species have been recorded (Bell, Lechowicz, and Waterway, 2000). Three of the species, *Carex backii* F. Boott., *C. communis* L.H. Bailey, and *C. platyphylla* Carey were chosen for study from a group of upland species that frequently co-occur at the study site (Bell, Lechowicz, and Waterway, 2000). The fourth species, *C. plantaginea* Lam., was investigated to determine the correlates and causes of its unique distribution among the *Car-*

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ex species at Mont St. Hilaire. It is associated neither with the upland species, nor with a group of lowland species. Rather, we found *C. plantaginea* most often along the edges of small streams and seepage areas within the upland habitat. *Carex plantaginea* and *C. platyphylla* are in the same section of *Carex* (*Careyanae*), while *C. communis* and *C. backii* are in different sections (*Acrocystis* and *Phyllostachys,* respectively) (Starr, Bayer, and Ford, 1999; Waterway, 1999). Distinct environmental distributions, particularly among the three upland species, may be interpreted as an indication that local variation in the composition and diversity of *Carex* species is at equilibrium with environmental gradients. However, *C. communis,* the only ant-dispersed species, was found in the broadest range of environmental conditions, overlapping considerably with *C. backii* and *C. platyphylla,* and we suggested that the distribution of *C. communis* may be determined more by its ability to disperse to unoccupied microsites than by specific environmental requirements.

In this paper, our primary objective was to experimentally test whether microsites (1 m²) where established individuals of a given species were found (''home'' sites) were more favorable to successful seedling establishment than sites where established individuals of one of the other species were found. Greater seedling establishment at home sites would support the hypothesis that species' distributions are in equilibrium with environmental gradients and that the diversity of *Carex* species at Mont St. Hilaire is maintained, at least in part, by interspecific variation in regeneration requirements combined with environmental heterogeneity. Absence of home-site advantage would indicate that species' distributions are not entirely in equilibrium with environmental gradients and that dispersal and colonization events exert an important control on local diversity. To investigate the possible causes of any advantage at home sites, experiments were conducted to isolate above- and belowground differences among the four plot types. In addition, we tested whether germination and establishment are negatively affected by leaf litter. Due to poor germination of *C. backii* and *C. plantaginea* in all experiments, and *C. platyphylla* in all but one experiment, our discussion is limited largely to *C. communis*. For *C. communis,* we consider Handel's (1978a) hypothesis that ant dispersal in forest-understory *Carex* species is associated with a suite of characteristics related to regeneration.

MATERIALS AND METHODS

Focal plots and seed collection—We conducted a series of experiments to test for home-site advantage, the possible causes of home-site advantage, and effects of leaf litter on germination and establishment. Seeds of *Carex backii, C. communis, C. plantaginea,* and *C. platyphylla* were planted either in the forest understory on the perimeter of 1-m² plots where an established individual (the focal plant) of one of the four species was found (Vellend, Lechowicz, and Waterway, 2000), or in a uniform lath-house environment using soil collected from these plots. Focal plants were chosen randomly within 15 sectors (1–30 ha/sector) of Mont St. Hilaire, a 1200-ha UNESCO biosphere reserve in southern Québec, Canada. Sectors in which each species occurred were identified during an intensive survey of the entire reserve in 1996. Field experiments were conducted at 32 *C. backii* plots (including six that also contained *C. communis* or *C. platyphylla*), 28 *C. communis* plots, 28 *C. plantaginea* plots (one of which contained *C. communis*), and 29 *C. platyphylla* plots (six of which also contained *C. backii* or *C. communis*).

Seeds from each species were collected as they matured: *C. plantaginea* during the first 2 wk of June; *C. communis* and *C. platyphylla* during the last 2 wk of June; and *C. backii* over 3 wk in late June and early July. We
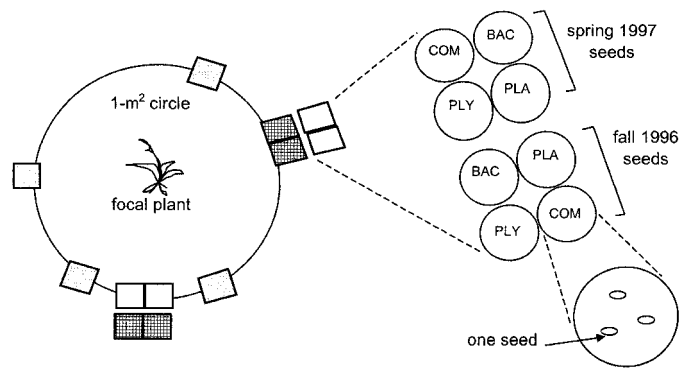

Fig. 1. Schematic diagram of one study plot illustrating the design of the field experiments. The location of all positions on the perimeter of each plot were chosen at random; this diagram is just one possible arrangement. Each square represents a group of four canisters: hatched squares = potting soil, covered by a mesh basket (litter exclusion); open squares = potting soil, not covered by a basket; light gray = native soil not covered by a basket.

Figure Abbreviations: BAC, *Carex backii*; COM, *C. communis*; PLA, *C. plantaginea*; PLY, *C. platyphylla*.

combined all seeds of a given species into a single composite batch. Seeds were allowed to air-dry from the time of collection until late October, at which time seeds were either planted in the field (see experiment 1), or stored over the winter in damp sterilized sand, in a sealed plastic container, buried just underneath the soil surface, in a lath house at Mont St. Hilaire (see experiments 2, 3, and 4). Prior to planting, ~ 10 moist seeds of each species were cut open; all seeds were found to be filled and apparently healthy. When we opened the container in spring 1997, the sand was saturated with water. Therefore, seeds used in experiments 2, 3, and 4 were submerged for an unknown period of time during the winter prior to planting; seed submersion was not deliberate.

Experiments 1 and 2: tests for home-site advantage with respect to aboveground environmental factors and effects of leaf litter on germination and establishment—Figure 1 illustrates the set-up of all field experiments. To ensure accurate relocation of seeds and identification of seedlings, all seeds were planted in bottomless plastic film canisters (3 cm diameter, 5 cm long), which had been pushed into the soil, beneath the leaf litter, leaving ~1 cm of each canister above the soil surface. Any leaf litter originally there was carefully replaced after seeds were planted. Though the canisters may have slightly modified the micro-environment where seeds were planted, differences in germination or seedling establishment among plot types are not likely to have been affected.

We planted seeds of each species at all plots in the field, but in potting soil that replaced the native soil removed for experiment 3 (see below) to eliminate edaphic differences among plots (Fig. 1). At each plot, seeds also were planted in a litter-exclusion treatment, in which inverted plastic mesh baskets were placed over groups of four canisters each, and in a control treatment, without baskets. Under a single mesh basket (litter-exclusion treatment), there was one canister per species (four canisters total), and each group of four litter-exclusion canisters was paired with an adjacent group of four control canisters. These pairs were located at random positions on the perimeter of each plot (Fig. 1). In experiment 1, we planted seeds in fall 1996 (18 October–1 November). Three seeds of each species were planted per canister, with two canisters per species per treatment at each plot. In experiment 2, we planted seeds in spring 1997 (20–23 May). The set-up of experiment 2 was identical to that of experiment 1, except that each canister was planted with one of the following: three seeds of *C. backii,* ten seeds of *C. communis,* five seeds of *C. plantaginea,* or three seeds of *C. platyphylla*.

Experiment 3: test for home-site advantage with respect to the total environment—In this experiment, seeds were planted in native soil at one of four randomly chosen positions on the perimeter of each focal plot (Fig. 1).

The time of planting and the number of seeds per canister were as in experiment 2. Four canisters were planted with seeds of each species at each plot, for a total of 12 seeds of *C. backii,* 40 seeds of *C. communis,* 20 seeds of *C. plantaginea,* and 12 seeds of *C. platyphylla.*

Censuses of experiments 1, 2, and 3—In all three field experiments, the number of seedlings present in each canister was counted at ∼ 2-wk intervals in 1997, starting on 15 June and ending on 7 October. Snow fell for the first time on 22 October and remained on the ground for the winter starting in early November. The final census was on 1 June 1998.

To assess the effect of naturally varying coverage of leaf litter on germination and establishment of seeds planted in the three field experiments, we scored the cover of leaf litter over each group of either four or eight canisters (see Fig. 1) not in a litter-exclusion treatment on 17 July 1997 in two categories: (1) visibility of the four or eight canisters was either completely or partially blocked by litter, or (2) all of the canisters could be seen clearly.

Experiment 4: test for home-site advantage with respect to edaphic conditions—During summer 1996, we collected a total of 2 L of soil at each plot from the same positions used in experiments 1 and 2. Soil samples were frozen at −4°C until 19 May 1997, at which time each 2-L sample was thawed, thoroughly mixed, and divided into two groups of four 250-mL subsamples each. We assigned each group of subsamples to one of two blocks set up in a lath house located at Mont St. Hilaire. In each block, the four subsamples were put into separate square pots (10 cm on a side) and planted with either three seeds of *C. backii,* ten seeds of *C. communis,* five seeds of *C. plantaginea,* or three seeds of *C. platyphylla.* The four pots of soil from a given plot were kept adjacent to one another, with the position of each group of four pots randomized within its block. We watered the whole experiment on all days without rain. Seedlings in each pot where germination occurred were thinned weekly to one seedling per pot. By early September, some of the plants became pot-bound, and the number of shoots and leaves on each plant were counted, and each plant was harvested between 12 September and 15 September. All samples were dried for 3 d at 70°C, and below- and aboveground plant parts were weighed separately to the nearest milligram.

Statistical analysis of experiments 1, 2, and 3: the field experiments—Of 5616 canisters at the 117 plots used in the field experiments, 18% were lost over the winter of 1996–1997 to either frost heaving or disturbance by animals. Throughout the remainder of the experiments a further 7% were lost, mostly to disturbance by animals. Any canister lost at any time was removed from the data set prior to analysis. For a given canister, we assumed that if no change in seedling number had occurred between censuses, then no germination or seedling mortality had occurred. An increase in seedling number was interpreted as germination; a decrease in seedling number was interpreted as mortality. All statistical analyses were conducted using SAS version 6.12 (SAS Institute, Cary, North Carolina, USA).

Germination responses were sufficient to allow statistical comparisons among treatments for *C. communis* and *C. platyphylla* in experiment 1, but only for *C. communis* in experiments 2 and 3. For experiment 1, we conducted separate analyses for each species. In each analysis we tested for differences among treatments for the following response variables: (1) total germination as of 7 October 1997, (2) total germination as of 1 June 1998, (3) number of seedlings remaining alive on 7 October 1997, and (4) number of seedlings remaining alive on 1 June 1998. Differences in seedling mortality among treatments may be inferred by comparing the results for germination and final seedling number for a given experiment.

For experiments 1 and 2 we tested for effects of plot type and litter exclusion on each response variable using analyses of variance as follows. If either canister in a given pair (litter exclusion canister plus control canister) was not present at the end of the experiments, both were removed from the data set prior to analysis. Data were averaged across replicate canisters. Total germination and number of seedlings were both expressed as proportions of the original number of seeds planted and subsequently arcsine-square-root transformed. For a given variable, we first tested for an effect of plot type on the *difference* between litter exclusion and control treatments with an intercept

included in the model. Thus, the intercept term tests for the main effect of litter exclusion, and the plot-type term tests for an interaction between litter exclusion and plot type. We then tested for an effect of plot type on the *sum* across litter exclusion and control treatments, thus testing for the main effect of plot type. For experiment 3, we averaged data across replicate canisters at each plot and conducted a one-way ANOVA testing for an effect of plot type on each variable.

To test for effects of naturally varying amounts of leaf litter in mid-summer (17 July) on germination and seedling number in the four data sets described above, we considered each canister not covered by a basket as an independent observation. Though each canister was not strictly independent (there was more than one at each plot), these tests were conducted only to augment the interpretation of the other experiments. Total germination and seedling number in each canister were tabulated as either zero, one, two, or three. For *C. communis* seeds in experiments 2 and 3, values >3 were assigned a value of 3. We then used categorical models (SAS, PROC CATMOD) to test for an effect of leaf litter cover in mid-summer on each variable in each data set described above.

Statistical analysis of experiment 4: the lath-house experiment—Germination occurred in <5% of the pots for all species except *C. communis* in this experiment, so statistical analyses were performed only for *C. communis.* We tested for differences among the four plot types for the following response variables: germination date, total dry mass, number of leaves, number of shoots, and the ratio of root-to-shoot mass. Germination date was the day of the year on which a seedling was first observed in a given pot; all other variables were determined on harvested plants. To improve normality, a square-root transformation was applied to all harvest variables prior to analysis. As there was no effect of block on any variable (paired-sample *t* test, *P* > 0.1), we analyzed the mean across blocks for soil from each plot. We conducted a one-way ANOVA to test for an effect of plot type on germination date, with multiple comparisons of plot type means using Ryan's *Q* procedure (Day and Quinn, 1989). Since it was apparent that germination date differed among plot types and was negatively correlated with all other variables, we conducted analyses of covariance (ANCOVA) with germination date as a covariate to test for differences among plot types for the remaining variables. Homogeneity of slopes was confirmed before conducting each ANCOVA. Following each ANCOVA, multiple comparisons of least-square means between each pair of plot types were made using Hochberg's (1974) GT2 test.

RESULTS

Overall germination—In experiment 1, overall germination was 3% for *C. backii,* 4% for *C. plantaginea,* 20% for *C. platyphylla,* and 45% for *C. communis.* In experiments 2 and 3, overall germination was 3% or less for *C. backii, C. plantaginea,* and *C. platyphylla.* For seeds of *C. communis,* overall germination was 13% in experiment 2 and 9% in experiment 3. Although *percentage* germination was relatively low for *C. communis* seeds in experiments two and three, the *number* of seeds that germinated in each canister was comparable to that for *C. communis* seeds planted in autumn because the numbers of seeds planted in each treatment at each plot in spring were 20 for experiment 2 and 40 for experiment 3, compared to six for experiment 1.

Experiments 1 and 2: tests for home-site advantage with respect to aboveground environmental factors, and effects of leaf litter on germination and establishment—For *C. communis* seeds in experiment 1, there was no significant effect of plot type on either total germination or final seedling number (*P* > 0.25), but a significant effect of leaf litter exclusion on seedling number both at the end of 1997, and in 1998 (*P* < 0.05; Table 1, Fig. 2). The number of seedlings in 1998 was greater in the leaf litter exclusion treatment than the con-

TABLE 1. Results of analysis of variance for effects of litter exclusion and plot type on germination and seedling survival in *Carex communis* (COM), and *C. platyphylla* (PLY). Plot types are *C. backii* (BAC), COM, *C. plantaginea* (PLA), and PLY. Results are presented for total germination and number of surviving seedlings as of 7 October 1997 and 1 June 1998. There was no litter exclusion treatment for COM seeds planted in native soil in spring; effects of litter and litter × plot type are thus not applicable (NA). Significant differences ($P < 0.05$) are indicated in boldface.

| Species of seed | Season of planting | Soil | Variable | Year | Sample size per plot type | | | | ANOVA effects | | | | | |
| | | | | | | | | | Litter | | Plot type | | Litter × Plot type | |
					BAC	COM	PLA	PLY	F	P	F	P	F	P
COM	fall	potting	germination	1997	23	23	20	26	0.19	0.6657	1.23	0.3041	0.55	0.6477
COM	fall	potting	no. seedlings	1997	23	23	20	26	**4.59**	**0.0349**	0.07	0.9767	0.60	0.6178
COM	fall	potting	germination	1998	23	23	20	26	0.24	0.6270	1.27	0.2909	0.68	0.5636
COM	fall	potting	no. seedlings	1998	23	23	20	26	**12.50**	**0.0007**	0.41	0.7451	**3.01**	**0.0344**
PLY	fall	potting	germination	1997	22	23	19	26	**4.13**	**0.0451**	0.71	0.5477	0.27	0.8436
PLY	fall	potting	no. seedlings	1997	22	23	19	26	**7.27**	**0.0084**	0.11	0.9554	**2.68**	**0.0520**
PLY	fall	potting	germination	1998	22	23	19	26	**3.85**	**0.0529**	1.13	0.3408	0.30	0.8264
PLY	fall	potting	no. seedlings	1998	22	23	19	26	**5.47**	**0.0217**	1.40	0.2487	2.05	0.1126
COM	spring	potting	germination	1997	27	24	23	27	2.87	0.0933	**4.97**	**0.0030**	0.48	0.6974
COM	spring	potting	no. seedlings	1997	27	24	23	27	0.30	0.5822	**3.28**	**0.0242**	0.57	0.6354
COM	spring	potting	germination	1998	27	24	23	27	0.01	0.9227	**6.93**	**0.0003**	0.90	0.4446
COM	spring	potting	no. seedlings	1998	27	24	23	27	**22.28**	**0.0001**	**5.42**	**0.0017**	**2.81**	**0.0433**
COM	spring	native	germination	1997	32	28	25	29	NA	NA	2.49	0.0639	NA	NA
COM	spring	native	no. seedlings	1997	32	28	25	29	NA	NA	0.42	0.7421	NA	NA
COM	spring	native	germination	1998	32	28	25	29	NA	NA	**3.32**	**0.0226**	NA	NA
COM	spring	native	no. seedlings	1998	32	28	25	29	NA	NA	**3.80**	**0.0123**	NA	NA

trol treatment at *C. backii, C. communis* and *C. plantaginea* plots, but opposite at *C. platyphylla* plots (plot type × litter exclusion, $P < 0.05$; Table 1, Fig. 2).

There were no significant differences among plot types for germination or establishment of *C. platyphylla* in experiment 1, but percentage germination was greater in the litter exclusion treatment than the control treatment at all plot types (Table 1, Fig. 3). At *C. backii, C. communis,* and *C. platyphylla* plots, seedling number in 1997 was also greater in the litter exclusion treatment than the control. However, the effect of litter exclusion on final seedling number varied among plot types in 1997 (plot type × litter exclusion, $P = 0.052$), with fewer seedlings in the litter exclusion treatment than in the control treatment at *C. plantaginea* plots.

For *C. communis* seeds in experiment 2, plot type had a significant effect on germination and seedling number both in 1997 and 1998 (Table 1), with greater germination and more seedlings at *C. plantaginea* plots, than at *C. backii, C. communis,* or *C. platyphylla* plots. There was no significant effect of litter exclusion on total germination (Table 1). However, the significant effect of litter exclusion on final seedling number in 1998 ($P = 0.0001$) was due, in part, to a flush of germination in the litter exclusion treatment in spring 1998 (Fig. 4). Germination occurred during spring 1998 in both treatments, but was greater in the litter exclusion treatment, whereas seedling mortality was greater in the control treatment (Fig. 4). The significant interaction term in the model for final seedling number in 1998 ($P < 0.05$, Table 1) was due to differences
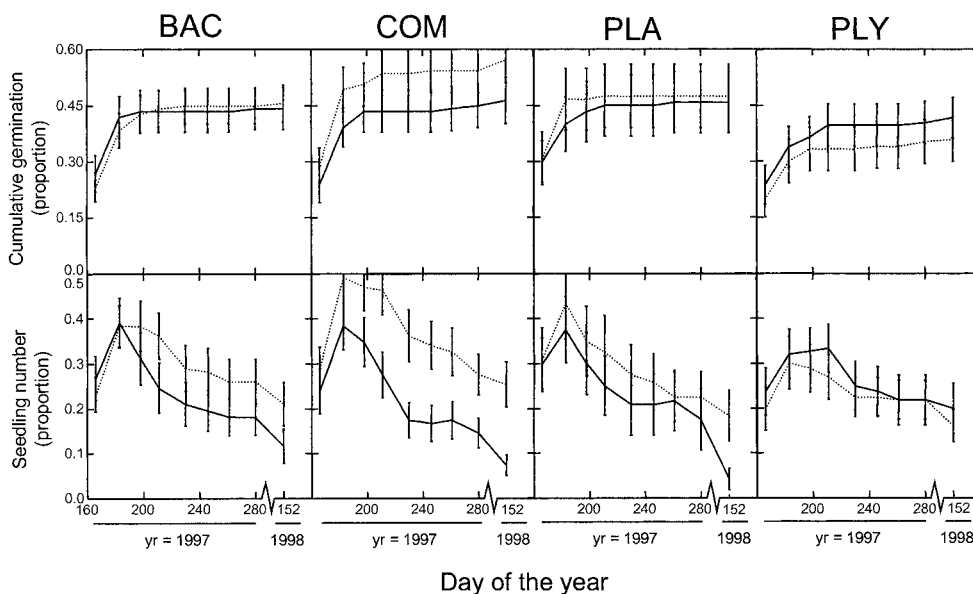

Fig. 2. Cumulative germination and seedling number (± 1 SE) for seeds of *Carex communis* planted in potting soil in autumn 1996 (experiment 1) at four plot types. At each plot, seeds were planted in two treatments, litter exclusion (·······), and control (——).
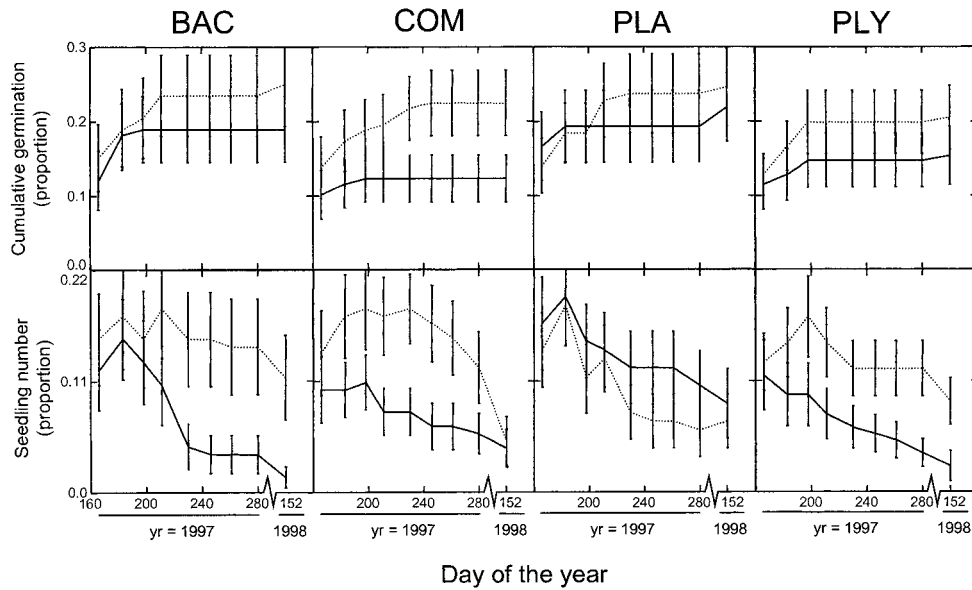
Fig. 3.   Cumulative germination and seedling number (± 1 SE) for seeds of *Carex platyphylla* planted in potting soil in autumn 1996 (experiment 1) at four plot types. At each plot, seeds were planted in two treatments, litter exclusion (········), and control (——).

among plot types in the magnitude, not the direction, of the effect of litter exclusion.

Experiment 3: test for home-site advantage with respect to the total environment—Percentage germination of *C. communis* seeds was greater at *C. plantaginea* plots than at *C. backii, C. communis,* or *C. platyphylla* plots in this experiment (Table 1, Fig. 5). However, seedling number at *C. plantaginea* plots decreased considerably during the summer of 1997 and ultimately was slightly less than that at *C. communis* and *C. platyphylla* plots in 1998 (Fig. 5), indicating that mortality was also greatest at *C. plantaginea* plots. Between autumn 1997 and spring 1998, there was a flush of germination at *C. com-*

munis, C. plantaginea, and *C. platyphylla* plots, but considerable mortality at *C. backii* plots (Fig. 5), thus causing the significant differences among plot types for final seedling number in 1998 (Table 1).

Effects of natural variation in leaf litter cover—For both *C. platyphylla* and *C. communis* in all experiments, germination and seedling number were greater where there was naturally no leaf litter than where leaf litter either partially or completely covered groups of canisters in mid-summer (Table 2). For experiments 2 and 3, the differences were not significant for germination ($P > 0.15$), but significant for final seedling number, both in 1997 and 1998 ($P < 0.005$). In experiment
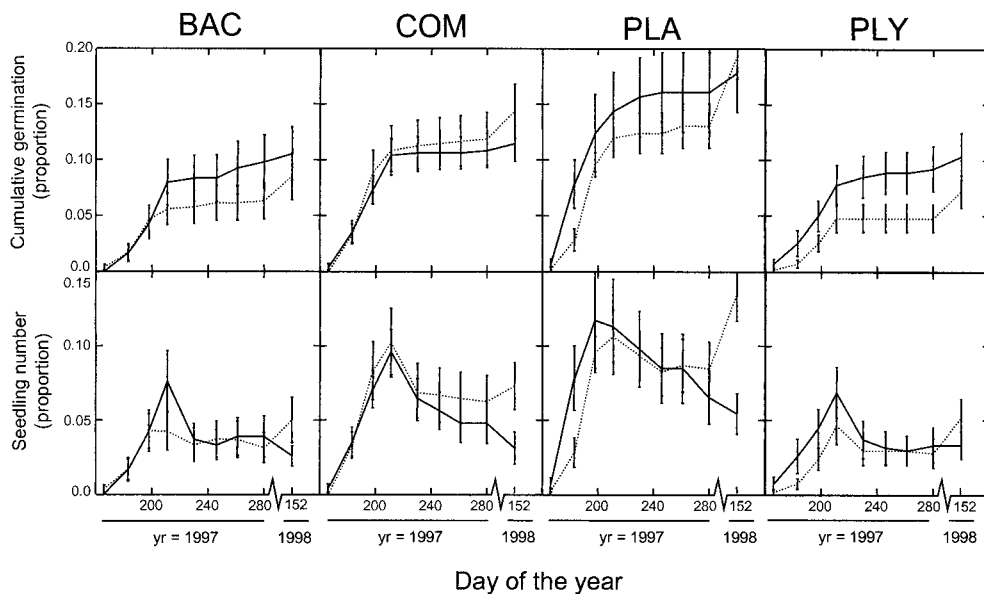

Fig. 4.   Cumulative germination and seedling number (± 1 SE) for seeds of *Carex communis* planted in potting soil in spring 1997 (experiment 2) at four plot types. At each plot, seeds were planted in two treatments, litter exclusion (········), and control (——).
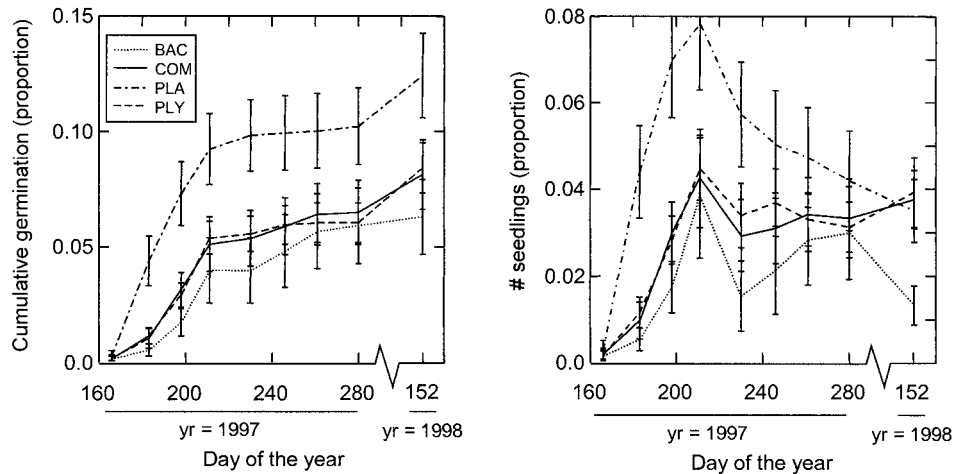
Fig. 5. Cumulative germination and seedling number (± 1 SE) for seeds of *Carex communis* planted in native soil in spring 1997 (experiment 3) at four plot types.

3, the differences were significant for both germination and seedling number in both 1997 and 1998.

Experiment 4: test for home-site advantage with respect to edaphic conditions—The first census of this experiment was on 11 June, and within 1 mo, 78% of the pots where seeds of *C. communis* had been planted contained a seedling, although the first germinant in some pots containing soil from *C. plantaginea* plots emerged as late as 3 August. Total dry mass, number of shoots, number of leaves, and root-to-shoot ratio were all negatively correlated with germination date ($P < 0.02$), and there was no heterogeneity of slopes among plot types for any variable regressed against germination date ($P > 0.6$). Germination date varied significantly among plot types, as did all other variables, even after including germination date as a covariate in the analyses of covariance ($P < 0.002$; Table 3). However, differences among plot types were driven entirely by the late germination date, small size, and high root-to-shoot ratio of *C. communis* plants in soil from *C. communis*.

plantaginea plots, with no significant differences among the other three plot types (Table 3).

DISCUSSION

The primary goal of our research on *Carex backii, C. communis, C. plantaginea,* and *C. platyphylla* (Vellend, 1999; Vellend, Lechowicz, and Waterway, 2000; this study) was to test whether the maintenance of diversity in forest-understory *Carex* species could be explained by the adaptation of each species to a different set of micro-environmental conditions within a spatially heterogeneous habitat, as proposed by equilibrium community theories (e.g., Pacala and Roughgarden, 1982; Tilman, 1982). Relatively distinct environmental distributions of the four species (Vellend, Lechowicz, and Waterway, 2000) suggested that this could be the case. Adaptations to micro-environmental conditions may be manifested either by competitive superiority or greater tolerance of specific biotic or abiotic stresses. We therefore predicted that, at some stage of

TABLE 2. Results of categorical models (SAS PROC CATMOD) testing for effects of litter cover on seed germination and seedling establishment of *Carex communis* (COM) and *C. platyphylla* (PLY). Maximum values for both germination and final seedling number are three. Each observation is a single bottomless canister in which three (season = fall) or ten (season = spring) seeds were planted. Significant differences ($P < 0.05$) are indicated in boldface.

Species of seed	Season of planting	Soil	Variable	Year	Mean ± 1 SE, no. canisters		χ^2	P
					No litter	Litter		
COM	fall	potting	germination	1997	1.36 ± 0.10, $N = 107$	1.22 ± 0.13, $N = 69$	0.81	0.3668
COM	fall	potting	no. seedlings	1997	0.65 ± 0.08, $N = 107$	0.29 ± 0.07, $N = 69$	**11.08**	**0.0009**
COM	fall	potting	germination	1998	1.39 ± 0.10, $N = 104$	1.22 ± 0.13, $N = 63$	1.14	0.2848
COM	fall	potting	no. seedlings	1998	0.42 ± 0.07, $N = 104$	0.10 ± 0.04, $N = 63$	**15.37**	**0.0001**
PLY	fall	potting	germination	1997	0.57 ± 0.08, $N = 112$	0.45 ± 0.09, $N = 69$	1.10	0.2938
PLY	fall	potting	no. seedlings	1997	0.29 ± 0.05, $N = 112$	0.09 ± 0.04, $N = 69$	**9.08**	**0.0026**
PLY	fall	potting	germination	1998	0.59 ± 0.08, $N = 107$	0.46 ± 0.09, $N = 63$	1.15	0.2834
PLY	fall	potting	no. seedlings	1998	0.21 ± 0.05, $N = 107$	0.03 ± 0.02, $N = 63$	**11.14**	**0.0008**
COM	spring	potting	germination	1997	1.08 ± 0.10, $N = 139$	0.87 ± 0.13, $N = 70$	1.66	0.1970
COM	spring	potting	no. seedlings	1997	0.60 ± 0.08, $N = 139$	0.23 ± 0.07, $N = 70$	**11.65**	**0.0006**
COM	spring	potting	germination	1998	1.39 ± 0.14, $N = 130$	1.10 ± 0.18, $N = 66$	1.73	0.1878
COM	spring	potting	no. seedlings	1998	0.45 ± 0.06, $N = 130$	0.17 ± 0.06, $N = 66$	**10.89**	**0.0010**
COM	spring	native	germination	1997	0.72 ± 0.05, $N = 350$	0.48 ± 0.08, $N = 103$	**6.32**	**0.0119**
COM	spring	native	no. seedlings	1997	0.37 ± 0.04, $N = 350$	0.21 ± 0.05, $N = 103$	**5.78**	**0.0162**
COM	spring	native	germination	1998	0.99 ± 0.08, $N = 338$	0.62 ± 0.11, $N = 99$	**7.45**	**0.0063**
COM	spring	native	no. seedlings	1998	0.34 ± 0.04, $N = 338$	0.15 ± 0.05, $N = 99$	**9.75**	**0.0018**

TABLE 3. Results of analysis of variance for an effect of plot type on germination date, and of analyses of covariance (with germination date as a covariate) testing for an effect of plot type on size and allocation measures for plants of *Carex communis* (COM) grown from seed in soil from four plot types: *C. backii* (BAC), COM, *C. plantaginea* (PLA), and *C. platyphylla* (PLY). Data are mean ± 1 SE of untransformed data. All variables except germination date were square-root transformed prior to analysis. For a given variable, different superscript letters indicate significant differences [$P < 0.05$, Ryan's *Q* procedure for germination date, Hochberg's (1974) GT2 method for analyses of covariance]. Significant differences ($P < 0.05$) are indicated in boldface.

Variable	Plot type				*F*	*P*
	BAC	COM	PLA	PLY		
Germination date (day of year)	175 ± 9[a]	175 ± 6[a]	182 ± 11[b]	178 ± 8[a,b]	5.4	**0.0016**
Total dry mass (g)	0.43 ± 0.16[b]	0.38 ± 0.17[b]	0.18 ± 0.09[a]	0.33 ± 0.17[b]	14.1	**0.0001**
Root mass/shoot mass	0.34 ± 0.09[a]	0.37 ± 0.11[a,b]	0.39 ± 0.13[b]	0.31 ± 0.09[a]	5.7	**0.0011**
Leaf number	31.2 ± 8.4[b]	31.6 ± 10.8[b]	20.0 ± 6.8[a]	29.6 ± 9.2[b]	9.9	**0.0001**
Shoot number	6.3 ± 1.8[b]	6.5 ± 2.1[b]	4.0 ± 1.6[a]	5.9 ± 2.0[b]	9.3	**0.0001**

the life cycle, each species would have an advantage at its "home sites" compared to sites where its congeners occurred. However, we found no evidence of home-site advantage for seed germination or seedling establishment in this study.

We have shown clearly that the environmental distribution of *C. communis* is not distinguished from that of its congeners by specific requirements for regeneration from seed or edaphic conditions for establishment. Because the response of *C. platyphylla* seeds was analyzed for only one experiment planted in potting soil, we cannot rule out the possibility that *C. platyphylla* seeds may respond to variation among plot types in edaphic conditions not addressed by that one experiment. However, *C. platyphylla* plots were distinguished from the other plot types mostly by occurring on the steepest slopes, rather than by soil conditions, which varied only minimally among *C. backii, C. communis,* and *C. platyphylla* plots (Vellend, Lechowicz, and Waterway, 2000). Furthermore, soil nutrients are generally of only minor importance for the germination of temperate herbs compared to temperature, light, and soil moisture (Baskin and Baskin, 1988), which should have been modified little, or not at all in the case of light, by the potting soil. It is likely that specific environmental conditions required for successful seed germination and establishment do not distinguish the distribution of *C. platyphylla* from that of its congeners. In a separate experiment, we observed the survival and growth of established ramet implants of the four species at all plots, and again found no evidence of home-site advantage, though survival of all species was lowest at *C. plantaginea* plots (Vellend, 1999). However, the two species with poor germination in all experiments, *C. backii* and *C. plantaginea,* may be more likely to exhibit home-site advantage than *C. communis* or *C. platyphylla,* given the evidence that *C. plantaginea* has a unique distribution among the *Carex* species at Mont St. Hilaire and that *C. backii* may depend on fire for successful regeneration.

Our results suggest that the number of *Carex* species in a small patch of forest floor is limited by the number of species whose seeds disperse there, thus indicating that stochastic dispersal and colonization events play an important role in maintaining the local diversity of *Carex* species in the forest understory. However, differences in environmental distribution among the four co-occurring congeners (Vellend, Lechowicz, and Waterway, 2000), as well as among other co-occurring forest herbs (e.g., Bratton, 1976; Beatty, 1985; Lechowicz, Schoen, and Bell, 1988), indicate that adaptations to different micro-environments also contribute to the maintenance of diversity in the forest understory. These results may seem, at first, to be in conflict. However, while the demonstration of

different microhabitat preferences among the four species justifies our previous conclusion (Vellend, Lechowicz, and Waterway, 2000), such data cannot be used to argue for or against the importance of other factors, such as stochastic dispersal and colonization events. In fact, several factors are quite likely to be important in maintaining species diversity within a given system (Huston, 1994; Palmer, 1994). Our studies on four *Carex* species in the forest understory indicate that abiotic or biotic constraints limit the range of micro-environments in which each species occurs, but for at least two species, there are likely to be many microsites within these limits that are unoccupied simply because seeds have not dispersed there.

Our results indicate that the carousel model of van der Maarel and Sykes (1993) may apply to forest herb communities, as suggested by Fröborg and Eriksson (1997). Van der Maarel and Sykes (1993) observed continual turnover of species through time on small-scale permanent plots in a limestone grassland and suggested that species move about freely within the community, with diversity maintained by the stochasticity of these processes. At Mont St. Hilaire, Holland (1978, 1981) observed continual immigration and emigration of forest herbs, including *C. communis, C. plantaginea, C. platyphylla,* and *C. pedunculata,* among 1-m² plots over 11 yr. At the end of the study, >20% of the species found in a given plot in the first year had been replaced by a different species, and there was no indication that the rate of replacement was slowing down (Holland, 1981). In Swedish deciduous forests, Fröborg and Eriksson (1997) observed a similar situation, and Eriksson and Ehrlén (1992) found that recruitment in most understory herbs was limited at least as much by dispersal to unoccupied microsites as the availability of suitable microsites.

As predicted, all of our field experiments showed a negative effect of leaf litter on seed germination and/or establishment. Leaf litter may have many interacting effects on the microenvironment at the soil surface (Facelli and Pickett, 1991). However, the two factors most likely to affect germination in understory *Carex* species are light (Bond, 1999; Schütz and Rave, 1999), which is blocked by litter, and temperature fluctuations (Schütz, 1999), which are dampened by litter (Facelli and Pickett, 1991). Both *C. communis* and *C. platyphylla* show greater germination in light than in darkness (Bond, 1999), and most *Carex* species from deciduous forests in central Europe respond positively to diurnally fluctuating temperatures (Schütz, 1999). Germination of *C. communis* and *C. platyphylla* was likely lower beneath leaf litter due to some combination of reduced light levels, and dampened temperature fluctuations at the soil surface. Reduced light levels may also partly explain the negative effects of litter on seedling estab-

lishment. However, it is the physical barrier to emergence that is thought to be the main inhibiting effect of litter on seedling establishment in forest herbs (Facelli and Pickett, 1991; Eriksson, 1995), particularly for grasses and sedges because of their growth from basal meristems (Sydes and Grime, 1981b). The negative effect of leaf litter on seedling establishment in this study was most likely due to the physical barrier to emergence.

The patterns of regeneration for *C. communis* may be part of an overall strategy (sensu Grime, 1979) related to its dispersal ecology. Among the four species that we investigated, *C. communis* is the only one that is dispersed by ants (Handel, 1978b), the only one that does not require overwinter stratification to germinate (Handel, 1978a; Bond, 1999), and the only one with a relative growth rate over two years that was significantly greater than zero (Vellend, Lechowicz, and Waterway, 2000). Among the studied species, *C. communis* was found in the widest range of environmental conditions (Vellend, Lechowicz, and Waterway, 2000), and showed the highest percentage germination both in the laboratory (Bond, 1999) and in the field (this study). Handel (1978a) observed a remarkably similar situation in his study of *Carex pedunculata*, also an ant-dispersed species (Handel, 1976). Compared to *C. plantaginea* and *C. platyphylla*, *C. pedunculata* is a poorer competitor, occurs in a wider range of local micro-environments, has a greater germination rate, and also does not require overwinter stratification to germinate (Handel, 1978a). Handel (1978a) hypothesized that the evolution of ant dispersal in *C. pedunculata* was a product of the adaptive advantage of dispersal into unoccupied microsites where establishment could occur in the relative absence of competition. Our data do not address the evolution of ant dispersal, but they do suggest an association between ant dispersal and plant strategies in forest understory *Carex* species. Along an axis of stress tolerance (Grime, 1979), ant-dispersed carices are less tolerant, relying on greater dispersal, higher germination rates, and faster growth to occupy, perhaps transiently, microsites in a wide range of environmental conditions. *Carex communis* and *C. pedunculata* are the two most frequently encountered sedges on Mont St. Hilaire (Bell, Lechowicz, and Waterway, 2000), and the only two we know to be dispersed by ants, although there may be others. These data are consistent with previous studies indicating that ant dispersal is a particularly successful strategy among herbaceous species in the forest understory (Handel, Fisch, and Schatz, 1981; Beattie, 1985).

In summary, we found no evidence for home-site advantage in either *C. communis* or *C. platyphylla*, suggesting that stochastic dispersal and colonization events are important in maintaining the diversity of *Carex* species in upland forests. As expected from previous work on forest herbs, we demonstrated negative effects of leaf litter on germination and establishment. Ant dispersal in *C. communis* appears to be part of an overall strategy associated with high germination rates and a broad tolerance of environmental conditions.

LITERATURE CITED

BASKIN, C., AND J. M. BASKIN. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California, USA.

BEATTIE, A. J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge, UK.

BEATTY, S. W. 1985. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65: 1406–1419.

———, AND O. D. SHOLES. 1988. Leaf litter effect on plant species composition of deciduous forest treefall pits. *Canadian Journal of Forest Research* 18: 553–559.

BELL, G., M. J. LECHOWICZ, AND M. J. WATERWAY. 2000. Environmental heterogeneity and species diversity of forest sedges. *Journal of Ecology* 88: 67–87.

BOND, A. 1999. Germination ecology of *Carex*: effects of stratification, light and soil moisture. M.Sc. thesis, Department of Plant Science, McGill University, Montréal, Québec, Canada.

BRATTON, S. B. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. *American Naturalist* 110: 679–693.

CHESSON, P. L., AND T. J. CASE. 1986. Overview: nonequilibrium community theories: chance, variability, history, and coexistence. *In* J. Diamond and T. J. Case [eds.], Community ecology, 229–239. Harper and Row, New York, New York, USA.

COLLINS, S. L., K. P. DUNNE, AND S. T. A. PICKETT. 1985. Responses of forest herbs to canopy gaps. *In* S. T. A. Pickett and P. S. White [eds.], The ecology of natural disturbance and patch dynamics, 217–234. Academic Press, New York, New York, USA.

DAY, R. W., AND G. P. QUINN. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* 65: 433–463.

ERIKSSON, O. 1995. Seedling recruitment in deciduous forest herbs: the effects of litter, soil chemistry and seed bank. *Flora* 190: 65–70.

———, AND J. EHRLÉN. 1992. Seed and microsite-limitation of recruitment in plant populations. *Oecologia* 91: 360–364.

FACELLI, J. M., AND S. T. A. PICKETT. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* 57: 1–32.

FRÖBORG, H., AND O. ERIKSSON. 1997. Local colonization and extinction of field layer plants in a deciduous forest and their dependence upon life history features. *Journal of Vegetation Science* 8: 395–400.

GRIME, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester, UK.

GRUBB, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107–145.

HANDEL, S. N. 1976. Dispersal ecology of *Carex pedunculata* (Cyperaceae), a new North American myrmecochore. *American Journal of Botany* 63: 1071–1079.

———. 1978a. The competitive relationship of three woodland sedges and its bearing on the evolution of ant dispersal of *Carex pedunculata*. *Evolution* 32: 151–163.

———. 1978b. New ant-dispersed species in the genera *Carex, Luzula,* and *Claytonia. Canadian Journal of Botany* 56: 2925–2927.

———, S. B. FISCH, AND G. E. SCHATZ. 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. *Bulletin of the Torrey Botanical Club* 108: 430–437.

HARVEY, P. H., AND M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford University Press, New York, New York, USA.

HOCHBERG, Y. 1974. Some generalizations of the T-method in simultaneous inference. *Journal of Multivariate Analysis* 4: 224–234.

HOLLAND, P. G. 1978. Species turnover in deciduous forest vegetation. *Vegetatio* 38: 113–118.

———. 1981. Eleven years of change in the species composition of permanent quadrats in deciduous forest on Mont St-Hilaire, Québec. *Naturaliste Canadien* 108: 311–323.

HUBBELL, S. P., R. B. FOSTER, S. T. O'BRIEN, K. E. HARMS, R. CONDIT, B. WECHSLER, S. J. WRIGHT, AND S. LOO DE LAO. 1999. Light-gap disturbance, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554–557.

HUSTON, M. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, UK.

LECHOWICZ, M. J., D. J. SCHOEN, AND G. BELL. 1988. Environmental correlates of habitat distribution and fitness components in *Impatiens capensis* and *Impatiens pallida*. *Journal of Ecology* 76: 1043–1054.

PACALA, S. W., AND J. ROUGHGARDEN. 1982. Spatial heterogeneity and interspecific competition. *Theoretical Population Biology* 31: 92–113.

PALMER, M. W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica et Phytotaxonomica* 29: 511–530.

SCHÜTZ, W. 1998. Seed dormancy cycles and germination phenologies in sedges (*Carex*) from various habitats. *Wetlands* 18: 288–297.

———. 1999. Germination responses of temperate *Carex*-species to diurnally fluctuating temperatures—a comparative study. *Flora* 194: 21–32.

———, AND G. RAVE. 1999. The effect of cold stratification and light on the seed germination of temperate sedges (*Carex*) from various habitats and implications for regeneration strategies. *Plant Ecology* 144: 215–230.

STARR, J. R., R. J. BAYER, AND B. A. FORD. 1999. The phylogenetic position of *Carex* section *Phyllostachys* and its implications for phylogeny and subgeneric circumscription in *Carex* (Cyperaceae). *American Journal of Botany* 86: 563–577.

SULTAN, S. E., A. M. WILCZEK, S. D. HANN, AND B. J. BROSI. 1998. Contrasting ecological breadth of co-occurring annual *Polygonum* species. *Journal of Ecology* 86: 363–383.

SYDES, C., AND J. P. GRIME. 1981a. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland I. Field investigations. *Journal of Ecology* 69: 237–248.

———, AND ———. 1981b. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland II. An experimental investigation. *Journal of Ecology* 69: 249–262.

TILMAN, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

VALERDE, T., AND J. SILVERTOWN. 1997. An integrated model of demography, patch dynamics and seed dispersal in a woodland herb, *Primula vulgaris. Oikos* 80: 67–77.

VAN DER MAAREL, E., AND M. T. SYKES. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *Journal of Vegetation Science* 4: 179–188.

VASSEUR, L., AND D. GAGNON. 1994. Survival and growth of *Allium tricoccum* Ait. transplants in different habitats. *Biological Conservation* 68: 107–114.

VELLEND, M. 1999. Environmental distribution and regeneration of four forest sedges. M.Sc. thesis, Department of Biology, McGill University, Montréal, Québec, Canada.

———, M. J. LECHOWICZ, AND M. J. WATERWAY. 2000. Environmental distribution of four *Carex* species (Cyperaceae) in an old-growth forest. *American Journal of Botany* 87: 1507–1516.

WATERWAY, M. J. 1999. Phylogenetic relationships within *Carex* based on DNA sequence data. *XVI International Botanical Congress Abstracts* p. 386.

WHIGHAM, D. F., J. O'NEILL, AND M. CIPOLLINI. 1993. The role of tree gaps in maintaining the population structure of a woodland herb: *Cynoglossum virginianum* L. *Plant Species Biology* 8: 107–115.