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COMPETITION AND DISPERSAL IN THE
REGULATION OF PLANT SPECIES RICHNESS
ON *CAREX STRICTA* TUSsockS

BY

LEONARD A. LORD
B.S., University of New Hampshire, 1986
M.S., University of New Hampshire, 1994

DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy

in

Plant Biology

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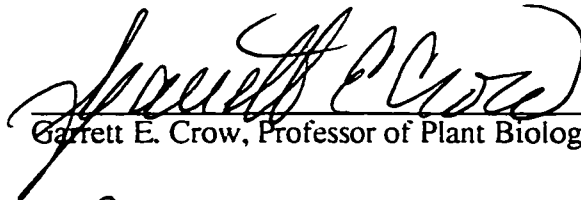
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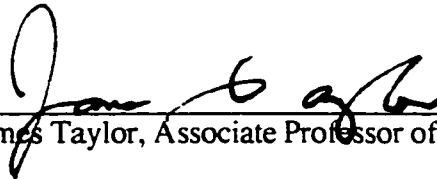
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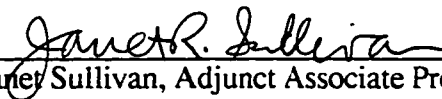
Alan L. Baker, Associate Professor of Plant Biology



Garrett E. Crow, Professor of Plant Biology



James Taylor, Associate Professor of Zoology



Janet Sullivan, Adjunct Associate Professor of Plant Biology

December 2, 1996

Date

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ABSTRACT

COMPETITION AND DISPERSAL IN THE REGULATION OF PLANT SPECIES RICHNESS ON *CAREX STRICTA* TUSSOCKS

by

Leonard A. Lord

University of New Hampshire, December, 1996

Many wetland plant species can be found growing on *Carex stricta* Lam. (tussock sedge) tussocks in freshwater marshes. Based on Grime's model of plant species richness, the objectives of this research were to: 1) examine if dispersal characteristics vary among *C. stricta* marshes in a manner that could potentially influence species richness on individual tussocks, and 2) examine how variation in propagule availability may interact with standing crop and leaf litter to regulate species richness on individual tussocks. All of the research was conducted in southeastern New Hampshire.

Dispersal characteristics were quantified in five wetlands representing a broad range of average species richness per tussock. In each wetland, I observed patterns of plant colonization on 50 artificial tussocks (10 per site) over a one year period. In wetlands with high numbers of species per *C. stricta* tussock, species arrived at artificial tussocks at higher rates than at sites with few species per *C. stricta* tussock. Therefore, it was possible that variation in dispersal characteristics among wetlands could contribute to the observed differences in average species richness per *C. stricta* tussock. In addition, I found that the variation among wetlands in the rates at which species arrived at artificial tussocks was due primarily to variation in numbers of dispersing species (species pool) rather than to variation in the densities of dispersing propagules per species.

In order to examine how variation in propagule availabilities may interact with standing crop and leaf litter to regulate species richness on *C. stricta* tussocks, I experimentally manipulated these factors using a factorial design involving 168 tussocks in three wetlands. Clipping of live *C. stricta*, removal of leaf litter, and addition of seeds from tussock inhabiting species all increased species richness on tussocks. Moreover, the magnitude of the limitation imposed by each was strongly dependent on the levels of each of the other factors. All of these relationships were consistent with Grime's model.

INTRODUCTION

One objective of community ecology is to describe and explain the structure of communities. A key element of community structure is species richness: the number of species present. Many different models have attempted to explain why species richness varies among plant communities, but no single model of plant species richness has emerged as being superior. Most of these models can be divided into two major groups. One group focuses on local processes, primarily in relation to plant competition, while the other group focuses on regional processes, primarily in relation to dispersal among communities. The authors of models in both groups generally acknowledge the importance of processes at both the local and regional scales, but most of the related research has focused on processes at one scale or the other. If processes at both local and regional scales are important to understanding the structure of plant communities, it is essential that research incorporate processes at both scales so that we may understand how these processes interact.

For my master's research, I conducted a correlative study in which I found that standing crop (community biomass) and leaf litter biomass were related to species richness—the number of plant species—on individual *Carex stricta* Lam. (tussock sedge) tussocks. I hypothesized that biomass influenced species richness through competitive effects. Although not measured directly, patterns in the data suggested that dispersal effects also may be important in regulating species richness in these communities. Dispersal effects may affect species richness by influencing the rate at which propagules from potential colonists come in contact with tussocks. With individual tussocks as the local communities, the most important scale of dispersal in the *Carex stricta* system is among tussocks within a wetland.

In order to better understand the influences of competition and dispersal in the tussock sedge system, I had two primary research objectives. The first objective was to examine whether or not there was variation among wetlands in the rate at which species come in contact with tussocks (species-tussock⁻¹·year⁻¹). This would establish whether or not dispersal effects could *potentially* influence species richness. If no variation was

found, then the contribution of dispersal effects to the variation among wetlands in species richness per tussock could be ruled out. However, the opposite would not be true; finding differences among wetlands would not necessarily indicate that dispersal affects species richness. This is because it is just as likely that dispersal *reflects* local community structure as it is that dispersal *affects* local community structure. In addition, the correlative work that I did for my master's research was not sufficient to conclude that standing crop and leaf litter directly influence species richness. Therefore, my second objective was to determine experimentally how variation in the rate at which species arrive at tussocks may interact with standing crop and leaf litter to influence species richness on *Carex stricta* tussocks.

Carex stricta Tussocks and Tussock Colonization

Carex stricta is a common sedge of freshwater wetlands and is native to eastern North America. In New England, I have found that *Carex stricta* often forms large, apparently even-aged populations that dominate marshes associated with beaver dams (Lord 1994). This sedge forms dense clumps or "tussocks" in which its culms and tillers emerge from discrete bases that are elevated above the surrounding water or saturated soil. These bases grow up to a meter or more in diameter and to just under a meter high and are made up of coarse roots, ascending rhizomes, and decomposing organic matter, all held together by tough, fine roots (Costello 1936; Lord 1994). As the tussocks age, there appear to be associated reductions in production of standing crop and in litter accumulation, increases in the areas of vegetation gaps on the tussocks, and partial decomposition of the emergent portions of the tussock bases. These changes are also likely to be influenced by the hydrological regime of the wetland, with large water level fluctuations associated with increases in the amount of decomposition.

In a wetland, the tussock growth form allows aerobic conditions to be maintained in roots that are held above the water level (Nishikawa 1990). In addition, tussock bases may provide a favorable nutrient medium (Nishikawa 1990) with both high levels of nutrients and rapid nutrient cycling (Chapin et al. 1979). This favorable rooting environment would benefit not only *Carex stricta*, but other wetland species that become established on the tussock bases as well. The association between *Carex stricta* and opportunistic colonists

has been observed by other researchers (Nichols 1915; Costello 1936; Jervis 1963, 1969; Niering 1987; Golet et al. 1993) and appears to be widespread.

Species Richness and Ecological Theory

Ecological theories that emphasize local scale processes related to productivity (e.g., Grime 1973a, 1973b, 1979 ; Huston 1979, 1994; Tilman 1982, 1988; Keddy 1990) are used to explain the frequently observed peak in species richness that occurs at moderately low biomass production (e.g., see review by Tilman & Pacala 1993). As live biomass reflects both the successful acquisition of resources in the past and the ability to acquire resources in the present, the low species richness associated with high biomass production is thought to reflect high levels of competitive exclusion by fast growing species; the low species richness associated with very low biomass production is thought to reflect species exclusions due to environmental stress or disturbance.

In contrast to theories emphasizing stress, disturbance, and competitive exclusion as the primary forces that shape community structure, a second group of theories emphasizes regional processes associated with dispersal (e.g., Mac Arthur & Wilson 1967; Horn & Mac Arthur 1972; Brown & Kodric-Brown 1977; Connell 1978; Caswell 1978; Hanski 1982, 1983; Tilman 1994). These models typically involve similar local habitat patches that are separated spatially and interact through dispersal. Species richness in the patches is a function of a balance between colonization and extinction rates (species-patch⁻¹·time⁻¹), both of which may be influenced by the rate at which species come in contact with patches.

Based on island biogeographic theory (Mac Arthur & Wilson 1967), the immigration rate of new species (λ) into a habitat patch is related to three factors: numbers of dispersing species that potentially could occupy the patch in the absence of competition (species pool: P), the number of species already present in the patch (species richness: S) and the rate at which species arrive at a patch (I).

$$\lambda = I - (I/P)S \quad (1)$$

In this theory, I is negatively correlated with patch distance from a mainland source of propagules. This is because propagule densities are reduced with increasing distance from a mainland, and therefore all species have lower probabilities of colonizing far patches (Mac Arthur & Wilson 1967: Fig. 1). At $S = 0$, $\lambda = I$, but as S increases, fewer species remain in the species pool as potential new colonists, and the immigration of new species declines. Equilibrium species richness occurs when colonizations equal extinctions.

In addition to having an effect on colonization, propagule densities also could affect extinction rates through effects on population subsidization (the “rescue effect”: Brown & Kodric-Brown 1977; Hanski 1982). Each species present in a given patch has a fixed extinction probability that is thought to be inversely related to its population size. Propagule inputs from external sources (individuals-patch⁻¹·time⁻¹) may buffer local populations from extinction during unfavorable periods when death rates exceed local regeneration rates (Fig. 2).

Although much of the theory related to the influences of regional dispersal on species richness was initially developed for mainland-island systems, these models may also have application for collections of habitat patches that interact through dispersal without distinct one-way mainland-island dispersal gradients (cf., Harrison 1991; Gotelli & Kelley 1993). For example, propagule densities are still likely to be important influences on I . Rather than being related to distance from a mainland, however, propagule densities may be related to conditions within a set of interacting patches. These conditions could include the average propagule production per ramet, average ramet number per species per patch, and average number of patches occupied per species (Hanski 1982), as well as the distances between patches.

Evidence from my master’s research indicated that the species richness of plant communities on *Carex stricta* tussocks may be influenced by the levels of living biomass production, leaf litter accumulations, and dispersal effects. Of all of the models I reviewed, only Grime’s (1973b, 1979) model of species richness included all three of these factors (Fig. 3). Grime’s emphasis on stress, disturbance, and exploitation competition in relation to productivity and species richness is typical of the models emphasizing local processes. However, Grime also included leaf litter accumulations in his models as a

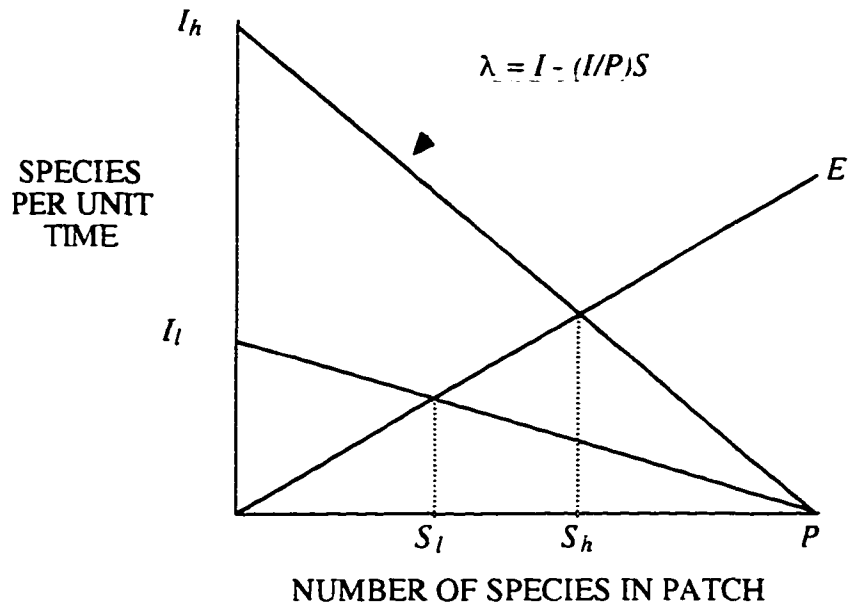


Figure 1. I is the rate at which species arrive at a patch. λ is the rate at which *new* species arrive at a patch. P is the number of dispersing species that could occupy the patch in the absence of competition. E is the maximum extinction rate. S is the balance between colonizations and extinctions: the equilibrium species richness. The subscript “l” refers to conditions where the species have low average dispersal densities, and “h” refers to conditions where the species have high average dispersal densities. In island biogeographic theory, low average dispersal densities are associated with islands far from a mainland source of propagules, and high average dispersal densities are associated with islands close to a mainland. With equivalent species pools, low average dispersal densities result in low equilibrium species richness. Adapted from Mac Arthur & Wilson 1967.

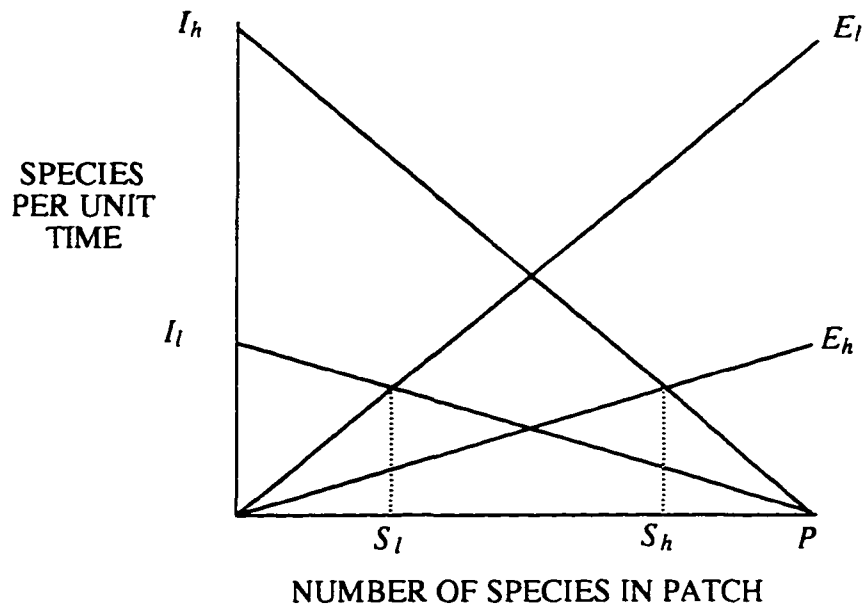


Figure 2. The rescue effect. Symbols are the same as in Figure 1. High average propagule densities result in both high immigration rates and low extinction rates. The reduced extinction rates (the rescue effect) results from high numbers of immigrants per species that may subsidize existing populations, thus reducing their extinction probabilities. Adapted from Brown & Kodric-Brown 1977.

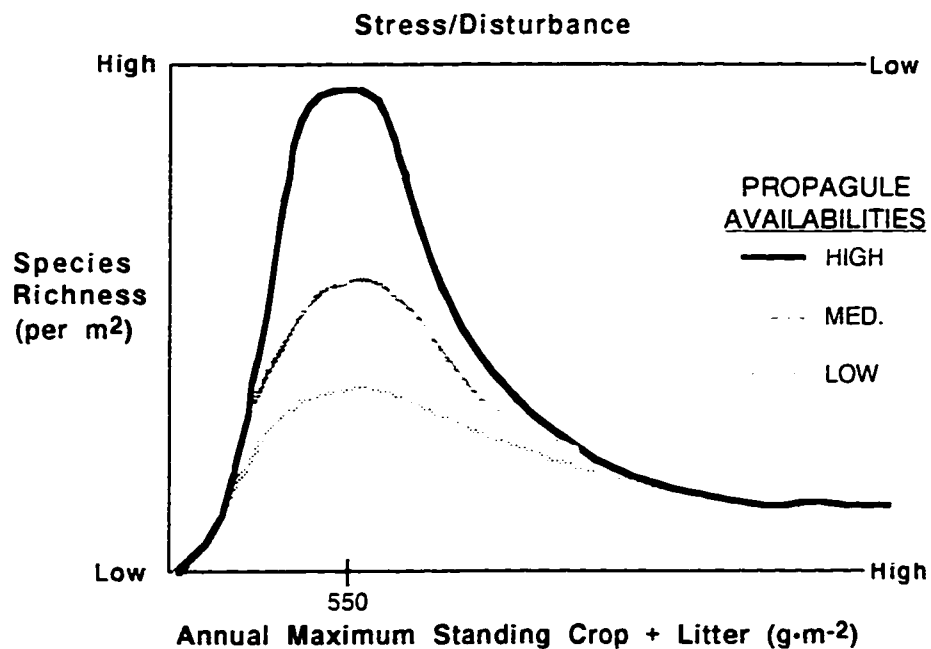


Figure 3. Grime's model of species richness in herbaceous vegetation. At high standing crop + litter, competition reduces richness. At very low standing crop + litter, stress or disturbance reduce richness. Maximum coexistence occurs at moderately low standing crop + litter (ca. 550 g·m⁻²), with the number of coexisting species directly related to propagule availabilities- the numbers of dispersing species and their immigration rates (adapted from Grime 1979).

factor that could contribute to the species richness-productivity relationship. Grime reasoned that heavy leaf litter production by fast growing species under favorable conditions could inhibit the establishment and growth of other species via physical or chemical interference competition and, like living biomass, would be greatly reduced in very stressful or disturbed environments. In addition, Grime argued that the magnitude of the peak in species richness associated with moderately low standing crop plus leaf litter levels was determined by the numbers of dispersing species and their immigration rates (Grime's "reservoir effects").

Because Grime's model appeared to reflect the processes at work in *Carex stricta* colonist communities, I used it as the basis of my hypotheses for this research. In my work, the local scale is that of the community of plants occupying a single *Carex stricta* tussock, and the regional scale is that of the group of tussocks that interact via dispersal within a wetland.

Literature Review

Correlative studies. Most of the studies in which Grime's model was specifically mentioned were correlative studies done across a number of different vegetation types to determine if a relationship existed between species richness and standing crop or standing crop plus leaf litter. While negative or unimodal relationships were revealed in most of these studies (e.g., Al-Mufti et al. 1977; Wheeler & Giller 1982; Vermeer & Berendse 1983; Wilson & Keddy 1988; Moore & Keddy 1989; Shipley et al. 1991; Wheeler & Shaw 1991; Tilman 1993; Gough et al. 1994), the relationships often were weak, with much scatter in the data. In some studies, no significant relationships were detected (Vermeer & Verhoeven 1987; Day et al. 1988), and in one study monotonic relationships were found (Wisheu & Keddy 1989). Of the correlational studies reviewed, only one included dispersal effects (Gough et al 1994). In that study, species pool and above ground biomass (standing crop plus litter) together explained 81% of the variation in species richness among local plots (species·m⁻²).

I also found several studies that examined only the effects of dispersal on species richness relationships by looking at the correlations between isolation and species richness. In all of these studies there were negative correlations between isolation (or factors related

to isolation) and plant species richness (Nilsson & Nilsson 1982; Kadmon & Pulliam 1993, 1995; Ouborg 1993; Reinartz & Warne 1993; Weiher & Boylen 1994), presumably because more isolated habitats had a lower rate of encounter by potential colonists than less isolated habitats.

Experimental studies. I could not find any experimental studies in which the effects of a competitive dominant, leaf litter levels, and dispersal on species richness were all examined together. Therefore, I have reviewed studies of each of these factors individually. Since my research did not involve examining the direct influences of stress and disturbance on species richness at very low standing crop plus leaf litter levels (the portion of Grime's model to the left of the peak in species richness, Fig. 3), I did not review experiments pertaining to those relationships.

Some researchers have examined the effects of dominant species by suppressing those dominants and noting the effects on species richness. These studies had mixed results. A number of studies found that suppression of dominants resulted in increased species richness (Abul-Fatih & Bazzaz 1979; Armesto & Pickett 1985; Gurevitch & Unnasch 1989; Cowie et al. 1992). In other cases, however, suppression of dominants did not result in increased richness (Pinder 1975; Allen & Forman 1976; Hils & Vankat 1982; Armesto & Pickett 1985; van der Valk 1986). Unfortunately, community productivity was not reported in most of these studies, making it difficult to relate the findings to Grime's model.

As with the competition studies, the results of leaf litter manipulations were mixed. Monk & Gabrielson (1985) and van der Valk (1986) found that leaf litter levels always were negatively associated with species richness. Penfound (1964), Carson & Peterson (1990), and Weiher & Keddy (1995) all had mixed results, where the effects of litter were determined by interactions with other factors.

I could not find any studies in which propagules from a number of species were manipulated simultaneously to examine the effects on species richness. However, I did find a number of experiments in which propagules from individual species were added to communities to determine if they could invade those communities. In several of these studies propagules were found to be limiting— species were absent until propagules were added (Gross & Werner 1982; Peart 1989; De Steven 1991a, 1991b; Robinson et al. 1995).

Not surprisingly, in two of these studies there were instances in which propagule additions did not lead to species' establishments, indicating that the absences of the species from the communities were not due to propagule limitation (Gross & Werner 1982; Peart 1989).

Taken together, these studies indicate that the living biomass of competitive dominants, leaf litter, and propagule supplies all have the potential to influence species richness. However, it is clear that more work must be done to determine the conditions under which these factors are important and what interactions may occur among them.

I. COLONIZATION OF ARTIFICIAL TUSSOCKS

Introduction

In my previous work, I examined the relationship between the number of vascular plant species found growing on individual *Carex stricta* tussocks and local environmental factors in five wetlands (Lord 1994). At the time of that study (1992), the average species richness in these wetlands ranged from 1.3 to 8.5 species per tussock. In the absence of competitive exclusion, the rate at which species from the species pool arrive at a tussock (I) would affect species establishment rates (number of species establishing-tussock⁻¹-time⁻¹), thus affecting the equilibrium species richness (Fig. 1). If I varied among sites, it could result in variation in average species richness per tussock. However, I was not measured as part of my 1992 study and, therefore, I did not know if variation in this factor contributed to the large differences in species per tussock found among the sites. This led to the present research, in which the primary objectives were to measure I in those same wetlands and to examine the nature of any variation in I that might exist. The purpose of the study was only to determine whether dispersal effects varied in a manner that could *potentially* contribute to variation among wetlands in the numbers of species colonizing *Carex stricta* tussocks. These patterns would not imply cause and effect, especially since there are likely to be feedbacks between local community structure and dispersal patterns.

In island biogeographic models, island community structure is a function of mainland community structure with no feedbacks. A *Carex stricta* marsh, however, is more likely to function as a set of interacting patches (a “metacommunity” Hanski & Gilpin 1991). This is because the species on the tussocks are usually reproductive and the tussocks are in close proximity to each other. The marshes are generally surrounded by upland forest that contains few of the species found to grow on tussocks, and therefore relatively few propagules from species that grow on tussocks are dispersed from outside the system. The high exchange of propagules among tussocks is likely to result in feedbacks in which propagule densities and the dispersing species pool are related to

conditions within the tussock population. For example, a species occupying a relatively large proportion of tussocks may have relatively high density of dispersing propagules (propagule density) and therefore relatively stable populations on all of the tussocks it is able to occupy due to the “rescue effect” (Fig. 2; Brown & Kodric-Brown 1977; Hanski 1982).

In island biogeographic theory, I is emphasized as being strongly related to the average colonization probability per species (i) as a function of patch distance from a mainland (Fig. 1). This assumes that propagule densities (propagules·species⁻¹·unit area⁻¹·time⁻¹) vary with patch distance from a mainland. In a set of interacting patches, propagule densities may vary with other factors, such as the average number of patches occupied per species, but the influence of propagule densities on I would be the same. Similarly, the effects of species pool (P) on I would be the same whether the system was a mainland-island system or a set of interacting patches. Although not specifically addressed in island biogeographic theory, I is a function of P , as well as of propagule densities. This is because each member of the species pool has an immigration probability per patch (i_j) that is related to the density of its dispersing propagules; the rate at which species arrive at a patch would be the sum of these probabilities:

$$I = \sum_{j=1}^P i_j$$

Among communities with equal average probabilities per species (e.g., patches at equal distances from a mainland), those with a greater species pool (P) would have more species because more species would contribute to the sum of the immigration probabilities (Fig. 4). Therefore, in order to understand how dispersal affects I , it is important to look at the influence of both propagule density and species pool.

Examining propagule densities was also important because propagule densities may affect extinction rates through effects on population subsidization (Fig. 2). Propagule inputs from external sources (individuals·patch⁻¹·time⁻¹) may buffer local populations from extinction during unfavorable periods when death rates exceed local regeneration rates.

To infer propagule densities and rates at which species arrive at tussocks, I looked

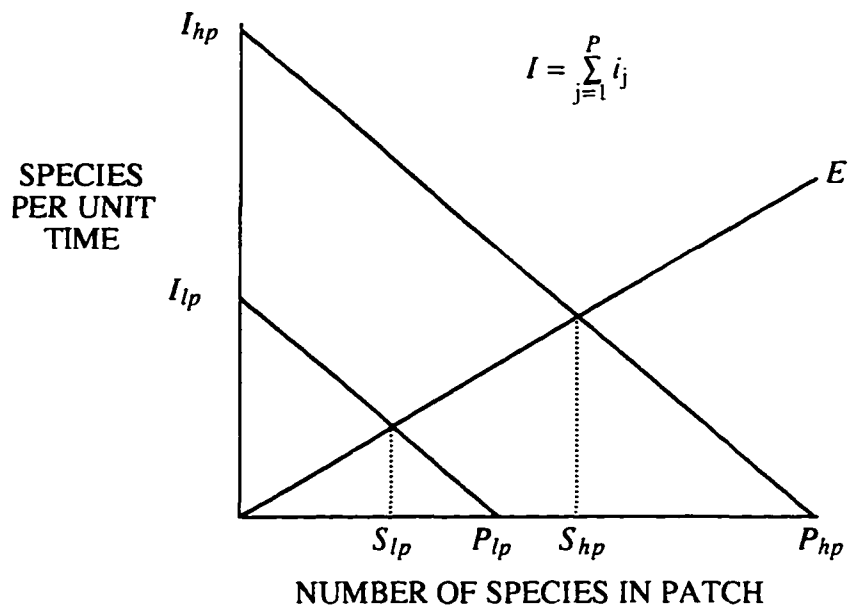


Figure 4. Effects of species pool on immigration and species richness. Symbols are as in Figure 1, except that the subscripts “lp” and “hp” refer to low species pool and high species pool respectively. Each species in the species pool has an immigration probability i . I is equivalent to the sum of these probabilities for all of the species in the species pool. In the example shown, the two patches have equivalent average i , but different species pools. The patch associated with the greater species pool has a greater equilibrium species richness.

at patterns of colonization on artificial tussocks. Colonization, in this case, is the arrival and germination of propagules. Artificial tussocks were used, rather than *Carex stricta* tussocks, in order to control for variation in environmental influences and existing seed banks. Species pools were determined by sampling established plants in the marshes. I tested the following hypotheses as they related to dispersal patterns in the five wetlands examined in my master's research. These wetlands were selected to represent a broad range of average species richness per tussock.

1a) Sites differ in the rates at which species arrive at tussocks (I).

1b) The pattern of variation in I among sites is one that could result in the observed differences in average species richness per *Carex stricta* tussock— that is, where the *C. stricta* tussocks each have high numbers of species, they also have greater levels of I .

2) Differences in I among sites are related to differences in the densities of dispersing propagules per species. Sites shown to have greater colonization rates per artificial tussock will therefore have more artificial tussocks colonized per species and higher densities of colonizing individuals per artificial tussock.

3) Differences in I among sites are due to differences in the numbers of dispersing species (P). Therefore, sites with greater numbers of established species will have greater colonization rates per artificial tussock.

In each hypothesis, the “species” referred to are those I have documented (Lord 1994; Part II) as occurring on *Carex stricta* tussocks. In addition, I use the more restrictive term “site” rather than “wetland” to refer to the limited portion (ca. 0.1 ha) of each *Carex stricta* population in which sampling took place.

Methods

The intent of the artificial tussocks was to provide a tussock-like substrate with physical conditions that did not vary within or among sites. They provided an environment for colonizations that was similar to *Carex stricta* tussocks, but with minimal competitive interactions and no preexisting seed bank. The artificial tussocks were designed to be approximately the same height above the water as *C. stricta* tussocks, but were slightly smaller in diameter (20 cm) than most of the *Carex stricta* tussocks found in the wetlands

where the tussocks were placed (ca. 23 cm, standard deviation = 17 cm; Lord 1994).

Construction of artificial tussocks. Fifty artificial tussocks (Fig. 5) were constructed, each using the following materials: 12 liters (loosely packed) rye straw, 9 liters (loosely packed) garden quality peat moss, 3 liters well water, 30 ml (loosely packed, ca. 43 g) ground dolomitic limestone, 1 piece of 2 x 0.4 m plastic "garden netting" (1.8 x 1.8 cm mesh, Ross Daniels, Inc., Lexington, KY), 1 length of 5 cm inner diameter x 25 cm long PVC pipe with 4 holes drilled 5 cm from one end, 2 pieces of 12 ga. galvanized wire, each 15 cm long, 3 pieces of nylon cord, each 1.1 m long, 1 piece of nylon cord 2.3 m long, 0-4 pieces of 2.5 x 20 x 20 cm polystyrene with 6.5 cm diameter holes in the centers (see below on the number of pieces used), and 1 oak stake, 2.5 x 2.5 cm x 1.2-1.4 m long.

First, a 2 x 0.4 m piece of plastic netting was laid out. Then, a 20 cm wide layer of rye straw was placed down the length of the netting, 10 cm from each edge. A mixture of peat, limestone, and water (to aid compaction) was then layered on top of the straw. The 10 cm of plastic netting on either side of the 20 cm wide strip of straw and peat was then folded in and tied down the center with a 2.3 m length of nylon cord. This material was rolled up around a piece of 25 cm long PVC pipe. The pipe had 4 holes that were pre-drilled 5 cm from one end. This end was left protruding from the peat and straw roll. The peat and straw roll was then tied in place using three pieces of nylon cord, each 1.1 m long. Two pieces of 15 cm long 12 ga. wire were each inserted through two of the holes to prevent the peat and straw from shifting along the pipe. Two pieces of 2.5 x 20 x 20 cm polystyrene with 6.5 cm dia. holes in the centers were then fit to the protruding PVC pipe, however, this number was later adjusted (see below). The entire assembly was then was slid, polystyrene end first, over an oak stake driven into the soil of the marsh.

The substrate portion of the artificial tussocks (i.e., the portion above the polystyrene) was cylindrical, ca. 20 cm in diameter, and ca. 20 cm tall. For tussocks that were in water > 20 cm deep, the buoyancy provided by the polystyrene allowed for a constant distance between the tops of the artificial tussocks and the water surface to be maintained (ca. 9-11 cm) despite water level fluctuations. For tussocks in < 20 cm of water, the distances between the tops of the artificial tussocks and the water surface were adjusted by adding and removing pieces of polystyrene (see below).

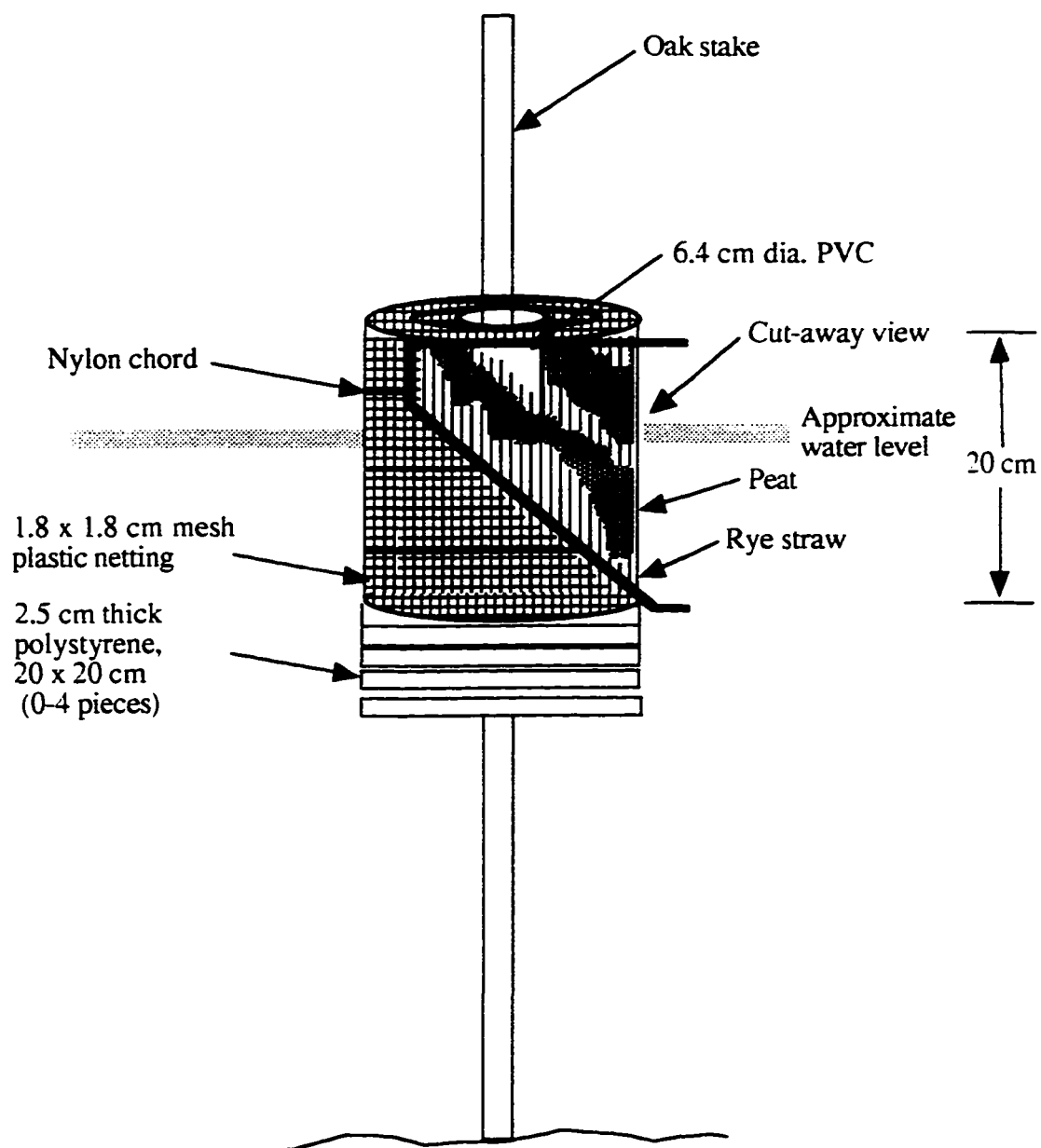


Figure 5. Artificial tussock. The artificial tussocks were provided a tussock-like substrate with physical conditions that did not vary within or among sites. They provided an environment for colonizations that was similar to *Carex stricta* tussocks, but with minimal competitive interactions and no preexisting seed bank. The artificial tussocks were designed to be approximately the same height above the water as *Carex stricta* tussocks, but were slightly smaller in diameter (20 cm) than most of the *Carex stricta* tussocks found in the wetlands where the tussocks were placed (ca. 23 cm, standard deviation = 17 cm; Lord 1994)

In constructing the artificial tussocks, limestone was added to the peat to bring the pH up to a level that was similar to *Carex stricta* tussocks. The average pH taken from six samples (two samples selected haphazardly from each of three bales) of the peat was 3.26 ± 0.05 SEM, whereas eight samples of partially decomposed (hemic-sapric) organic matter taken from two haphazardly selected *Carex stricta* tussocks at each of four of the sites (AT-2, -3, -4, -5) had an average pH of 5.27 ± 0.19 SEM. After the study was completed, pH tests were done on peat samples taken from three randomly selected artificial tussocks at site AT-1 and three at AT-5 to verify that an appropriate amount of limestone had been added. For AT-1, the pH was found to be 6.9 ± 0.06 SEM and for AT-5 it was 6.8 ± 0.03 SEM. Although in October the pH of the artificial tussocks was higher than the *Carex stricta* tussocks, it may have been closer to the pH of the *Carex stricta* tussocks earlier in the growing season, but continued to rise due to the continuous action of the limestone.

Sites. The sites chosen for assessment of propagule supplies were the same five sites that were sampled for my master's research in 1992 (Lord 1994). Site numbers for this study are preceded by AT (artificial tussocks) to distinguish them from sites used in the tussock manipulation (MT) study (see Part II). No two study sites *within* each group (AT or MT) were located closer than 1 km of each other, nor were any of them hydrologically connected. All of the sites were located in palustrine emergent marshes (see Cowardin et al. 1979) dominated or codominated by *Carex stricta*. In addition, all of the sites were within 20 km of Durham, NH and were selected to represent a broad range of average species richness per tussock. See Lord (1994) for more a more detailed description of site selection.

Site AT-1 (Fig. 6) was located between two beaver dams in a small (0.3 ha) section of a 1.5 ha marsh complex along a brook running between Scruton Pond and the Isinglass River in Barrington, NH. Site AT-2 (Fig. 7) was located in the northern end of a 2.5 ha marsh along Spruce Brook, in Barrington. Only about 0.5 ha of the marsh in the vicinity of the study site was dominated by *Carex stricta*. Site AT-3 (Fig. 8) was located in a 2 ha marsh complex along a tributary of the Little River in Nottingham. Approximately 0.3 ha of the marsh in the vicinity of my research was dominated by *Carex stricta*. Site AT-4 (Fig. 9) was located in the northern portion of a 2 ha marsh

along a tributary feeding into the eastern end of Round Ponds in Barrington. Site AT- 5 (Fig. 10) was part of a 19 ha marsh complex along a tributary to the Little River in Lee. The hydrology in all of these wetlands was controlled by beaver. From aerial photography, it appeared that the occupation of these wetlands by beaver occurred sometime between 1953 and 1974 for all of the sites (no photography could be located between those years). Sites AT-1, AT-4, and AT-5 were forested prior to beaver flooding, while site AT-2 had been cleared and site AT-3 appeared to have been dominated by a scrub-shrub community.

Location and maintenance of artificial tussocks. At each of the five sites, 10 artificial tussock locations were selected along parallel transects spaced 10 m apart and offset at least 5 m from the original transects used in 1992. These transects ran approximately perpendicular to the marsh-upland boundary.

The transects were broken into 10 m segments, each of which had 10 points, 1 m apart. Within each segment, one of these 10 points was selected randomly within each 10 m section, with no two selected points from adjacent segments within 3 m of each other. Artificial tussocks were placed in open areas within 1 m of the selected points. To minimize edge effects, none of the artificial tussocks were placed within 5 m of forest edge, within 2 m of other non-forested vegetation types, within 0.5 m of inclusions of dense shrubs within the sampling area, or within 2 m of stream channels or open water.

The artificial tussocks were set out August 23-24, 1994. Where water levels were less than 20 cm, the artificial tussocks rested on the soil substrate, in deeper water they floated on two pieces of polystyrene. In late October, 1994, the tops of the floating tussocks had dropped from ca. 9 cm to ca. 5-6 cm above the water. At that time two more pieces of polystyrene were added, bringing the elevations of the tops of the artificial tussocks to ca. 10 cm above the water. An emergent height above water levels of 10 cm corresponds closely with the heights of *Carex stricta* tussock bases above water levels as measured at these same sites in 1992 (Lord 1994).

The floating artificial tussocks maintained a continuous emergent height relative to water levels despite water fluctuations, however, artificial tussocks in less than 20 cm of water rested on the bottom, and elevations were adjusted by adding or removing the 2.5 cm thick pieces of polystyrene. During the 1995 growing season, the artificial tussocks that



Figure 6. Site AT-1 was located between two beaver dams in a small (0.3 ha) section of a 1.5 ha marsh complex along a brook running between Scruton Pond and the Isinglass River in Barrington, NH.



Figure 7. Site AT-2 was located in the northern end of a 2.5 ha marsh along Spruce Brook, in Barrington. Only about 0.5 ha of the marsh in the vicinity of the study site was dominated by *Carex stricta*.



Figure 8. Site AT-3 was located in a 2 ha marsh complex along a tributary to the Little River in Nottingham. Approximately 0.3 ha in the vicinity of the study site was dominated by *Carex stricta*.



Figure 9. Site AT-4 was located in the northern portion of a 2 ha marsh along a tributary feeding into the eastern end of Round Ponds in Barrington.



Figure 10. Site AT- 5 was part of a 19 ha marsh complex along a tributary to the Little River in Lee.

were not floating were checked and adjusted relative to water levels after significant rain events or dry periods. Where water levels dropped below 10 cm, all of the polystyrene was removed and no further reduction in the elevations of the artificial tussocks was possible. Even though water levels fell below the soil surface in some instances, the artificial tussocks were able to absorb moisture directly from the muck on which they rested. All of the artificial tussocks remained moist throughout the study.

In order to assure favorable growing conditions for colonizing species, overhanging vegetation was clipped within 0.5 m of the artificial tussocks as necessary to reduce shading, and low concentrations of Peters Professional® plant food (20-20-20 plus micronutrients) were applied to the seedlings and artificial tussocks using a mist bottle. In mid-July, 30 ml of 0.065% (by volume) fertilizer solution was applied to each artificial tussock. Two weeks later, 120 ml of 0.13% fertilizer solution was applied to each artificial tussock. The latter application rate was continued at one week intervals for two more weeks. Note that the 0.13% concentration is recommended by the manufacturer for indoor houseplants.

Sampling of artificial tussocks. The artificial tussocks were surveyed for vascular plants known to be *Carex stricta* colonizing species. The surveys were conducted in mid-July, 1995 and then again in mid-September, 1995. Tussock colonizing species were defined as those recorded on at least one *Carex stricta* tussock in my 1992 surveys of these same five sites, or on a tussock in one of the sites used in my field experiment (MT sites) in 1994 or 1995. *Galium trifidum* and *G. tinctorium* were found to have overlapping vegetative morphologies and so were not distinguished (*Galium* spp.). *Spiraea latifolia* and *S. tomentosa* also were not distinguished because of the similarities in seedling morphologies (*Spiraea* spp.) Taxonomy followed Crow & Hellquist (in press) except for *Aster novi-belgii* and *Erechtites hieraciifolia*, which followed Gleason & Cronquist (1991).

In addition to noting species presences and absences, during the September survey colonization densities were estimated for each species on each artificial tussock and were classified into four groupings: 1-3, 4-10, 11-30 and >30 individuals. It was impractical to estimate densities for some graminoid seedlings (*Calamagrostis canadensis*, *Carex canescens*, and *Carex lasiocarpa*) because of their large numbers and vegetative similarities to each other and to *Carex stricta*.

The purpose of the July survey was to aid in assessing whether or not extinctions occurred over the summer. The number of colonizing species per artificial tussock was calculated as the combined set of species from both the July and September surveys. In the few cases where species were present on an artificial tussock in July, but absent in September, the densities of the extinct species were assumed to have been in the lowest density class (1-3). Species losses occurred on three artificial tussocks at site AT-2, seven at AT-4, and on one at AT-5, with each occurrence but one involving the loss of only a single species.

The intent of the artificial tussocks was to create conditions that were conducive to the establishment of *Carex stricta* colonizing species, and to have these conditions equivalent both within and among sites so that variation in establishment could be attributed solely to variation in propagule supplies. Similarities in growing conditions among the artificial tussocks were assessed using the three most common species to create a measure of plant vigor for each artificial tussock. The heights of the tallest *Carex stricta*, *Carex canescens*, and *Triadenum virginicum* individuals were measured for each artificial tussock. Then, for each species, the heights from all of the observations were combined and standardized to have a mean of zero and a standard deviation of one. A vigor score for each artificial tussock was then derived by averaging the standardized measurements among the indicator species growing on it. The indicator species were not all present on every artificial tussock; scores were generated from all three species for 28 of the 50 artificial tussocks, from two species for 15 of the artificial tussocks, and from only a single species for seven of the tussocks. I later determined that the vigor score for one of the tussocks at site AT-2 was an outlier and had very high leverage (i.e., disproportionately high influence) in the statistical analyses. This score was dropped and the standardized values used in the vigor index were recalculated without the measurements associated with that artificial tussock.

At each wetland a fixed point was established from which water levels were monitored on an opportunistic basis during the 1995 growing season (April 8 - September 21). The longest interval between water level measurements was 25 days. In order to obtain readings associated with equivalent intervals at all of the sites, I used the numerous readings that were taken irregularly to interpolate seven water level

measurements for equivalent 25 day periods (April 9 - September 6). These seven water levels were then combined with locally measured water depths to calculate the minimum, maximum, and median water depths at each artificial tussock.

Sampling of established species abundances. Though not directly related to my hypotheses, I examined the general relationships between the individual species' artificial tussock colonization rates, their abundances of established plants in the marshes, and the frequencies with which they occurred as established plants on *Carex stricta* tussocks. The frequencies with which species occurred on *Carex stricta* tussocks in these sites were taken from the 1992 survey (Lord 1994). Species abundances of established plants were assessed using percent foliage cover estimates. These cover estimates were conducted in September, 1994, using 20, 0.25 m² quadrats per site, and included plants rooted in all substrates (i.e., both on and off *Carex stricta* tussocks).

The sampling of abundances was done along the same transects that were used to locate the artificial tussocks. Two 0.25 x 1.0 m quadrats were laid out on opposite sides of the transects at each artificial tussock using a compass and plastic quadrat frame. The closest corner of each quadrat to an artificial tussock was established 1.0 m in a direction perpendicular to the transect. The length of the quadrats also ran perpendicular to the transects unless one end came within 0.5 m of a shrub patch. In order to be consistent with other aspects of sampling, shrub patches were avoided. This was done by rotating the quadrats 45°. Because of this procedure, the abundances of some of the woody species were slightly underestimated.

As in my 1992 surveys of plant species growing on *Carex stricta* tussocks, only individuals that had developed beyond the seedling stage were included in the abundance estimates. This was because seedlings were often difficult to identify without destructive methods, and because I felt that species that were represented only by seedlings that late in the growing season were not established enough to be considered members of the community.

The following traits were used to distinguish between seedlings and individuals of more mature stages. For herbaceous dicots, seedlings were differentiated by having disproportionate leaf size or shape, a delicate appearance, under-developed leaf

characteristics (e.g., lack of lobing, teeth, or stem clasping), the presence of cotyledons or cotyledon remains, or, in most cases, the development of three or fewer nodes. Although heights of the herbaceous dicot seedlings were not measured in this survey, I have found in subsequent surveys that seedlings excluded using these criteria were nearly always less than 2 cm tall.

Due to morphological similarities among young graminoids, height rather than morphological criteria was used to separate seedlings from established individuals. Graminoids shorter than 15 cm were considered to be seedlings unless they could be identified as species that normally have a short stature. It was predetermined that if this were the case, individuals less than 1/3 of the low end of the range of mature heights described for the species in Gleason & Cronquist (1991) would be considered seedlings. The only species that this last criterion was applied to was *Carex canescens* (mature height 2-6 dm), with individuals less than 7 cm tall classified as seedlings.

Data analysis. All statistical analyses were run using SYSTAT 5.2 for the Macintosh (SYSTAT, Inc. © 1990-92). In all of these analyses, the selected alpha level (i.e., the probability of making a Type I error) for significance was $P < 0.05$. For the parametric analyses, distributions of the dependent variables and residuals were examined visually to verify normality. In addition, variances and plots of residuals against continuous independent variables were examined to verify homoscedasticity.

The general relationships between species' artificial tussock colonization rates (percentage of artificial tussocks colonized by a species), their abundances of established plants in the marshes (percent foliage cover), and the frequencies with which they occurred as established plants on *Carex stricta* tussocks (1992 percentage of tussocks occupied) were analyzed using Spearman rank correlations. In this analysis, each species in each wetland was an individual observation. Woody species were not included because of the underestimates in their foliage cover estimates (see above). A nonparametric correlation was used because the variables were not normally distributed.

Analysis of variance (ANOVA) was used to examine whether the number of colonizing species per artificial tussock (I) varied among the sites. Then, analysis of covariance (ANCOVA) was used to examine whether this colonization was affected by variation in vigor or in water levels associated with each artificial tussock. Sites were

modeled as fixed effects in these analyses because they had been selected to represent a broad range of average species richness per tussock. The terms for vigor and water levels were included separately in the models because they were correlated. The ANCOVA's were stepped back by first checking for significant interactions, then pooling nonsignificant terms with the error term. Bonferroni adjusted multiple t-tests were then used to examine differences among individual sites in the average number of colonizing species per artificial tussock.

After examining whether or not variation existed among sites in the numbers of species colonizing artificial tussocks, I examined whether this variation was due to differences in average propagule densities or to differences in the numbers of dispersing species. I used two analyses to examine variation among sites in propagule densities per species. First, I assumed that species with higher regional propagule densities per species would colonize more artificial tussocks than species with low regional densities. I used a Kruskal-Wallis analysis to test for differences in the number of artificial tussocks colonized per species among sites. Then, I examined how the densities of individuals per species per artificial tussock varied among the sites. The number of individuals of each species on each artificial tussock was assigned a density class: 1-3, 4-10, 11-30, or >30 individuals. All species were pooled together and the number of observations in each of the four density classes was tabulated for each site. Regardless of the numbers of dispersing species, sites with higher levels of propagule densities per species should have greater *proportions* of observations in the higher density classes than sites with low densities per species. Differences among sites in the proportions of density class observations were examined using a contingency Table analysis. As no density values were estimated for *Calamagrostis canadensis*, *Carex canescens*, or *Carex lasiocarpa* (see above), these species were excluded from the contingency analysis. Lastly, I examined the influence of species pools on the numbers of species colonizing artificial tussocks. This was done by regressing the numbers of colonizing species associated with each of the individual tussocks against the total numbers of species known to colonize *C. strica* tussocks that were recorded at each site during the quadrat sampling of abundances.

Results

General patterns. Thirty tussock colonizing species were noted on artificial tussocks over all five sites, with 4-18 species noted per site (Table 1). Of the 10 species found on artificial tussocks in three or more sites, some consistently colonized a high proportion of artificial tussocks (e.g., *Bidens discoidea*, *Carex canescens*, *Spiraea* spp.), while others were common at one site but uncommon at another (e.g., *Calamagrostis canadensis*, *Galium* spp., *Lycopus uniflorus*). Only one species, *Lysimachia terrestris*, was consistently uncommon at three or more sites.

Within sites, the numbers of tussocks colonized per species were consistently distributed bimodally (Fig. 11). Most species at most sites occurred on either a few (<5) or on many (>6) artificial tussocks. Only one species at one site was found on five artificial tussocks (*Juncus canadensis* at site AT-4), and none of the species at any of the sites were found on six artificial tussocks. Another consistent pattern was the relatively low variation in numbers of colonizing species per artificial tussock within each site (standard deviation = 0.97-1.37 species).

Individual species' artificial tussock colonization rates (percentage of artificial tussocks occupied), their abundances of established plants in the marshes (percent foliage cover), and the frequencies with which they occurred as established plants on *Carex stricta* tussocks (1992 percentage of tussocks occupied), were all positively correlated (Spearman $r = 0.547-0.626$, Table 2; see Table 1 for individual observations).

Species per artificial tussock. The primary objective of this study was to determine if dispersal characteristics varied among wetlands in a way that could contribute to variation in average species richness per *Carex stricta* tussock. Variation in the rates at which species arrived at *Carex stricta* tussocks among sites was inferred by examining the colonization of artificial tussocks. I found that the number of species arriving at artificial tussocks (I) varied significantly among sites ($r^2 = 0.931$; Table 3), with all of the sites differing from each other (Bonferroni adjusted t-tests, $P < 0.05$ for all comparisons). In general, variation among site in the average number of species colonizing artificial tussocks paralleled variation in the 1992 average species richness per *Carex stricta* tussock (compare Figs. 12 & 13).

Table 1. Abundance and dispersal of species that become established on *Carex stricta* tussocks. The 1992 data are frequencies of occurrence on *C. stricta* tussocks from Lord (1994), 1994 data are foliar cover estimates from 0.25 m² quadrats, and 1995 data are frequencies of artificial tussock colonization.

	SITE AT-1			SITE AT-2			SITE AT-3			SITE AT-4			SITE AT-5		
	1992 % Freq. (n = 12)	1994 % Cover (n=20)	1995 % Freq. (n = 10)	1992 % Freq. (n = 15)	1994 % Cover (n=20)	1995 % Freq. (n = 10)	1992 % Freq. (n = 15)	1994 % Cover (n=20)	1995 % Freq. (n = 10)	1992 % Freq. (n = 14)	1994 % Cover (n=20)	1995 % Freq. (n = 10)	1992 % Freq. (n = 15)	1994 % Cover (n=20)	1995 % Freq. (n = 10)
<i>Acer rubrum</i> †	0.03	14.3	10
<i>Agalinis paupercula</i>	13.3	100
<i>Aster novi-belgii</i>	6.7	0.78	70
<i>Bidens connata</i>	42.9	0.12	30	6.7	0.03	10
<i>Bidens discoides</i>	60.0	1.77	100	78.6	1.15	100	100.0	2.92	100
<i>Calamagrostis canadensis</i>	75.0	14.53	80	100.0	10.15	10	60.0	6.12	90	14.3	1.12	40	86.7	8.03	90
<i>Calla palustris</i>	50.0	0.88	70
<i>Carex canescens</i>	8.3	1.43	90	26.7	0.03	100	92.9	28.82	100	86.7	0.45	100
<i>Carex lacustris</i>	6.7
<i>Carex lasiocarpa</i>	0.05	80
<i>Carex utriculata</i>	13.3	0.95
<i>Cephalanthus occidentalis</i> †	0.05	30	6.7	0.62	100	10
<i>Cicuta bulbifera</i>	13.3	53.3	0.33	90	86.7	0.55	90
<i>Decadon verticillatus</i>	7.1	1.70	80	1.75	70
<i>Dryopteris cristata</i>	8.3
<i>Epilobium leptophyllum</i>	0.05	10	20.0	0.30	80
<i>Erechtites hieracifolia</i>	0.05	20
<i>Galium spp.*</i>	16.7	0.05	20	6.7	0.03	86.7	3.48	100	71.4	0.07	100	100.0	2.10	100
<i>Hypericum boreale</i>	30	0.20	10	0.03
<i>Impatiens capensis</i>	6.7	6.7	6.7
<i>Iris versicolor</i>	7.1
<i>Juncus canadensis</i>	0.12	40	1.30	50	20
<i>Lycopus uniflorus</i>	20	20.0	0.15	100	42.9	0.53	100	86.7	3.08	100
<i>Lysimachia terrestris</i>	13.3	0.15	10	78.6	4.28	30	13.3	0.07	20
<i>Lysimachia thyrsiflora</i>	80.0	0.90	30
<i>Scutellaria galericulata</i>	40.0	0.23	20
<i>Sparganium androcladum</i>	0.20	0.10	2.15	7.1	15.70	40	0.05	10
<i>Spiraea spp.†**</i>	1.45	100	6.7	0.95	70	0.03	90	0.75	100	20.0	0.15	100
<i>Triadenum virginicum</i>	16.7	3.73	100	6.7	0.10	40	6.7	0.12	100	92.9	15.00	100	66.7	1.20	100
<i>Typha latifolia</i>	0.05

† Woody species may be slightly under-represented in 1992 & 1994 (see methods). * Includes *G. tinctorium* & *G. rigidum*. ** Includes *S. latifolia* & *S. tomentosa*.

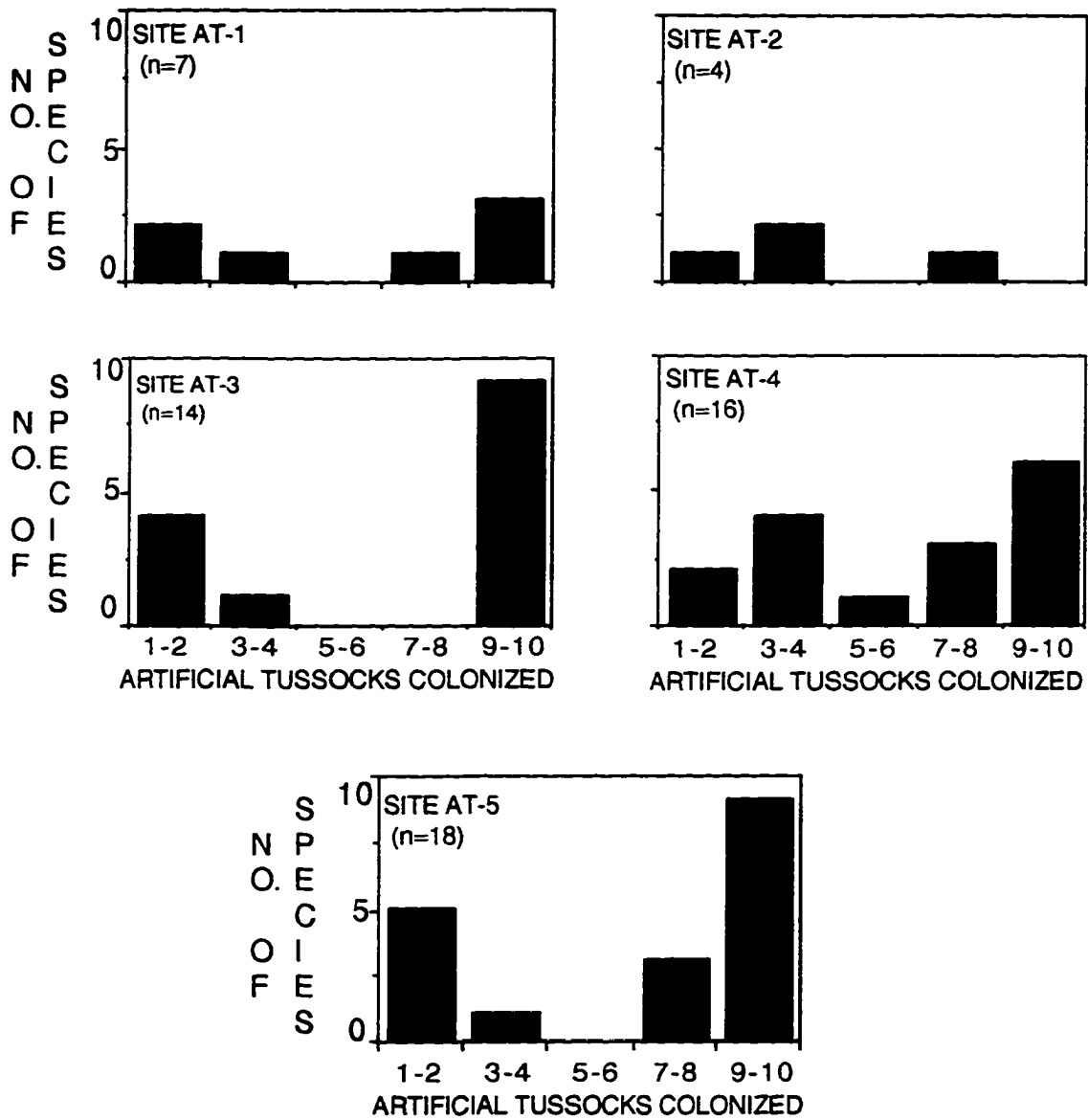


Figure 11. Distributions of plant species colonization frequencies on artificial tussocks (n= total number of species sampled). Site numbering reflects an increasing average species per *Carex stricta* tussock as determined in 1992 (see Fig. 12).

Table 2. Spearman rank correlations of abundance and dispersal characteristics of species that become established on *Carex stricta* tussocks. The 1992 data are frequencies of occurrence on *Carex stricta* tussocks from Lord (1994). 1994 data are foliar cover estimates from 0.25 m² quadrats, and 1995 data are frequencies of artificial tussock colonization (see Table 1 for individual observations).

	1992	1994	1995
	% Frequency	% Cover	% Artificial Tussocks
1992 % Frequency on <i>Carex stricta</i>	1.000		
1994 % Foliar Cover	0.626	1.000	
1995 % of Artificial Tussocks Colonized	0.597	0.547	1.000

*Woody species were excluded from the analysis (see Methods).

Each species at each site is one observation. N=65.

P<0.001 for all individual comparisons.

Table 3. Analysis of variance: differences among sites in rates of artificial tussock colonization. Data are from five sites represent a broad range of average species richness per *Carex stricta* tussock (n=10 artificial tussocks per site).

DEPENDENT VARIABLE: NUMBER OF COLONIZING SPECIES PER ARTIFICIAL TUSSOCK

N=50 r=0.965 r²=0.931

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
SITE	795.400	4	198.850	152.701	0.000
ERROR	58.600	45	1.302		

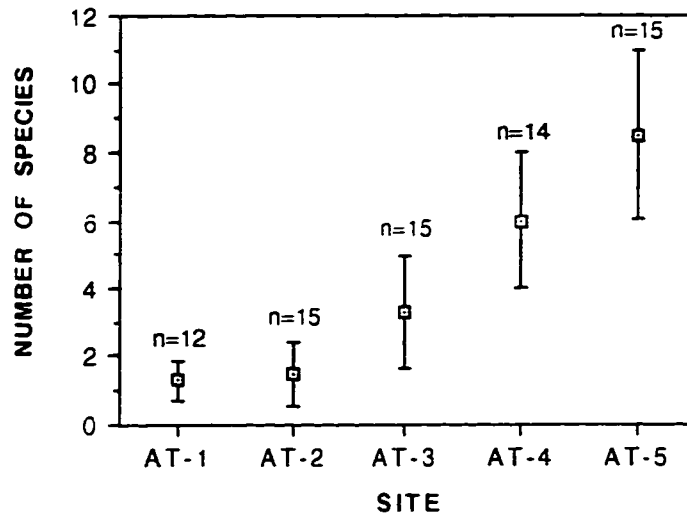


Figure 12. Means and standard deviations of the numbers of plant species colonizing individual *Carex stricta* tussocks in 1992. Sites were selected to represent a broad range of species richness per tussock. Data are from Lord (1994).

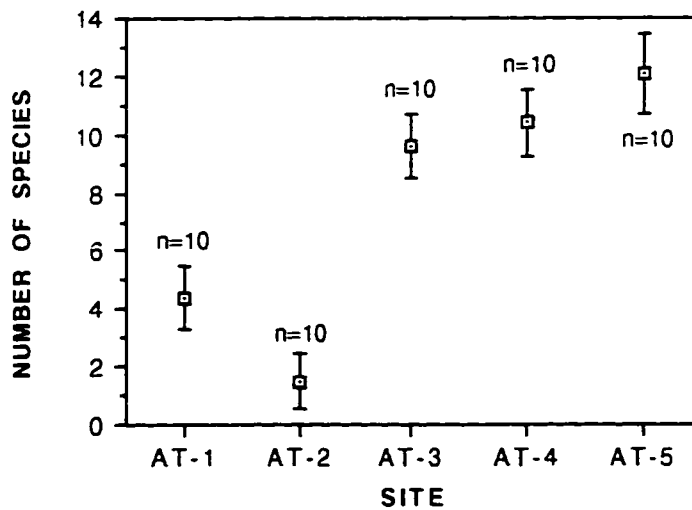


Figure 13. Means and standard deviations of the numbers of plant species colonizing artificial tussocks (1995). Note the low variation within all sites. Sites are the same as those examined in 1992 (see Figure 12 and Lord 1994).

Conditions on the artificial tussocks were designed to be as similar as possible so that any variation among artificial tussocks in the numbers of colonizing species would be due to differences in regional dispersal characteristics rather than to differences in local conditions. The effects of local conditions were checked using variables associated with water levels and the plant vigor score associated with each artificial tussock. When the effects of these variables on the number of species colonizing artificial tussocks were tested using ANCOVAs, each initially had significant explanatory power; however, inspection of the leverages associated with these analyses indicated that the significance of these factors was due to measurements associated with a single artificial tussock at site AT-2 (leverages $>>0.2$). When the models were reanalyzed (and the index of vigor recalculated) without that observation, neither water levels nor vigor scores explained significant variation in the numbers of colonizing species per artificial tussock.

Dispersal densities and species pools. Variation in the numbers of species colonizing the artificial tussocks (and therefore arriving at *Carex stricta* tussocks) could result if sites had different overall densities of dispersing propagules per species, if they had different numbers of dispersing species (species pools), or if there were variation in both of these factors. Two statistical analyses were used to examine variation among the sites in dispersal densities per species— neither of these indicated important differences in dispersal densities.

First, a Kruskal-Wallis test indicated no significant differences among sites in the number of artificial tussocks colonized per species ($H=2.58$, 4 df, $P=0.63$). The mean at site AT-2, however, was less than that at the other sites (Fig. 14).

In the second analysis, the densities of individuals per species per artificial tussock were examined. The number of individuals of each species on each artificial tussock was assigned a density class: 1-3, 4-10, 11-30, or >30 individuals. All species were pooled together and the number of observations in each of the four density classes was tabulated for each site. When all sites were considered, differences in the proportions of observations in each density class were found to be significant ($G = 49.10$, $P < 0.001$). Observations were relatively evenly distributed among density classes at sites AT-1, AT-3, and AT-4 (Fig. 15), and the distribution patterns among these three sites were not significantly different ($G = 10.34$, $P = 0.111$). The distributions of density classes at both

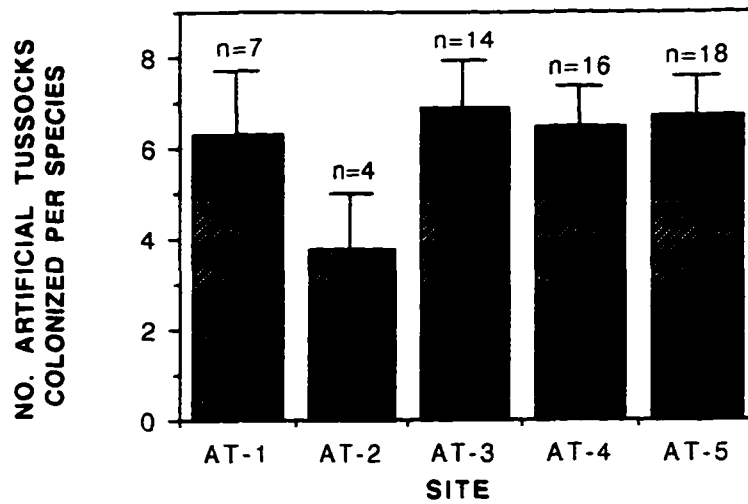


Figure 14. A average numbers of artificial tussocks colonized per plant species in each of five wetlands representing a gradient in average species richness per *Carex stricta* tussock (see Fig. 12). A Kruskal-Wallis test indicated no significant differences among sites.

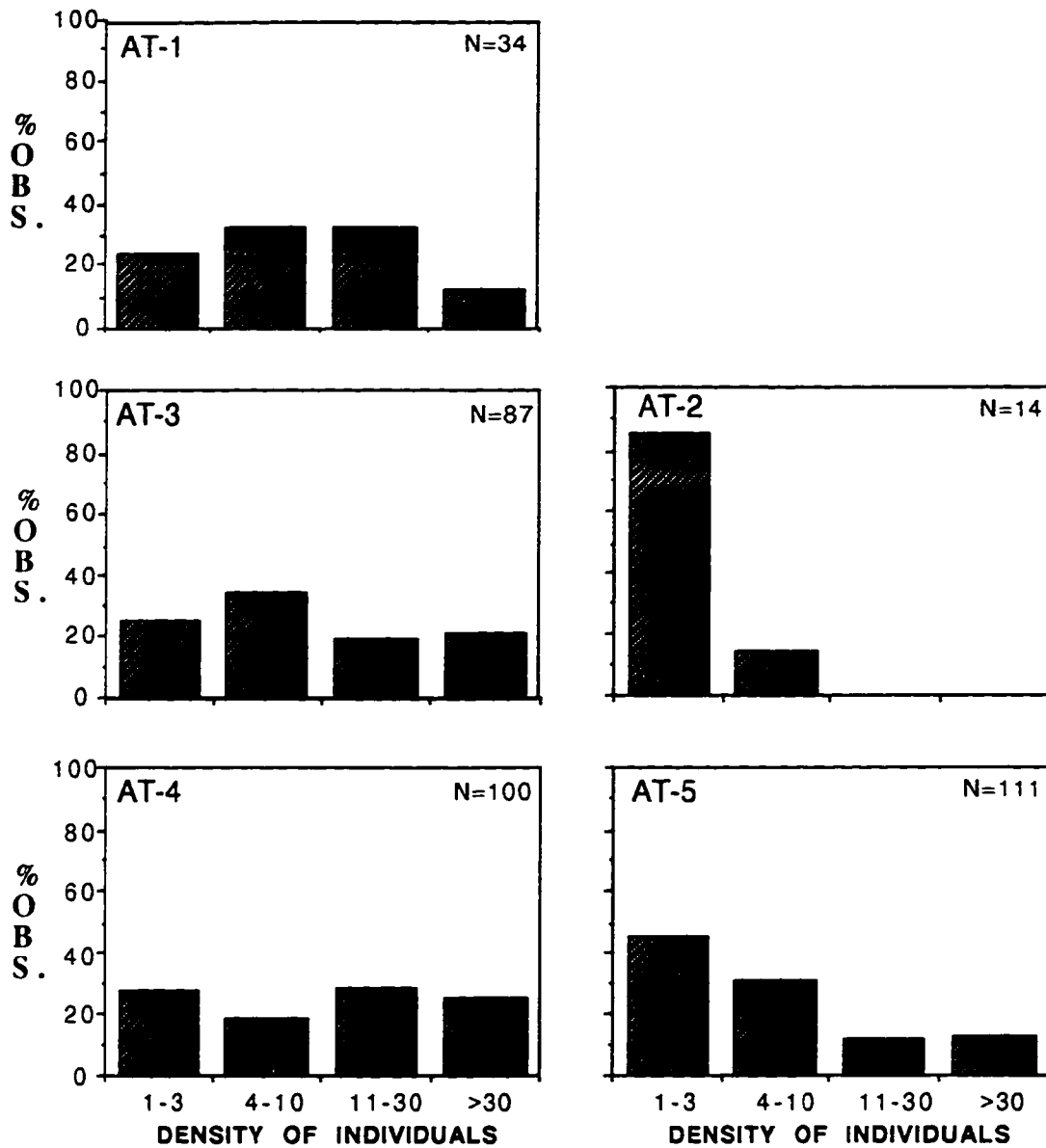


Figure 15. Proportions of density class observations (each species on each artificial tussock is one observation, N = the total number of observations per site). Contingency table analyses indicated that the proportions of observations at sites AT-1, AT-3, and AT-5 did not differ from each other, however those at sites AT-2 and AT-5 differed from the other sites. Differences between AT-2 and AT-5 could not be validly tested due to the high number of sparse observations at site AT-2. The sites with high average species per *Carex stricta* tussock (AT-4 and AT-5) did not have greater proportions of observations in the high density classes.

sites AT-2 and AT-5 (the sites with the lowest and highest numbers of species per artificial tussock respectively) were similar in that they were concentrated in the two lowest density classes. Differences in the patterns among these two sites could not be tested due to the relatively high number of sparse observations at site AT-2. The sites with more colonizing species per artificial tussock generally did not have greater proportions of high density observations than those with low propagule supplies.

The effect of the size of the species pool on the number of species arriving at *Carex stricta* tussocks was assessed by regressing the numbers of colonizing species on each of the artificial tussocks against the total number of species known to colonize *Carex stricta* tussocks recorded during the quadrat sampling of foliage cover that at each site. Seventy-six percent of the variation in species numbers among artificial tussocks was associated with the variation among sites in total number of species sampled in quadrats (Table 4, Fig. 16).

Discussion

Species per artificial tussock. The primary objective of this study was to determine if dispersal characteristics varied among wetlands in a way that could explain variation in average species richness per *Carex stricta* tussock. Variation in the rates at which species arrived at *Carex stricta* tussocks among sites was inferred by examining the colonization of artificial tussocks. My hypothesis that sites differed in the rates at which species arrive at tussocks (*I*) was supported (Table 3, Fig. 13). In addition, my hypothesis that the pattern of variation in *I* among sites is one that could result in the observed differences in average species richness per *Carex stricta* tussock was also supported (compare Figs. 12 & 13); where the *C. stricta* tussocks each had high numbers of species, greater levels of *I* were detected on the artificial tussocks. It is unlikely that the trend was due to variation in environmental factors among sites because variables used to measure these differences—water levels and plant vigor—were not significant covariates in the ANCOVA's.

Dispersal densities and species pools. Having established that average values of *I* varied among sites, I then sought to determine whether this was due to variation in the propagule densities per species, in numbers of dispersing species (species pools), or to variation in both factors. My hypothesis that differences in average values of *I* among sites

Table 4. Regression analysis: Number of species colonizing artificial tussocks as a function of the number of species in the species pool. The species pool for each site was estimated as the total number of species known to colonize *Carex stricta* tussocks that were sampled in 20, 0.25 m² quadrats at each site.

DEPENDENT VARIABLE: NUMBER OF COLONIZING SPECIES PER ARTIFICIAL TUSSOCK				
N=50	r=0.877	r ² =0.768	ADJ r ² =0.764	
VARIABLE	COEFFICIENT	STD ERROR	T	P (2 TAIL)
CONSTANT	-2.445	0.846	-2.889	0.006
SPECIES POOL	0.823	0.065	12.619	0.000

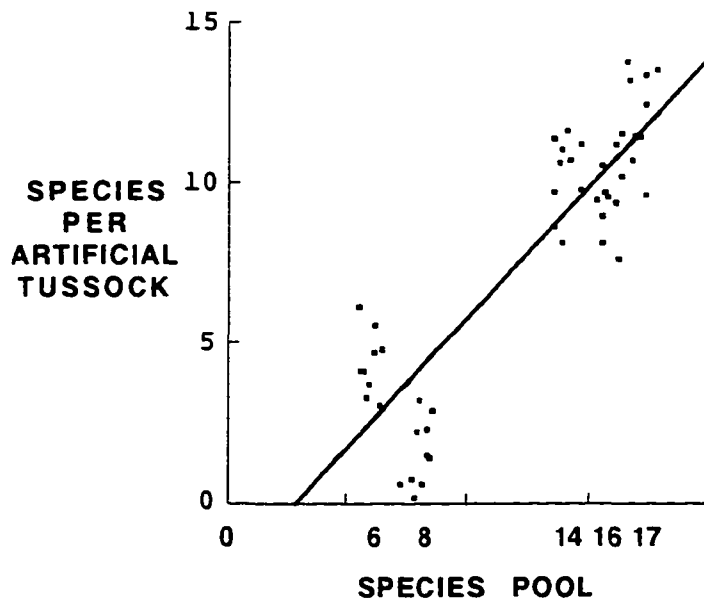


Figure 16. Number of species colonizing artificial tussocks as a function of the number of species in the species pool. The species pool for each site was estimated as the total number of species known to colonize *Carex stricta* tussocks that were sampled in 20, 0.25 m² quadrats at each site. All species in a site have the same species pool corresponding to the values on the X axis. For purposes of display, the points have been “jittered”. Refer to Table 4 for the corresponding statistical analysis.

were related to differences in the densities of dispersing propagules per species was not supported. Sites shown to have greater average values of I did not have significantly more artificial tussocks colonized per species (Fig. 14), nor did they have higher densities of colonizing individuals per artificial tussock (Fig 15). These results indicated that the variation in I among sites was not related to variation in the densities of propagules per species. Nevertheless, artificial tussocks at site AT-2 had both the lowest average I and the lowest average number of tussocks colonized per species. In addition, nearly every observation of the number of individuals per species per artificial tussock was in the lowest density class (1-3 individuals). It appears that the low average I found at site AT-2 was at least partially due to low propagule densities, but the differences could not be detected with the research design and analyses used (Type II error).

My hypothesis that differences in I among sites were due to differences in the numbers of dispersing species (P) was supported. Sites with more species growing in them had greater average levels of I (Table 4, Fig. 16). Therefore, assuming that the interception of propagules by the artificial tussocks was closely related to that by *Carex stricta* tussocks, any variation in species richness among the *Carex stricta* tussocks in these sites that was due to variation in I would be almost completely due to variation in the numbers of dispersing species. If the average colonization probability per species is a function of propagule densities, and variation in I among sites was not found to be significantly related to variation in propagule densities, then variation in I must be related to variation in P . At site AT-2, however, I was lower than would be expected from species pool effects (Fig. 16). This may have been due to propagule densities per species that were lower than at other sites (though not statistically different).

Many models that focus on the effects of regional dispersal characteristics on local species richness have emphasized the influence of propagule densities on these processes (e.g., Mac Arthur & Wilson 1967; Brown & Kodric-Brown 1977; Caswell 1978; Hanski 1982; Tilman 1994). The importance of the size of the species pool, however, has not been overlooked (e.g., Grime 1973b, 1979; Taylor et al. 1990; Zobel 1992; Eriksson 1993) and has been correlated with local species richness in two recent studies (Gough et al. 1994; Partel et al. 1996). Undoubtedly, both factors contribute to the rates at which species come in contact with local communities; with variation in one or the other being

more important under different circumstances. Dispersal densities (isolation) could be more important in mainland-island systems, while species pools might be more important in systems of closely linked communities (metacommunities). I have not found any other studies that examined the relative effects of propagule densities and species pools in determining the rates at which species arrive at local patches.

General patterns. Although not directly related to my hypotheses, general patterns in the data were explored in order to better understand regional (wetland scale) dispersal dynamics in this system. First, I found very little variation within each site in the numbers of colonizing species per artificial tussock (Fig. 13; standard deviation = 0.97-1.37 species). This indicates that the dispersal of propagules was relatively homogeneous within each site, with no directional gradients in propagule supplies. Such gradients would be expected if dispersal patterns followed those predicted by island biogeographic theory (Mac Arthur & Wilson 1967), with most of the propagules originating from a single concentrated source either outside of the tussock populations, or from a group of tussocks acting as a single “mainland” source (Harrison 1991).

Several patterns in the data were suggestive of the “core and satellite species hypothesis” (Hanski 1982, 1985; Hanski & Gyllenberg 1993). The first of these was the significant ranked correlation (Table 2) between individual species’ rates of artificial tussock colonization (percentage of artificial tussocks occupied), their abundances of established plants in the marshes (percent foliage cover), and the frequencies with which they occurred as established plants on *Carex stricta* tussocks (percentage of tussocks occupied in 1992). Next, the distributions of individual species’ probabilities of colonizing artificial tussocks had strongly bimodal distributions at all of the sites (Fig. 11). And last, I had previously observed (Lord 1994) that, for some sites, the frequencies with which species occurred as established plants on *Carex stricta* tussocks also had bimodal distributions.

In core and satellite models, feedbacks between dispersal densities and the proportion of patches occupied result in two distinct groups of species— those that are common (core species), and those that are uncommon (satellite species). The core species have high propagule densities and the satellite species have low propagule densities. These models assume that high dispersal rates among patches result in low extinction rates of

local populations. This is because high dispersal densities imply large within-patch population sizes, and because propagule inputs make local populations more extinction resistant during locally unfavorable periods (the rescue effect). The result is that species that are uncommon tend to remain uncommon because they have relatively low dispersal densities and therefore low colonization rates but relatively high extinction rates. Conversely, species that do manage to become established beyond a threshold number of patches will have large population sizes with high dispersal densities and, therefore, will rapidly colonize most of the patches in a region and will be extinction resistant within those patches. However, core and satellite models were not specifically tested in this study, and alternate explanations for these patterns exist.

First, the correlations between species abundances, frequencies, and propagule supplies do not necessarily imply feedbacks. For example, high abundances may result in high dispersal densities, however, the high dispersal densities may not translate into lower extinction rates.

Second, a more parsimonious explanation of the bimodal patterns of dispersal densities (i.e., artificial tussock colonizations) and species occurrences on *Carex stricta* tussocks is that these were the result of presence/absence sampling from logarithmic distributions of propagule and population abundances. Logarithmic distributions have many low abundance observations and a long, positively skewed “tail” of high abundances, with very few observations associated with each high abundance value. At low and moderate abundances, presence/absence sampling parallels the abundance distribution, with many species having low frequency observations and fewer species occurring more commonly. At some level of abundance, however, the species are likely to be present in all plots. All of the species exceeding this abundance are also likely to be present in all plots (or all tussocks) resulting in a high number of species with high occurrence frequencies (Gleason 1929). The degree that this results in a bimodal distribution depends on the area sampled per observation and number of observations obtained (Williams 1950).

II. TUSSOCK MANIPULATIONS

Introduction

Grime's model (1973b, 1979) relates the species richness of plant communities to standing crop, leaf litter, and dispersal effects (species pools and immigration rates). During my master's research, I determined that factors related to standing crop and leaf litter were correlated with variation in the numbers of species on individual *Carex stricta* tussocks (Lord 1994). In the study using artificial tussocks described above (Part I), I determined that variation in dispersal characteristics was associated with variation in species richness per tussock among wetlands. The objective of the following study was to examine whether standing crop of the dominant species (*Carex stricta*), leaf litter, and propagule availabilities have direct effects on plant species richness in plant communities occupying individual *Carex stricta* tussocks, and whether these effects occur in a manner that is consistent with Grime's model.

Based on a study of a number of herbaceous systems in Great Britain (Al-Mufti et al. 1977), Grime had predicted that the peak species richness in his model would correspond to a seasonal maximum standing crop plus leaf litter of approximately 550 g·m⁻². Using data taken during my master's research from a broad range of *Carex stricta* populations, I determined that the seasonal maximum standing crop plus leaf litter that occurred on most *Carex stricta* tussocks was well in excess of 550 g·m⁻² (Fig. 17). Therefore, the scope of this study was restricted to the portion of Grime's model in which species richness is limited by highly productive, competitive species (the area to the right of the peak in species richness, Fig. 3).

To examine the relationships predicted by Grime's model, I selected tussock populations that had high standing crop plus litter levels, and then selectively reduced the biomass of *Carex stricta* without directly affecting any other species on the tussocks. In addition, leaf litter was removed and propagules were supplemented. I tested the following

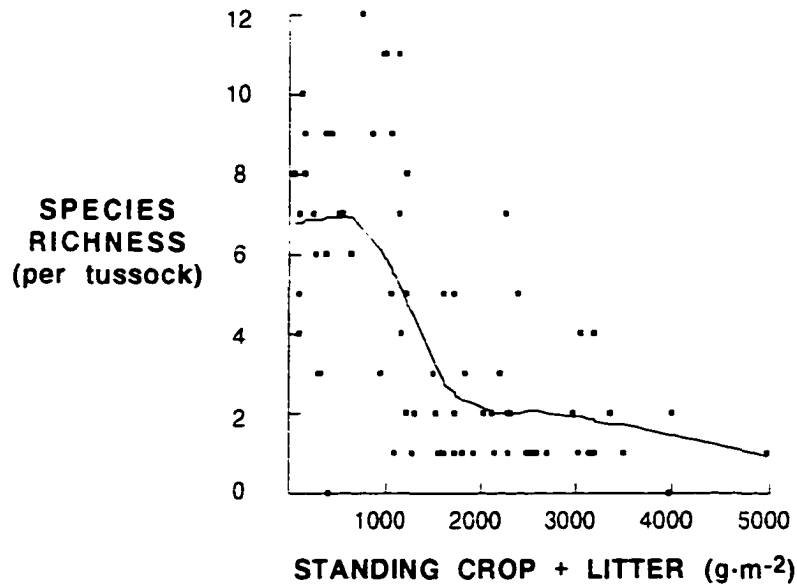


Figure 17. The relationship between maximum seasonal standing crop + leaf litter and the number of species occupying individual *Carex stricta* tussocks. Tussocks were sampled from five New Hampshire wetlands representing a broad range of average species richness per tussock (N=71 tussocks, see Lord 1994 for methods). The smoothed trend line was fit using locally weighted regression (lowess).

hypotheses:

1) High levels of *Carex stricta* standing crop production, high levels of leaf litter accumulation, and low propagule availability all limit species richness on *Carex stricta* tussocks.

2) The magnitudes of species richness limitation by *Carex stricta* standing crop and leaf litter are both affected by propagule availability, with greater effects occurring where propagules from more species known to colonize *Carex stricta* are present.

Methods

Site selection. *Carex stricta* populations consist of tussocks at similar developmental stages and, therefore, having similar levels of standing crop and leaf litter (Lord 1994). The primary consideration in selecting *Carex stricta* marshes to study was that the tussocks involved have levels of peak standing crop plus litter that would result in high levels of competitive exclusion under Grime's model. From my earlier research, peak species richness levels were found to occur on individual tussocks at approximately 750 g·m⁻² standing crop plus leaf litter (Fig. 17), slightly higher than the levels in Grime's model. Two tussock populations in that study appeared to be in earlier stages of development and had average standing crop plus litter levels of approximately 2300 and 2500 g·m⁻². In order to assure that the tussocks within the selected sites had high initial standing crop plus leaf litter levels, I selected three palustrine emergent wetlands dominated by *Carex stricta* populations that were visually similar to the two previously studied populations with high standing crop plus leaf litter levels.

Secondary site selection criteria were related to the practical aspects of conducting the experiment. I had predetermined that all of the *Carex stricta* populations involved would be at least 0.1 ha in size, within 20 km of the UNH campus, within 1 km of a road, and would be at least 0.5 km from any other population used in the same experiment.

Site descriptions. Site numbers associated with this experiment are preceded by MT (manipulated tussocks) to distinguish them from sites used in the artificial tussock (AT) colonization study. As in the previous section, I use the term "site" to refer to the limited

portion (ca. 0.1 ha) section of a tussock sedge population in which sampling took place. Site MT-1 (Fig. 18) occurred within a small (0.2 ha) section in the northern end of a 1.5 ha marsh complex associated beaver impoundments between Scruton Pond and the Isinglass River in Barrington. Site MT-2 (Fig. 19) was located in the northern portion of a 2 ha marsh along a tributary feeding the eastern end of Round Ponds, also in Barrington. Site MT-3 (Fig. 20) was part of a 19 ha marsh complex along a tributary of the Little River in Lee. The hydrology in all of these wetlands was controlled by beaver. Aerial photos and site evidence indicate that sites MT-1 and MT-2 were forested prior to beaver flooding, while site MT-3 had been cleared and partially ditched. The occupation by beaver occurred sometime between 1953 and 1974 for all of the sites (no aerial photography could be located between those years).

Tussock selection. Fifty-six tussocks were selected for study at each of the three sites. These represented seven replicates associated with each of eight treatments (see below), for a total of 168 tussocks. Tussocks were selected at 3 m intervals along transects spaced 3 m apart within each site. The transects were established approximately perpendicular to the wetland edge. In order to minimize edge effects, none of the selected tussocks were located within 5 m of forested vegetation types, within 2 m of bordering non-forested vegetation types, within 0.5 m of inclusions of dense shrubs in the sampling area, or within 2 m of stream channels or open water.

The tussock closest to each 3 m point was selected. If no tussock was found within 1 m, the point was abandoned. The selected tussocks were divided into groups of eight in sequential order along the transects. One of each of the eight treatments outlined below was assigned randomly to each of the tussocks within each group.

In order to be selected, tussocks had to meet the following minimum requirements. The bases had to be at least 10 cm in diameter and at least 15 cm tall. They had to be at least 0.5 m from clumps of dense shrubs to minimize shading effects, at least 1 m from any poison sumac (*Toxicodendron vernix*), and at least 3 m from any tussock containing a hornets nest. In addition, tussocks were rejected if they had woody individuals > 50 cm tall. This was because large woody individuals are likely to differ from herbaceous species in how they both affect, and are affected by, community dynamics on the tussocks. Thirty-two of the original 168 tussocks selected did not meet all of the above criteria and alternate



Figure 18. Site MT-1 occurred within a small (0.2 ha) section in the northern end of a 1.5 ha marsh complex associated with beaver impoundments between Seruton Pond and the Isinglass River in Barrington.



Figure 19. Site MT-2 was located in the northern portion of a 2 ha marsh along a tributary feeding into the eastern end of Round Ponds in Barrington.



Figure 20. Site MT-3 was part of a 19 ha marsh complex along a tributary to the Little River in Lec.

tussocks were selected to replace them. One of the selected control tussocks at site MT-3 was severely disturbed by beaver during the course of the study and was therefore omitted from all analyses.

Treatments. All combinations of the following manipulations were performed on the selected tussocks using a fully crossed experimental design. These manipulations involved two levels for each of the three factors, resulting in a total of eight treatment combinations.

1) Litter removal: At the end of the growing season in 1994 (September through November), I removed the standing crop (i.e., what would become the litter in the next year), bryophytes, and undecomposed litter from the tops of the selected tussocks. Work was alternated haphazardly among sites to ensure that the timing of the removals did not vary among sites. The standing crop and litter were cut with grass clippers and then raked up with a small, three-pronged hand cultivator. New, overwintering *Carex stricta* shoots extended 5-10 cm above the tops of the tussock bases, therefore the clipping was done ca. 5 cm above this to prevent damage to the new shoots. In the few cases where they were observed, I avoided removing propagules that were in the leaf litter; however, it is likely that some propagules, and possibly some established plants, were removed during this procedure.

2) Clipping of *Carex stricta*: Clipping of *Carex stricta* leaves began in late April, 1995, when the leaves were 15-20 cm long. Since litter depths were generally in the range of 8-12 cm thick, all clipping was done at 10-12 cm above the tussock surface, whether litter was present or had been removed. Clippings were done every 1-1.5 weeks until the third week in July. By that time, *Carex stricta* leaf densities had been reduced to approximately 50% of their original densities and, therefore, only one additional clipping was done (second week of August). Depending on the timing of tiller initiation in the spring, each of the selected tussocks was clipped 10-11 times during the experiment. In addition to the *Carex stricta* foliage, all foliage of the surrounding vegetation within 0.5 m of the clipped tussocks was also clipped as necessary to reduce shading.

I felt that the effects of clipping *Carex stricta* leaves would reduce competition for all resources, making these resources more available for other species to utilize. Due to reasons of practicality, only the effects of the treatment on light levels were checked. This

was done using a LI-COR model LI-185B quantum sensor. Three replicates from each of the eight treatments were randomly selected at each of the three sites (N=72). At site MT-2, two tussocks were inadvertently selected from the wrong treatments, however this did not alter the numbers of clipped and unclipped tussocks selected. Light levels were measured at the estimated peak standing crop, August 9-14, 1995. All measures were done between 10:30 am and 3:30 pm EDT on clear days. Light measurements were taken at a height above the tussock bases equivalent to the upper surface of the leaf litter layer. Since litter depths were generally in the range of 8-12 cm thick, the measurements were taken at 12 cm above the tussock surface whether the litter had been removed or not. At each tussock, three readings were taken: one at the northern edge, one in the center, and one at the southern edge of the tussock. These readings were then averaged. Ambient light levels were measured immediately before and immediately after the tussock measurements, and then were averaged. In order to standardize for variations in ambient light, the light levels on the tussocks were converted to percent reductions of ambient light.

3) Seed additions: During the summer of 1994, seeds from eight tussock colonizing species (Table 5) were collected from outside of the study areas. To the extent practical, excess vegetative material was screened and winnowed from the seeds. The seeds were stored dry at room temperature until January 31, 1995, at which time they were stored cold (ca. 5° C) dry for 10 weeks.

The amount of seeds added to the selected tussocks was determined for each species based on dividing the total amount of seeds collected into equal portions. However, the supplementation level per tussock did not exceed visual estimates of seed levels that might be produced by a relatively large population of the species on an average sized tussock. Although the application rates varied among species, equivalent weights for each species were applied to all of the tussocks selected for seed addition. Net seed weights were estimated using three haphazardly obtained samples of the cleaned seeds from each species. The remaining chaff, damaged seeds, and dispersing appendages were separated from 50 seeds per sample (25 per sample for *Calamagrostis canadensis* and *Carex canescens* due to the work involved in removing appendages). The weights of the seeds were then compared to the gross weights associated with the samples.

Beginning April 15, 1995, seeds were lightly rubbed into the tops of only those

Table 5. Species and application rates used in seed addition treatments. Gross weights were used in application rates. Net weights and standard errors estimated from samples of 25-50 seeds (n=3 samples per species). Germination and standard errors estimated from samples of 0.5-0.1g net weight (n=5 samples per species).

Species	Gross (g)	Net (g)	No. Germinating
<i>Bidens connata</i>	1.23	0.75 ± 0.08	6 ± 3
<i>Bidens discoidea</i>	1.04	0.50 ± 0.04	0
<i>Calamagrostis canadensis</i>	2.11	0.25 ± 0.03	2712 ± 153
<i>Carex canescens</i>	1.20	0.50 ± 0.01	1180 ± 68
<i>Galium trifidum</i>	1.78	1.50 ± 0.02	606 ± 26
<i>Lycopus uniflorus</i>	1.96	1.50 ± 0.12	2790 ± 680
<i>Lysimachia terrestris</i>	0.42	0.25 ± 0.01	112 ± 22
<i>Triadenum virginicum</i>	1.23	0.50 ± 0.03	1786 ± 125

selected tussock bases that were ≥ 5 cm above the water level. Additions to the remaining tussocks were postponed 1-2 weeks until water levels dropped. By April 29, all of the seeds had been distributed to the selected tussocks. At site MT-1, water levels had been elevated above the tops of many of the tussock bases due to a newly constructed beaver dam. In order to make conditions similar to those at the other sites, and to prevent supplemented seeds from floating away, I lowered water levels 10 cm at the site by inserting four pieces of 10 cm diameter plastic PVC pipe into the top of the beaver dam.

In order to estimate germination of the seeds, I conducted germination tests using 5 samples of 0.05 g net weight per species (0.025 g for *Calamagrostis canadensis* due to the small seed size and large volume of callus hairs, and 0.10 g for *Bidens connata* due to the high weight per achene). On April 17, 1996, two days after the initial field application of seeds, the germination samples were placed in petri dishes on two layers of moistened filter paper and then placed outside in an area where they were protected from direct sunlight. The samples were checked at least twice a week and were watered with deionized water as necessary. Germinating seedlings were counted and removed from the petri dishes for three months. The results of these tests were used to estimate the number of seeds added per tussock in the seed addition treatments that would potentially germinate (Table 5).

Sampling. In September and October, 1994, plant species were surveyed on all of the selected tussocks prior to applying the treatments. The tussocks were then resurveyed in late August and early September, 1995, four months after the propagule additions. At the time of the second survey, species densities were estimated and classified into three groupings: 1-3 stems, 4-10 stems, and >10 stems. In addition, the presence of reproductive structures was noted. Nomenclature followed Crow & Hellquist (in press) except for *Aster novi-belgii* and *Erechtites hieraciifolia*, which followed Gleason & Cronquist (1991).

The surveys were restricted to the tops of the tussocks. This is because some tussocks had thick growths of *Sphagnum* spp. or floating mats attached to their sides, making it difficult ascertain which plants were actually rooted into the tussock bases and which were rooted into the mats of *Sphagnum*. The perimeter of the top surface of a tussock base was normally defined by the outer edge of *Carex stricta* tillers. In those cases where stress or disturbance caused tillers to be absent along horizontal portions of the

perimeter, the edge was defined as the outermost area that was less than 45° from horizontal, less than 10 cm below an adjacent vegetated portion of the tussock, and at least 15 cm above the surrounding soil.

Only individuals that had matured beyond the seedling stage were included in the tabulations of species richness. The criteria for establishing whether or not an individual was a seedling are the same as those used in the surveys of species frequencies (1992) and percent cover (1994) at the five artificial tussock study sites (see Part I).

The response variable measured was the change in species richness (ΔS) on each tussock. This was calculated by subtracting the number of species counted in 1994 from those counted in 1995. *Carex stricta* and *Calamagrostis canadensis* were not included in these calculations. *Carex stricta* was not considered to be a colonizing species. *Calamagrostis canadensis* densities were used as an independent variable to test for suspected competitive effects; including *Calamagrostis canadensis* in the calculation of the dependent variable could have biased the statistical relationships. The change in species richness was used rather than the post-treatment number of species because initial numbers of species on the tussocks were not equal; using ΔS was a way of compensating for initial differences.

As the criterion for plant establishment (development beyond the seedling stage), as well as the morphological criteria that I used for defining seedlings, were somewhat subjective, I also calculated the change in species richness using more stringent criteria. In this second calculation, I only used species that were new colonists in 1995 and had developed to a stage where flowers, fruits, or bulbils had been initiated (ΔS_r). New colonists that were reproducing had the potential to remain in the communities indefinitely under the treatment conditions, and thus could clearly be considered “established”. In addition, determining the presence or absence of reproductive structures did not have the subjectivity associated with determining which individuals were seedlings and which were not. An important difference between ΔS and ΔS_r is that ΔS included extinctions of species that were established prior to the manipulations and was a negative value if the number of extinctions exceeded the number of newly established species. In contrast, ΔS_r included only newly established species, therefore, was never less than zero. This difference turned

out to be unimportant as there were relatively few extinctions during the experiment (see Results).

In addition to the observations made to calculate the dependent variables, I also measured a number of factors that were used as covariates in my analyses. All of the tussocks were measured for length and width, and tussock area was calculated using the formula of an ellipse. Water depths were obtained at three points around each tussock, and the height of the top of the tussock relative to the water level was obtained at two representative points. Tussock height was calculated as the sum of the average water depth plus the average height above the water at the time of measurement. The total area of vegetation gaps that were each $>25 \text{ cm}^2$ at the tussock surface (i.e., gaps in the stem cover) was estimated visually with the aid of a ruler, and the percent gap area was calculated by dividing by the total horizontal tussock area. Gap area estimates were made prior to conducting litter removals in order to assure estimates were made with equal precision among the treatments.

The water level measurements taken at each tussock were related to a fixed point at each site. From this fixed point, water levels were monitored on an opportunistic basis April 8 - September 8, 1995. The longest interval between water level measurements was 21 days. In order to obtain readings associated with equivalent intervals at all of the sites, I used the numerous readings that were taken irregularly to interpolate eight water level measurements for equivalent 21 day periods (April 8 - September 1). These eight water levels were then used to calculate the median distance between the top of each tussock base and surface water. In cases where the water Table dropped below the surface of the muck, the distance was equivalent to the height of the tussock as moisture levels on the tussocks should be more closely related to the distances above the wet muck than to the distances above the free water table.

At site MT-3, one tussock had a small amount of muck placed on it by a beaver (105 cm^2) and another had otter feces on it (162 cm^2). These minor disturbances were not associated with any extinctions, and species establishments on the organic materials were excluded from the results. In addition, the disturbed areas were subtracted from the tussock surface areas in statistical analyses. A third tussock at that site was severely

disturbed by beaver, and the measurements associated with that tussock were dropped from all of the analyses.

Data analysis. All statistical analyses were run using SYSTAT 5.2 for the Macintosh (SYSTAT, Inc. © 1990-92). Except where noted, the selected alpha level (i.e., the probability of making a Type I error) for significance was $P < 0.05$. For the parametric analyses, distributions of the dependent variables and residuals were examined visually to verify normality. In addition, variances and plots of residuals against continuous independent variables were examined to verify homoscedasticity.

The effects of clipping on light levels were tested using a mixed model ANOVA, with the percent reduction in ambient light as the dependent variable, "site" as a random effect, and terms for clipping and *Calamagrostis canadensis* densities as fixed effects. *Calamagrostis canadensis* densities were tabulated as categories (absent, 1-3 stems, 4-10 stems, >10 stems) and were included in the analysis because this was the tallest and most abundant of the tussock colonizers and could affect light levels. An interaction between the treatment and *Calamagrostis canadensis* densities was expected because clipping *Carex stricta* probably had less effect on light levels in the presence of high *Calamagrostis canadensis* densities. However, this could not be tested because some cells had too few observations. An interaction between the treatment and "site" was tested to determine if the clipping effects varied among sites. The analysis was first run as a Model I ANOVA (all factors fixed) and then appropriate adjustments to F and P values were calculated following Zar (1984).

The effects of the treatments on the change in species richness of each tussock (ΔS , ΔS_r) were analyzed using ANOVA with "site" as a random effect. None of the interactions with "site" were significant and were dropped from the model in a stepwise manner. Pooling the sums of squares and degrees of freedom from these nonsignificant terms was done to simplify the model and to improve the error mean square as an estimate of the population random error. In addition, dropping the interactions with the random effect meant that all of the F and P calculations were equivalent to a Model I ANOVA and, therefore, adjustments to those calculations were not required.

The additional effects of initial species richness (1994), tussock area, tussock volume, gap area, percent gap area, along with minimum, maximum, and median heights

of the top of the tussock above the water surface water were examined using analysis of covariance (ANCOVA) with ΔS and ΔS_r used separately as dependent variables. Initial species richness was tested because it was likely to be negatively correlated with the number of potential colonists arriving at a tussock (i.e., high initial richness means fewer species left as potential new colonists in the dispersing species pool). Tussock area was tested because species number has been shown to be strongly related to the size of the area measured (e.g., Mac Arthur & Wilson 1967; Connor & McCoy 1979). Tussock volume may be related to tussock age and had been a significant predictor of species richness in my earlier study (Lord 1994). Gap area could be related to the area available as potential establishment sites and percent gap area was significantly correlated with species richness in my master's study. Moisture status is an important habitat variable related to germination and survivorship of plants, thus it was important to see how variation in water levels relative to the tops of the tussocks affected the experiment.

These covariates were added or dropped from the ANCOVA models interactively based on associated significance levels of $P < 0.005$. Highly correlated variables were not included in the models together. The "best" models were selected as those with the highest adjusted r^2 .

The conservative alpha level for individual variables was chosen to help protect the overall significance of the analyses. This was because the "best" ANCOVAs were actually created by running a number of analyses. However, the P-values associated with each term in each analysis do not take this into account (e.g., Philippi 1993). The benefit of using the lower significance level was that it minimized the probability that spurious covariates would be included in the models (reduced probability of Type I errors). The tradeoff was a reduction in power of the ANCOVAs, increasing the likelihood that significant relationships would not be detected (increased probability of Type II errors). Because they had greater power, I used the ANOVAs to interpret the effects of the treatment factors, and limited my interpretations of the ANCOVAs to examining the effects of additional (non-treatment) factors on species richness.

Examination of the leverages associated with the ANCOVAs resulted in the omission of one covariate from the analyses. Percent gap area was originally found to be

significant, however, it had observations with high leverages (>0.2). Three tussocks with very high proportions of gap ($\geq 50\%$) as compared to the mean (11.0%, standard deviation = 0.9%) had a disproportionate influence on the outcome of the analyses. When these observations were omitted from the analyses, percent gap was no longer significant. Because the significance of this variable was dependent on three outliers, it was dropped from further consideration.

Results

General patterns. Prior to the manipulations, the average species richness per tussock was 0.9 (standard deviation = 0.8) at site MT-1, 2.0 (standard deviation = 1.3) at site MT-2, and 2.8 (standard deviation = 1.6) at site MT-3. Nearly twice as many species were found on tussocks at site MT-3 (19 species from 55 tussocks totaling a 10.2 m² sample area) than at sites MT-1 (11 species from 56 tussocks totaling 4.5 m²) or MT-2 (11 species from 56 tussocks totaling 7.1 m²). All of the individual sites had net gains in the numbers of species surveyed over the course of the experiment (Table 6). These increases ranged from four species at site MT-3 to eight species at site MT-2. Approximately half of the new species occurrences at each site were species included in the seed additions.

When all sites were considered together, 25 species were encountered on tussocks in 1994, and 30 were encountered in 1995 (Table 6). This reflects the loss of two species, and the gain of seven new species. Most of the new species that appeared over the course of the experiment were wind dispersed species (*Aster novi-belgii*, *Epilobium leptophyllum*, *Erechtites hieraciifolia*, and *Solidago* sp.). Only one of the new species appeared to be related to the seed addition treatments (*Bidens connata*).

It is important to note that *Bidens connata* and *Bidens discoidea* both showed moderate gains in the numbers of tussocks occupied: *Bidens connata* increased from 0% to 16.2% and *Bidens discoidea* increased from 0.6% to 10.2% of all of the tussocks surveyed (Table 6). This occurred despite the very low estimates of germination rates used in the seed additions (Table 5).

Light levels. Based on a significance level of $P < 0.05$, I found that 82% of the variation in light levels among the tussocks could be attributed to the clipping treatment,

Table 6. Percentage of *Carex stricta* tussocks occupied before (1994) and after (1995) factorial manipulations involving clipping of *Carex stricta* leaves, removal of leaf litter, and addition of seeds.

	SITE MT-1		SITE MT-2		SITE MT-3		ALL SITES	
	(n=56)		(n=56)		(n=55)		(n=167)	
	1994	1995	1994	1995	1994	1995	1994	1995
	%	%	%	%	%	%	%	%
<i>Acer rubrum</i>	5.4	5.4	8.9	12.5	1.8	1.8	5.4	6.6
<i>Asclepias incarnata</i>	3.6	5.5	1.2	1.8
<i>Aster novi-belgii</i>	1.8	0.6
<i>Bidens connata</i> †	5.4	17.9	25.5	16.2
<i>Bidens discolor</i> †	1.8	12.5	18.2	0.6	10.2
<i>Calamagrostis canadensis</i> †	48.2	48.2	75.0	73.2	60.0	69.1	61.1	63.5
<i>Carex canescens</i> †	1.8	17.9	37.5	33.9	18.2	45.5	19.2	32.3
<i>Carex lacustris</i>	3.6	5.5	1.2	1.8
<i>Carex lasiocarpa</i>	19.6	21.4	7.3	5.5	9.0	9.0
<i>Cicuta bulbifera</i>	3.6	9.1	50.9	3.0	18.0
<i>Dryopteris cristata</i>	1.8	3.6	1.8	5.5	1.2	3.0
<i>Epilobium leptophyllum</i>	1.8	0.6
<i>Erechtites hieraciifolia</i>	1.8	0.6
<i>Galium spp.*†</i>	39.3	5.4	48.2	74.5	87.3	26.3	58.1
<i>Hypericum boreale</i>	1.8	1.8	1.2
<i>Impatiens capensis</i>	3.6	23.2	5.4	1.2	9.6
<i>Juncus canadensis</i>	1.8	0.6
<i>Lycopus uniflorus</i> †	25.0	32.1	1.8	25.5	0.6	27.5
<i>Lysimachia terrestris</i> †	1.8	5.4	10.7	5.5	7.3	3.6	6.6
<i>Rosa palustris</i>	1.8	1.8	0.6	0.6
<i>Rubus hispidus</i>	3.6	1.2
<i>Scutellaria galericulata</i>	1.8	1.8	40.0	50.9	13.8	17.4
<i>Solidago sp.</i>	1.8	0.6
<i>Spiraea latifolia</i>	25.0	5.4	30.4	7.3	5.5	4.2	20.4
<i>Spiraea tomentosa</i>	1.8	5.4	1.8	17.9	1.8	1.2	8.4
<i>Thelypteris palustris</i>	1.8	1.8	3.6	5.5	1.8	2.4
<i>Toxicodendron vernix</i> **	1.8	1.8	0.6	0.6
<i>Triadenum virginicum</i> †	17.9	33.9	32.1	42.9	32.7	54.5	27.5	43.7
<i>Typha latifolia</i>	3.6	3.6	1.2	1.2
<i>Vaccinium corymbosum</i>	1.8	0.6
<i>Vaccinium macrocarpon</i>	1.8	1.8	0.6	0.6
<i>Viburnum recognitum</i>	1.8	1.8	0.6	0.6

* Includes *G. tinctorium* and *G. trifidum*.

** This species was avoided (see methods).

† Propagules were added.

Calamagrostis canadensis densities, and the site in which the tussocks were located (Table 7). A significant interaction indicated that the effect of clipping *Carex stricta* leaves varied among the sites. Light levels on unclipped tussocks were much higher at site MT-2 (41% of ambient) than at MT-1 (17%) or MT-3 (12%). Clipping *Carex stricta* leaves increased light to similar levels at all sites (75–86% of ambient). Since light levels were initially higher at site MT-2, the increases in light due to clipping were not as dramatic as they were at the other sites (Fig. 21). In addition, *Calamagrostis canadensis* densities significantly affected light levels on the tussocks. When the variation due to clipping was factored out, the adjusted mean light levels averaged 28% lower on tussocks with *Calamagrostis canadensis* densities of ≥ 10 stems than on tussocks without *Calamagrostis canadensis* (Fig. 22). Interactive effects of *Calamagrostis canadensis* densities were not tested because some cells had too few observations ($n \leq 2$).

Species richness (ΔS). The effects of the treatments on species richness were examined using an ANOVA (Table 8) with a significance level for individual terms set at $P < 0.05$. From this analysis I determined that 39% of the change in species richness (ΔS) was attributable to the treatments, and all of the two-way interactions among the factors were significant. Increases in species richness were not shown to differ significantly among the sites, and the effects of the treatments did not vary significantly among sites (all interactions with “site” were nonsignificant and were dropped from the model).

The pattern of the means reflected the interactions among the factors (Fig. 23A). Manipulation of each factor alone resulted in little or no increase on species richness; manipulation of two factors resulted in increases that were greater than the additive effects of manipulating each factor alone; and the greatest increase resulted when all three factors were manipulated (L+C+S: removal of leaf litter, clipping *Carex stricta* leaves, and addition of seeds). The means associated with each treatment ranged from an increase of 0.71 species for the treatment that only involved clipping *Carex stricta* leaves, to an increase of 4.52 species for the treatment involving manipulation of all three factors. From the ANOVA, it is clear that the magnitude of the L+C+S mean was due to the additive effects of each factor under the influence of the two way interactions, and was not due to a three-way interaction.

Since ΔS represented the net effect of new establishments and extinctions, I

Table 7. Analysis of variance*: effects of clipping *Carex stricta* and of *Calamagrostis canadensis* densities on the percentage of ambient light 12 cm above the tussock base. This height (12 cm) corresponds to the top of the leaf litter.

DEPENDENT VARIABLE: PERCENT OF AMBIENT LIGHT

N=72 r=0.94 r²=0.818

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
SITE	0.117	2	0.058	2.401	0.099
CLIP	5.093	1	5.093	22.336†	0.0025-2<0.05†
C. CANADENSIS	0.815	3	0.272	11.154	0.000
SITE*CLIP	0.457	2	0.228	9.379	0.000
ERROR	1.534	63	0.024		

VARIABLES

SITE: Categorical variable (three sites)
 CLIP: Clipping of *C. stricta* tillers (clipped/unclipped)
 C. CANADENSIS: Density class of *C. canadensis* (0, 1-3, 4-10, >10 ramets)

*Mixed model ANOVA with SITE as a random factor.
 †Adjusted for mixed model following Zar (1984)

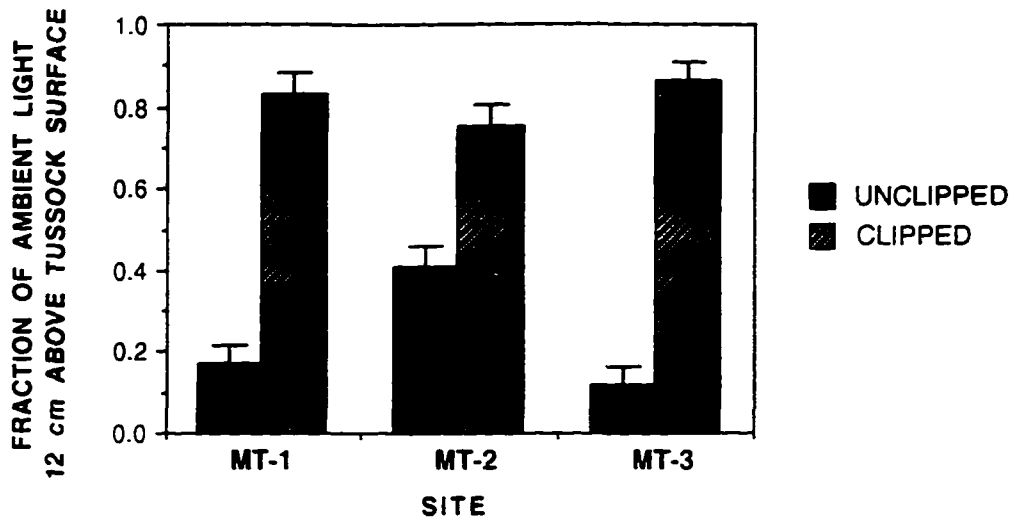


Figure 21. Adjusted means (effects of *Calamagrostis canadensis* densities removed) and standard errors of light levels on clipped and unclipped tussocks. Observations were subsamples (N=72 tussocks) taken among the eight factorial treatment combinations. The high light levels on unclipped tussocks at MT-2 resulted in different effects of clipping among sites (see Table 7).

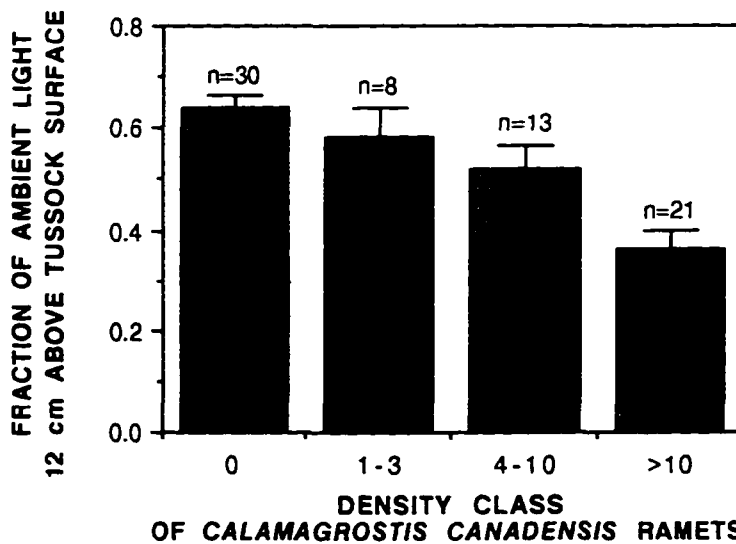


Figure 22. Adjusted means (effects of SITE removed) and standard errors of light levels associated with *Calamagrostis canadensis* ramet densities (includes both clipped and unclipped tussocks). Observations were subsamples (N=72 tussocks) taken among the eight factorial treatment combinations.

Table 8. Analysis of variance: effects of treatments (clipping *Carex stricta* leaves, removing leaf litter, adding seeds) on the change in plant species richness (ΔS) on individual *Carex stricta* tussocks over one year (1994-1995).

DEPENDENT VARIABLE: CHANGE IN SPECIES RICHNESS (ΔS)					
N=167	r=0.625	r ² =0.390			
SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
SITE	7.453	2	3.726	1.605	0.204
LITTER	71.546	1	71.546	30.810	0.000
CLIP	28.968	1	28.968	12.474	0.001
SEED	74.172	1	74.172	31.941	0.000
LITTER*CLIP	16.006	1	16.006	6.893	0.010
LITTER*SEED	14.799	1	14.799	6.373	0.013
CLIP*SEED	14.799	1	14.799	6.373	0.013
LITTER*CLIP*SEED	4.631	1	4.631	1.994	0.160
ERROR	364.583	157	2.322		

VARIABLES

SITE: Categorical variable (three sites)
 LITTER: Leaf litter (present/removed)
 CLIP: *C. stricta* tillers (clipped/unclipped)
 SEED: Seeds from eight colonizing species (added/not added)

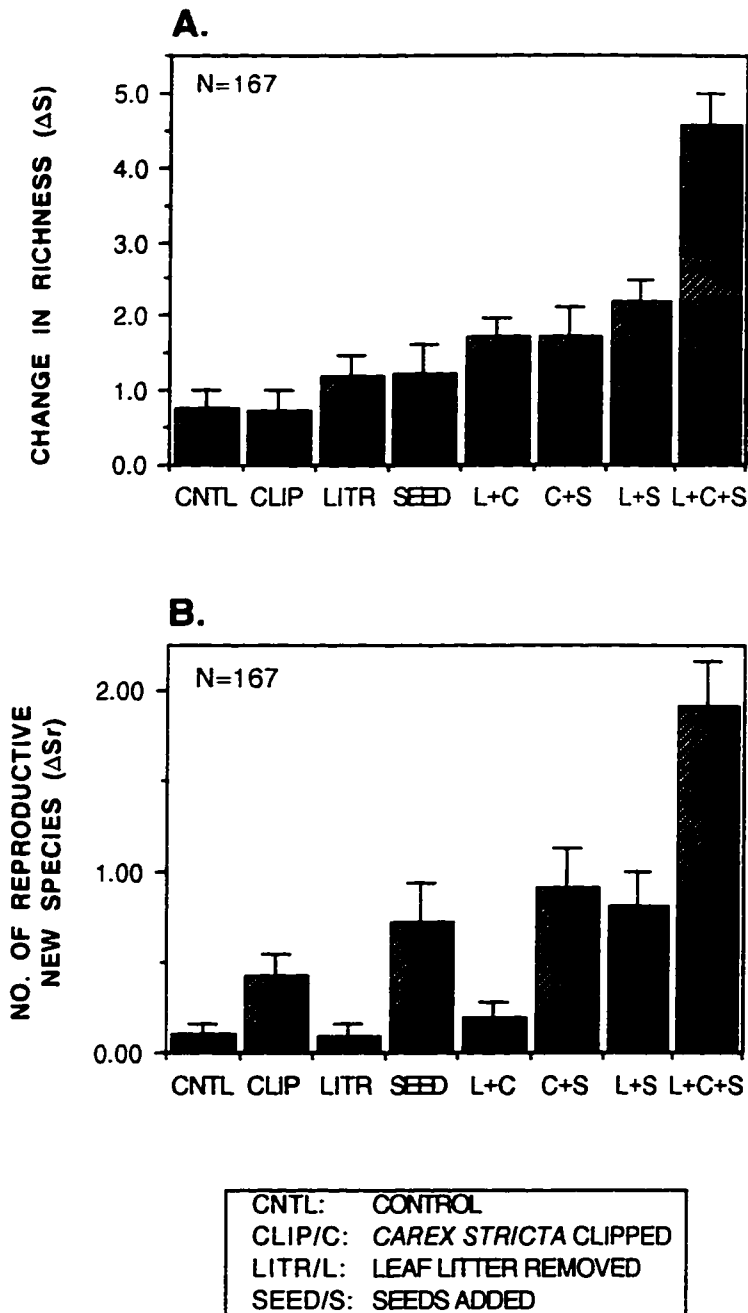


Figure 23. Means and standard errors by treatment for: **A.** the change in plant species richness (establishment-extinctions, see Fig. 12), and **B.** the number of newly established plant species that initiated dispersing reproductive structures (flowers, fruits, or bulbils).

examined the treatment means in terms of both of these factors (Fig. 24). There were few extinctions among any of the treatments, with nearly all of the variation in ΔS coming from variation in establishment of new species.

The influence of additional variables was explored using analysis of covariance (ANCOVA). The significance level used for these analyses was $P < 0.005$ and, due to their low power, these models were not used to examine treatment effects other than those involving interactions with covariates. The model created with the highest r^2 (0.61) included variables for initial species richness, the median distance between water levels and the top of the tussock base, and the density class of *Calamagrostis canadensis* stems (Table 9). Of these additional variables, only one of them was involved in a significant interaction with any of the treatments— the effects of seed additions varied with *Calamagrostis canadensis* densities. High *Calamagrostis canadensis* densities were associated with high natural recruitment, and this recruitment was not enhanced through seed additions (Fig. 25). The covariates also apparently explained enough within-site variation that “site” was significant in this analysis ($P < 0.005$), whereas it was not in the ANOVA ($P > 0.05$). Increases in species richness were greater at site MT-2 than at the other sites (Fig. 26).

Species richness of newly established, reproductive species (ΔS_r). The same analyses that were run using ΔS as the dependent variable were also done for ΔS_r . This was done as a means of verifying that similar results would be obtained using more stringent criteria of plant establishment. The results of the analyses were indeed similar to those described for ΔS . In an ANOVA, 42% of the variation in new establishments could be explained by the treatments and, in this case, by significant differences among sites (Table 10). As with the ΔS ANOVA, there were significant interactions among the treatment factors, however, in this case it was a three-way interaction rather than three two-way interactions.

The pattern of the means associated with ΔS_r was similar to the pattern associated with ΔS , with the main difference being that the litter removal plus clipping treatment (L+C) had little effect on ΔS_r (compare Figs. 23A & B). The means associated with each treatment ranged from an increase of 0.10 species for the control to an increase of 1.91

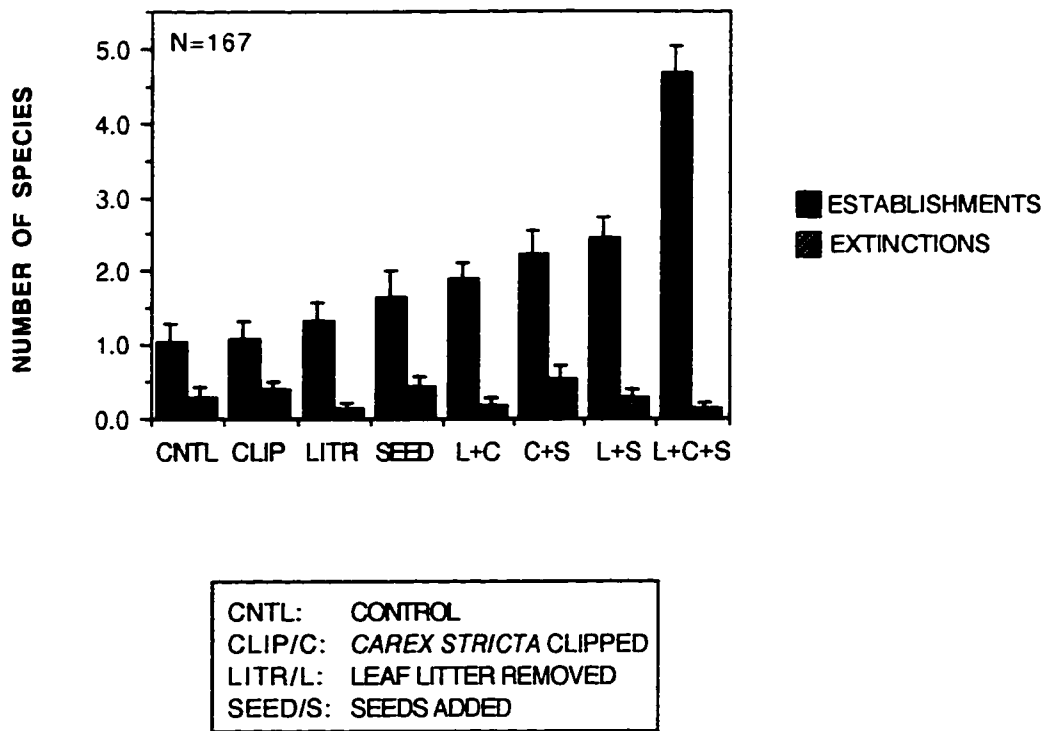


Figure 24. Means and standard errors for establishments and extinctions of species by treatment. Each tussock had counts of both new establishments and extinctions associated with it. Note that the change in richness (ΔS , Fig. 23 A.) was calculated as new establishments-extinctions for each tussock.

Table 9. Analysis of covariance: effects of treatments (clipping *Carex stricta* leaves, removing leaf litter, adding seeds), and covariates (initial species richness, water levels, and *Calamagrostis canadensis* densities) on the change in plant species richness (ΔS) on individual *Carex stricta* tussocks (1994-1995).

DEPENDENT VARIABLE: CHANGE IN SPECIES RICHNESS (ΔS) N=167 $r=0.790$ $r^2=0.624$					
COEFFICIENTS (effects coding):					
CONSTANT		4.492	LITTER	0.000	
			CLIP	0.000	0.360
SITE	1.000	-0.348	LITTER	0.000	
SITE	2.000	0.649	SEED	0.000	0.267
LITTER	0.000	-0.587	CLIP	0.000	
			SEED	0.000	0.269
CLIP	0.000	-0.411	LITTER	0.000	
SEED	0.000	-0.806	CLIP	0.000	
			SEED	0.000	-0.079
RICHNESS 94		-0.565	CALCANS	0.000	
MEDIAN WATER		-0.104	SEED	0.000	-0.083
C. CANADENSIS	0.000	-0.580	CALCANS	1.000	
			SEED	0.000	-0.171
C. CANADENSIS	1.000	0.155	CALCANS	2.000	
C. CANADENSIS	2.000	0.131	SEED	0.000	-0.377

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
SITE	24.368	2	12.184	8.075	0.000
LITTER	56.565	1	56.565	37.491	0.000
CLIP	25.387	1	25.387	16.826	0.000
SEED	82.954	1	82.954	54.982	0.000
RICHNESS 94	66.195	1	66.195	43.874	0.000
MEDIAN WATER	45.783	1	45.783	30.345	0.000
C. CANADENSIS	20.232	3	6.744	4.470	0.005
LITTER*CLIP	21.328	1	21.328	14.136	0.000
LITTER*SEED	11.714	1	11.714	7.764	0.006
CLIP*SEED	10.789	1	10.789	7.151	0.008
LITTER*CLIP *SEED	1.000	1	1.000	0.663	0.417
CALCANS*SEED	24.297	3	8.099	5.368	0.002
ERROR	224.805	149	1.509		

VARIABLES

SITE: Categorical variable (three sites)
 LITTER: Leaf litter (present/removed)
 CLIP: *C. stricta* tillers (clipped/unclipped)
 SEED: Seeds from eight colonizing species (added/not added)
 RICHNESS 94: Number of species present prior to manipulation
 MEDIAN WATER: Median distance from top of tussock base to water (cm)
 C. CANADENSIS: Density class of *C. canadensis* (0,1-3,4-10,>10 ramets)

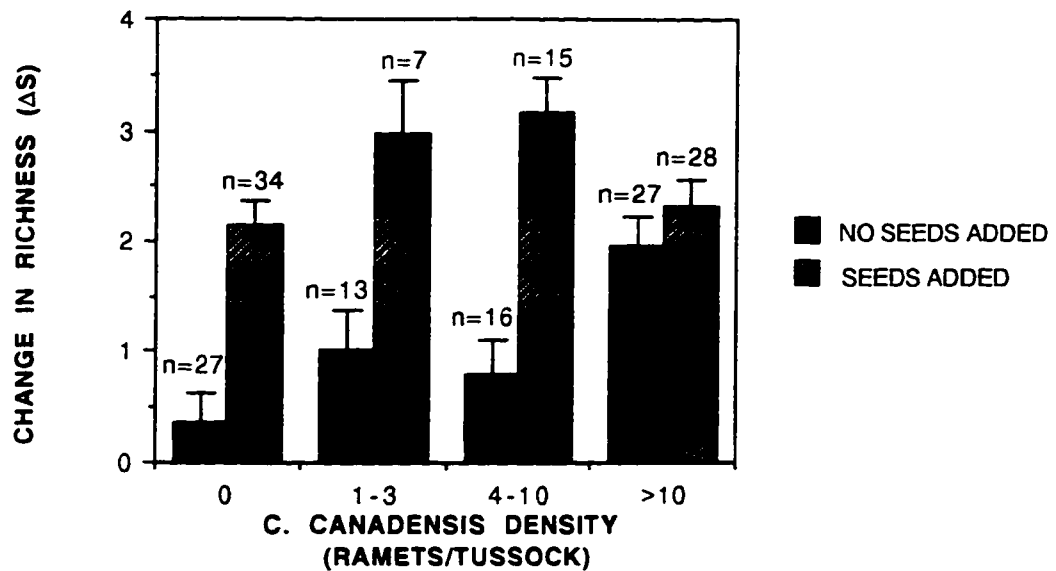


Figure 25. Adjusted means and standard errors of the change in plant species richness (ΔS) associated with *Calamagrostis canadensis* densities with, and without, seed addition. High *Calamagrostis canadensis* densities are associated with large increases in species richness without seed additions. When seeds were added, it resulted in increased species richness only at *Calamagrostis canadensis* densities of ≤ 10 ramets per tussock. This reflects the significant *Calamagrostis canadensis**seed interaction (Table 9).

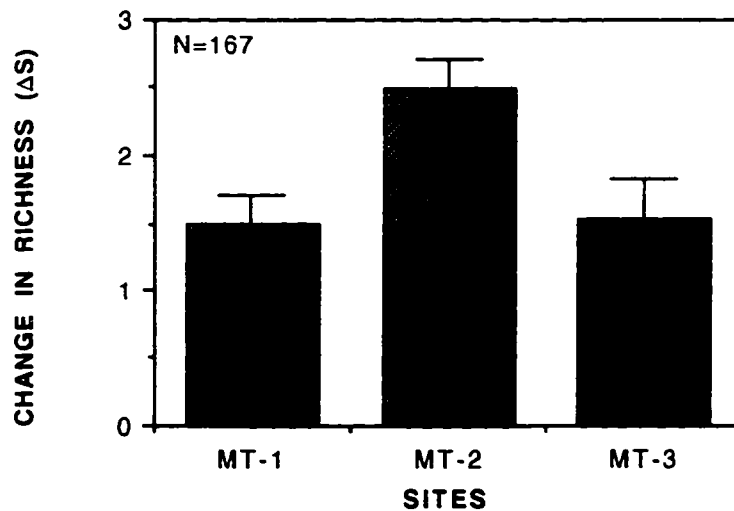


Figure 26. Adjusted means and standard errors of the change in plant species richness (ΔS) among sites. Site MT-2 had significantly greater increases than the other sites (Table 9).

Table 10. Analysis of variance: effects of treatments (clipping *Carex stricta* leaves, removing leaf litter, adding seeds) on the new establishment of reproductive species (ΔS_r) on individual *Carex stricta* tussocks (1994-1995).

DEPENDENT VARIABLE: NUMBER OF NEW SPECIES THAT INITIATED REPRODUCTIVE STRUCTURES (ΔS_r)

N=167 r=0.647 r²=0.418

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
SITE	9.747	2	4.873	8.756	0.000
LITTER	1.899	1	1.899	3.412	0.067
CLIP	7.631	1	7.631	13.710	0.000
SEED	32.318	1	32.318	58.063	0.000
LITTER*CLIP	1.173	1	1.173	2.107	0.149
LITTER*SEED	4.665	1	4.665	8.381	0.004
CLIP*SEED	1.934	1	1.934	3.475	0.064
LITTER*CLIP*SEED	3.384	1	3.384	6.079	0.015
ERROR	87.386	157	0.557		

VARIABLES

SITE: Categorical variable (three sites)
LITTER: Leaf litter (present/removed)
CLIP: *C. stricta* tillers (clipped/unclipped)
SEED: Seeds from eight colonizing species (added/not added)

species when all three factors were manipulated (L+C+S). As with the ΔS means, the L+C+S mean was more than twice as large as the next highest mean.

Using ΔS_r as the dependent variable, an ANCOVA model was constructed in the same manner as in the analysis of ΔS (Table 11). The ANCOVA with the highest r^2 explained an additional 4% of the variation in ΔS_r ($r^2=0.46$) as compared to the ΔS_r ANOVA. The only covariate that was significant in this ANCOVA, however, was the median difference between the top of the tussock base and water levels. This variable was not involved in any significant interactions. As in the ΔS ANCOVA, increases in ΔS_r at site MT-2 were greater than at the other sites.

Discussion

Treatment effects on species richness. The data support my hypothesis that high levels of *Carex stricta* standing crop production, high levels of leaf litter accumulation, and low propagule supplies all limit species richness on *Carex stricta* tussocks (Table 8, Fig. 23). Experimental reduction of the limitations imposed by each of the three factors resulted in increases in species richness (ΔS) when the limitations imposed by at least one other factor were also reduced. The treatment in which limitations by all three factors were reduced resulted in an increase in species richness that was twice as great as the next highest treatment, indicating the importance of all three factors. The pattern of the means was similar for ΔS_r .

Although I assumed that clipping *Carex stricta* leaves would increase the availabilities of all resources, only the effects on light levels were tested. Clipping did increase light levels (Table 7). In addition, a significant interaction indicated that the effects of clipping varied among the sites—unclipped tussocks at site MT-2 had much higher light levels than unclipped tussocks at the other sites (Fig. 21). In the field, *Carex stricta* appeared to be more productive at sites MT-1 and MT-3, perhaps explaining the differences in light levels. However, this difference among sites was apparently not enough to alter the effects of the *Carex stricta* on species richness, otherwise there should have been a significant interaction between clipping and “site”.

The increases in species richness that resulted from clipping, leaf litter removal, and

Table 11. Analysis of covariance: effects of treatments (clipping *Carex stricta* leaves, removing leaf litter, adding seeds), and covariates (initial species richness, water levels, and *Calamagrostis canadensis* densities) on the new establishment of reproductive species (ΔS_T) on individual *Carex stricta* tussocks (1994-1995).

DEPENDENT VARIABLE: NUMBER OF NEW SPECIES THAT INITIATED REPRODUCTIVE STRUCTURES (ΔS_T)						
N=167 r=0.676 r ² =0.457						
COEFFICIENTS (effects coding):						
CONSTANT		1.195		LITTER	0.000	
				CLIP	0.000	0.377
SITE	1.000	-0.151		LITTER	0.000	
SITE	2.000	0.547		SEED	0.000	0.155
LITTER	0.000	-0.096		CLIP	0.000	
				SEED	0.000	0.085
CLIP	0.000	-0.196				
SEED	0.000	-0.432		LITTER	0.000	
				CLIP	0.000	
				SEED	0.000	-0.149
MEDIAN WATER		-0.036				

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
SITE	14.903	2	7.451	14.253	0.000
LITTER	1.541	1	1.541	2.948	0.088
CLIP	6.373	1	6.373	12.191	0.001
SEED	31.110	1	31.110	59.509	0.000
MEDIAN WATER	5.832	1	5.832	11.156	0.001
LITTER*CLIP	0.984	1	0.984	1.881	0.172
LITTER*SEED	4.007	1	4.007	7.665	0.006
CLIP*SEED	1.185	1	1.185	2.266	0.134
LITTER*CLIP*SEED	3.690	1	3.690	7.058	0.009
ERROR	81.554	156	0.523		

VARIABLES

SITE: Categorical variable (three sites)
 LITTER: Leaf litter (present/removed)
 CLIP: *C. stricta* tillers (clipped/unclipped)
 SEED: Seeds from eight colonizing species (added/not added)
 MEDIAN WATER: Median distance from top of tussock base to water (cm)

seed additions could have resulted from increased establishment of new species, reduced extinction rates, or both. However, it is clear from an analysis of the establishments and extinctions associated with the treatments that the primary effect of all three of the factors was on establishment rather than extinction (Fig. 24).

Another interesting pattern was that the treatments not only affected local scale species richness, but may also have affected regional (site) scale richness as well. The number of species increased by 4-8 at each of the sites (Table 6). However, the effects on site scale richness were not part of this study, and as such, there were no control sites with which to compare these increases.

Finding that the standing crop of the dominant, leaf litter, and propagule availability are all important in regulating species richness is consistent with Grime's model of species richness (1979). However, this experiment was not designed to test Grime's model relative to other models, and the results are not inconsistent with other models that predict competition or dispersal effects influence species richness. The reason that Grime's model has been emphasized is that it was the only one that included all three factors—standing crop, leaf litter, and dispersal—that my earlier research (Lord 1994) had indicated might be important in regulating plant species richness on *Carex stricta* tussocks. If all three factors are shown to be important in other systems, then Grime's model may prove to be more complete, and therefore more predictive, than other models.

The data also support my second hypothesis that the magnitudes of species richness limitation by *Carex stricta* standing crop and leaf litter are both affected by propagule availabilities, with greater effects occurring where propagules from more species known to colonize *Carex stricta* are present. Clipping or litter removal alone each had little effect on species richness (ΔS or ΔS_r), but when seeds were added in conjunction with either of these manipulations there was a substantial increase in species richness (Fig. 23). This is consistent with Grime's model in which the slope of the relationship between standing crop plus litter and species richness is dependent on the number of species in the system (Fig. 3).

No hypothesis was made on whether there would be a significant interaction between clipping and litter removal; however, the significant clipping*litter relationship (Table 8) is also consistent with Grime's model. This is because most of the curve to the

right of the peak is exponential rather than linear— reductions in both standing crop and litter therefore result in exponentially greater increases in species richness than would come about by the reduction of either factor alone (Fig. 3).

Although this study was restricted to a single system, there is a theoretical basis for suspecting that the relationships uncovered have broad applicability. The significant interactions between standing crop, leaf litter, and dispersal effects indicate that the effects of these factors should not be studied in isolation. This could be one of the reasons that manipulations of standing crop and leaf litter have yielded mixed results. In addition, the correlational studies between species richness and productivity have typically yielded relationships with very high unexplained variation. This variation would be predicted from Grime's model, as supported by my experiment, if the observations come from communities that vary in dispersal characteristics. This was demonstrated in a correlational study by Gough et al. (1994) in which species richness (species·m⁻²) was sampled in coastal marshes along gradients of salinity and elevation. In that study, standing crop plus litter biomass was only weakly correlated ($r^2 = 0.02$) with species richness (species·m⁻²) in a univariate regression; whereas, "potential species richness" (species pool) and standing crop plus litter biomass together explained 81% of the variation in species richness. Visual analysis of the published data suggested that there was a significant interaction between species pool and biomass. Unfortunately, the interaction was not included in the statistical analyses and the authors concluded that biomass effects were unimportant relative to factors related to species pools. Rather than dismissing biomass effects (and the predictive ability of Grime's model), a more complete analysis might have yielded the conclusion that biomass effects become more important with increasing species pools— a conclusion fully consistent with Grime's model!

Additional influences on species richness. The median water levels relative to the tops of the tussock bases were negatively correlated with both ΔS and ΔS_r . This means that tussock bases associated with higher relative water levels during the growing season were associated with larger values of ΔS and ΔS_r . Higher water levels could have increased species richness by having positive effects on dispersal, germination, and vigor of tussock colonizing species. If wetter conditions allowed more species to become

established without affecting competitive interactions, this would mean that tussocks associated with higher water levels effectively had a greater species pool (a greater number of dispersing species able to become established in the absence of competitive interactions) than drier tussocks in the same wetlands. High water levels could also have increased richness by having negative effects on *Carex stricta*, thus inhibiting its ability to exclude other species. In either case, the effects would be consistent with Grime's model. It is likely that the effects of water level vary from year to year, depending upon precipitation levels and the conditions of the beaver dams. The year of the experiment (1995) was relatively dry, and water levels may have greater effects than if precipitation had been closer to average levels. Water levels were not significantly correlated with species richness in the five sites I examined in 1992 (Lord 1994).

The negative association between the number of species originally present on the tussocks and ΔS (Table 9) probably resulted because there was a finite species pool. All else being equal, tussocks with higher initial numbers of species would then have a lower probability of new species establishments (λ) than tussocks with few initial species (Equation 1). This relationship was not detected with ΔS_r .

The relationship between *Calamagrostis canadensis* density and species richness (ΔS) was surprising. *Calamagrostis canadensis* density was included in the analyses because this plant was suspected of being a competitive species that could influence species richness on the tussocks. *Calamagrostis canadensis* is a productive grass that was the most frequently occurring species found growing on *Carex stricta* tussocks (Table 6). As suspected, high densities of *Calamagrostis canadensis* were shown to significantly reduce light levels (Table 7; Fig. 22). Despite the reduced light levels, however, high densities of *Calamagrostis canadensis* were associated with *increased* species richness (ΔS) from natural propagule inputs. Seed additions to tussocks with high *Calamagrostis canadensis* density did not increase this high level of natural recruitment to the same extent that the additions increased recruitment at lower *Calamagrostis canadensis* density (Table 9; Fig. 25). Although I suspect that this relationship merely indicates that *Calamagrostis canadensis* establishes well on tussocks that also favor the establishment of other species, the data were not collected in a manner that could test whether any facilitative

effects of *Calamagrostis canadensis* were involved. *Calamagrostis canadensis* density was not found to explain significant variation in ΔS_r .

The inclusion of the covariates (initial richness, water level, and *Calamagrostis canadensis* density) in the ANCOVA model explained enough within-site variation in ΔS that significant differences among sites were revealed (Table 9). The larger increase in richness at site MT-2 (Fig. 26) was probably not due to differences in unmanipulated levels of *Carex stricta* standing crop, leaf litter levels, propagule availabilities (dispersed or in seed banks), or in any of the covariates, as these differences should have resulted in significant interactions between the other independent variables and “site” in the analyses. The cause of these site differences is unknown, but it is interesting that higher light levels on unclipped tussocks were also noted at site MT-2 (Fig. 21). The significance of site differences and lack of interactions with “site” were also found in the analyses of ΔS_r (Tables 10&11).

It was also puzzling that no interactions between site and the treatments were found in relation to site MT-3 because that site appeared to have a larger potential species pool (19 species total) than the other sites (11 species each) based on the surveys conducted prior to the manipulations (Table 6). In the artificial tussock study (Part I), I found that species pools were positively correlated with the rates at which species arrive at tussocks. If natural levels of dispersal resulted in more species arriving at tussocks at MT-3 than at the other sites, then standing crop and leaf litter biomass removals would be expected to have more of an effect on species richness at site MT-3. Seed additions could have less of an effect at site MT-3 if a greater percentage of the species used in the seed additions were already present in the seed banks or arrived the tussocks through natural dispersal. However, the perceived differences in species pools are likely to be at least partly due to a sampling artifact because the tussocks were much larger at site MT-3 (55 tussocks totaling a 10.2 m² sample area) than at sites MT-1 (56 tussocks totaling 4.5 m²) or MT-2 (56 tussocks totaling 7.1 m²). The positive relationship between sample area and number of species encountered is well established (e.g., Mac Arthur & Wilson 1967; Connor & McCoy 1979). In addition, the total number of species recorded on the tussocks in each wetland may not reflect the actual species pools associated with each tussock. The species

pool for each tussock is the number of dispersing species that could potentially occupy it in the absence of competition. It is possible that *individual* tussocks at site MT-3 had species pools that were similar to those at the other sites, but that the tussocks at MT-3 covered a broader range of conditions so that the combined set of species on the tussocks was larger at MT-3.

SYNTHESIS AND CONCLUSIONS

Based on a model proposed by J.P. Grime (1973a, 1973b, 1979), and my earlier study (Lord 1994), the objective of this research was to determine whether or not *Carex stricta* standing crop, leaf litter levels, and dispersal regulate the numbers of species found growing on individual *Carex stricta* tussocks. Previously, I had found that variables related to standing crop and leaf litter were correlated with variation in species richness among *Carex stricta* tussocks located in five sites representing a broad range of species richness per tussock (Lord 1994). Then in the current study (Part I), I found that at sites with high numbers of species per *Carex stricta* tussock, potential tussock colonizing species arrived at artificial tussocks at higher rates (I) than at sites with few species per *Carex stricta* tussock; therefore, it was possible that variation in I among sites could contribute to the observed differences in average species richness per *Carex stricta* tussock. In addition, I found that the variation in I was primarily due to variation in the species pools rather than in the densities of dispersing propagules per species.

In order to more directly establish cause and effect relationships of standing crop, leaf litter, and dispersal on species richness on individual tussocks, I experimentally manipulated these factors using a factorial design (Part II). From this experiment I found that each of the factors limit species richness, and the magnitude of the limitations imposed by each factor was dependent on the levels of each of the other factors. All of these relationships were consistent with Grime's (1979) model. These results do not contradict other models that predict relationships between species richness and biomass or dispersal effects; rather, they indicate that Grime's model may be a better predictor of species richness because his model includes factors not considered in the other models.

Taken as a whole, my research has shown that standing crop, leaf litter, and propagule supplies vary among *Carex stricta* tussocks and tussock populations, and that variation in these factors is likely to be responsible for variation in species richness among *Carex stricta* tussocks. This is the first experiment of its kind to examine the interactions of resource competition by a dominant species, interference effects by leaf litter, and

establishment limitation related to propagule supplies as they affect species richness. Many other researchers have examined the effects of each of these factors in isolation, with mixed results. These conflicting results may be due, at least in part, to the effects of interactions that were not accounted for in those studies.

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