

INTERACTIONS OF LOCAL AND REGIONAL PROCESSES: SPECIES RICHNESS IN TUSSOCK SEDGE COMMUNITIES

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Abstract. Grime's model of plant species richness was used as a basis for examining how local and regional processes interact in the regulation of the species richness of vascular plants growing on individual *Carex stricta* (tussock sedge) tussocks in New Hampshire, USA. We first used a correlational study of 71 tussocks in five marshes to examine the relationships between species richness and standing crop + leaf litter biomass. We found humped (unimodal) relationships with a wide variation in peak species richness per tussock among sites. Then, using a factorial design involving 167 tussocks in three marshes, we performed *Carex stricta* standing crop removals, leaf litter removals, and seed additions to examine how these factors interacted to influence species richness. The results of both studies supported Grime's model, which implies that the magnitude of local competitive effects on plant species richness is dependent on regional propagule availability.

Key words: biomass; *Carex stricta*; competition; dispersal, leaf litter; local or regional scale; propagule availability and limitation; seed addition; species richness; standing crop.

Many different models have attempted to explain why species richness varies among plant communities. Most of these models can be divided into two major groups. One group has focused on local (i.e., within-community) processes, primarily in relation to plant competition (e.g., Grime 1973a, b, 1979, Huston 1979, 1994, Tilman 1982, 1988, Keddy 1990). The second group has focused on regional processes, primarily in relation to dispersal among communities (e.g., MacArthur and Wilson 1967, Horn and MacArthur 1972, Brown and Kodric-Brown 1977, Caswell 1978, Connell 1978, Hanski 1982, 1983, Tilman 1994). The authors of models in both groups generally acknowledge the importance of processes at both the local and regional scales, but most research has concentrated on processes exclusively at one scale or the other. It is essential that research incorporate processes at both local and regional scales if we are to determine the relative importance of these processes and their interactions.

We studied plant communities growing on individual *Carex stricta* Lam. (tussock sedge) tussocks. *Carex stricta* is a common sedge of freshwater wetlands in eastern North America. It often forms large, apparently even-aged populations that dominate marshes associated with beaver (*Castor canadensis*) impoundments (Lord 1994). This plant gets its common name from the dense clumps or "tussocks" that it forms, in which its culms and tillers emerge from discrete bases formed of dense roots and rhizomes that can reach ≤ 1 m tall and 1 m in diameter. In addition to elevating *Carex stricta* foliage above the water or saturated soils of a

wetland, the elevated tussock bases provide habitat islands on which other common marsh species become established.

Initial observations in *Carex stricta* marshes indicated a wide range among tussock populations in the number of species per tussock as well as in standing crop, leaf litter accumulation, and apparent propagule inputs of colonizing species. Variation in these factors is also central to Grime's (1973b, 1979) model of species richness (Fig. 1). Variation in above-tussock biomass is likely to be related to tussock age. Larger, presumably older, tussocks have reduced above-tussock biomass per unit area. The reduced biomass appears to be related to cumulative stress and disturbance from factors such as disease, flooding stress, and small-mammal nesting, which weaken the *Carex stricta* (Lord 1992). Variation in within-site species pools and propagule densities are also likely to be related to differences in ages of the tussock populations. In older tussock populations, reduced biomass may provide more establishment sites for a wider range of species, there will have been more time for accumulation of species, and colonizing species are likely to have larger populations with higher densities of propagules dispersing among tussocks (Lord 1996).

As do several theories that emphasize local scale processes related to productivity, Grime uses competition to explain the frequently observed peak in species richness that occurs at moderately low biomass production (e.g., Grime 1973a, b, 1979, Huston 1979, 1994, Tilman 1982, 1988, Keddy 1990, Tilman and Pacala 1993). The low species richness associated with high standing crop + leaf litter biomass reflects high levels of competitive exclusion by fast-growing species, while the low species richness associated with

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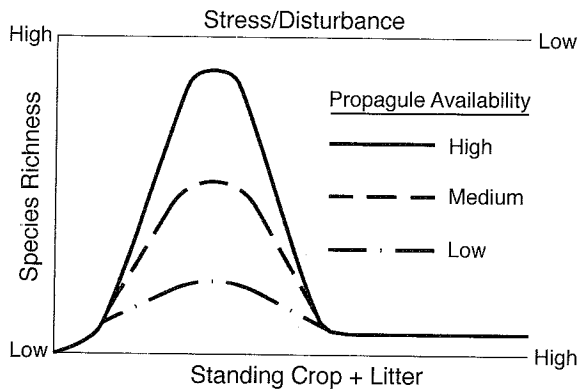


FIG. 1. Grime's model of species richness in herbaceous vegetation (adapted from Grime 1979). Propagule availability is related to the size of the species pool and densities of dispersing propagules.

very low standing crop + leaf litter levels reflects species exclusions due to environmental stress or disturbance. The highest level of coexistence is achieved between these extremes.

Though not central to his model, Grime also considered the regional scale effects of dispersal. Grime argued that the magnitude of the peak in species richness associated with moderately low standing crop + leaf litter levels was determined by "... the availability and rate of ingress of potential constituent species from the surrounding landscape" (Grime 1979). We have termed this last attribute "propagule availability," which is related to the number of potential colonist species (species pool) and the densities of their dispersing propagules (also see MacArthur and Wilson 1967, Huston 1999).

Most tests of Grime's model have used nonmanipulative field observations to examine relationships between species richness and standing crop or standing crop + leaf litter. Our study began similarly so that we could ascertain the general nature of the relationship between species richness and standing crop + litter in this system. We then followed up on our correlative work with an experimental test of the direct effects of standing crop, leaf litter, propagule availability, and most importantly, their interactions on species richness. In our research, the local scale was that of the plant community growing on an individual tussock. The "regional" scale of dispersal and propagule availability was related to propagule inputs originating anywhere outside of the local community. Our experimental examination of local and regional interactions involved testing the following hypotheses:

- 1) *Carex stricta* standing crop production, leaf litter accumulation, and 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 colonizing species are present.

METHODS

In 1992, we sampled five marshes dominated by *Carex stricta* in southeastern New Hampshire, USA. Marshes were selected to represent a wide range in the average number of plant species per tussock. In each marsh, 15 tussocks were randomly selected and vascular plant species surveyed between 22 August and 1 September. Individual tussocks were treated as entire communities and, due to their relatively small sizes, were sampled completely rather than subsampled. As uniform sample areas were not used, variation in tussock area was accounted for statistically (see below). Seedlings (generally dicots <2 cm, monocots <15 cm, see Lord 1994, 1996) were not included in richness estimates. Standing crop (living biomass growing above the tussock base) and leaf litter were collected, oven dried at 60°C for 2.5 d, and weighed. The resulting masses were divided by the area of the top of the tussock base to standardize them. This yielded relatively high standing crop mass/area, as *Carex stricta* leaves can extend well beyond the tussock base. For simplicity, species surveys and biomass collections were restricted to the tops of the tussock bases. Of the original 75 tussocks selected, four were later dropped due to problems with data collection.

The relationships between species richness per tussock, tussock area, and standing crop + leaf litter biomass were examined using ANCOVA with "site" as a fixed effect and a $P < 0.05$ significance level. A parabolic model was tested to reflect the curved nature of the relationship between richness and biomass in Grime's model. Variations of the model were run using both untransformed and log-transformed tussock area, with nearly identical results. The analysis was run using SYSTAT 5.2 for the Macintosh (Wilkinson 1992). The nonsignificant interaction between site and biomass was dropped to improve the error mean square as an estimate of the population random error.

For graphing, each datum was standardized to the average tussock area of the entire data set ($0.165 \pm 0.090 \text{ m}^2$; mean $\pm 1 \text{ SD}$) using the partial regression coefficient from the ANCOVA. Regression lines of species richness vs. tussock area were constructed for each site using the ANCOVA coefficients. Tussock area effects were removed by using the average tussock area for the entire data set in constructing each line.

In 1994, three additional *Carex stricta*-dominated marshes were utilized in a field experiment in southeastern New Hampshire. Grime's model suggests that competition is a strong force structuring high biomass communities. Therefore, we selected tussock populations that had apparently high levels of standing crop + leaf litter to test the effects of competition. These populations were visually similar to Sites 1 and 2 from the 1992 study, which averaged $\sim 2400 \text{ g/m}^2$ standing

TABLE 1. Analysis of covariance for the relationship of species richness on individual *Carex stricta* tussocks to standing crop + leaf litter biomass, with tussock area as a covariate.

Source	SS	df	MS	F	P
Site	201.754	4	50.439	21.420	0.000
Tussock area	11.967	1	11.967	5.082	0.028
Biomass	15.595	1	15.595	6.623	0.013
(Biomass) ²	22.458	1	22.458	9.537	0.003
Site × (Biomass) ²	35.397	4	8.849	3.758	0.009
Error	138.933	59	2.355		

Notes: Sites were selected to represent a broad range of species richness per tussock (1992). $N = 71$, $r^2 = 0.813$.

crop + leaf litter. Fifty-six tussocks were randomly selected along transects at each of the three sites, representing seven replicates for each of the eight treatments outlined below. To avoid possible clumping of treatments, the tussocks were divided into groups of eight along the transects, and randomly assigned one of eight treatments within each group.

In September and October 1994, plant species were surveyed on the tussocks using methods consistent with the 1992 study. The following manipulations were then performed on the selected tussocks using a fully crossed $2 \times 2 \times 2$ experimental design.

1) Litter removal. At the end of the growing season in 1994 (September through November), we removed the standing crop and litter from the tops of the selected tussocks. Clipping of preformed overwintering *Carex stricta* shoots was avoided, and the treatment did not have any noticeable effect on standing crop the following year.

2) Clipping of *Carex stricta*. Clipping of *Carex stricta* leaves began in late April 1995, and continued throughout the summer. Each of the selected tussocks was clipped 10–11 times. The selective clipping did not damage other species.

3) Seed additions. During the summer of 1994, seeds of eight tussock-colonizing species (*Bidens connata*, *Bidens discoidea*, *Calamagrostis canadensis*, *Carex canescens*, *Galium trifidum*, *Lycopus uniflorus*, *Lysimachia terrestris*, *Triadenum virginicum*) were collected from outside of the study areas. The seeds were stored dry at room temperature until 31 January 1995, at which time they were stored cold ($\sim 5^\circ\text{C}$) and dry for 10 wk. Equivalent masses of 0.25–1.5 g of seed for each species were applied to all of the tussocks selected for seed addition between 15 and 29 April 1995.

The tussocks were resurveyed in late August and early September 1995 and the change in species richness (ΔS) was calculated. The change in richness was used rather than final species richness to help account for differences in initial species richness. At the time of the second survey the presence of reproductive structures on new colonizers was noted.

Statistical analyses were run using SYSTAT 5.2 for the Macintosh (Wilkinson 1992). The effects of the treatments on ΔS were analyzed using ANCOVA with "site" as a random effect. Interactions between the

blocking variable and the treatments were tested to determine if the treatments had similar effects at all sites. None of the interactions with "site" were significant at $P < 0.05$, and were dropped from the model in a stepwise manner to simplify the model and to improve the error mean square as an estimate of the population random error. Variations of the model were run using both untransformed and log-transformed tussock area, with nearly identical results. One tussock, severely disturbed by beaver during the experiment, was not used.

RESULTS

In our 1992 correlational study we found that tussock area, standing crop + leaf litter biomass, and site explained 81% of the variation in species richness, with a significant interaction between site and (biomass)² (Table 1). The relationship between species richness and tussock area was linear (slope = 5.78 species/m²); nonlinear transformations of area did not improve the model. The relationship between species richness per tussock and biomass (standing crop + leaf litter) was hump shaped (Fig. 2). Sites 4 and 5, with the highest average species richnesses per tussock, showed relatively steeply humped curves. Sites 1–3 had relatively shallow curves. The average at each site was 1.3 ± 0.6 species per tussock at Site 1 (mean ± 1 SD, $n = 12$), 1.5 ± 0.9 at Site 2 ($n = 15$), 3.3 ± 1.7 at Site 3 ($n = 15$), 6.0 ± 2.0 at Site 4 ($n = 14$), and 8.5 ± 2.5 at Site 5 ($n = 15$). The average tussock area at each site (mean ± 1 SD) was 0.074 ± 0.038 m² at Site 1 ($n = 12$), 0.153 ± 0.092 m² at Site 2 ($n = 15$), 0.144 ± 0.076 m² at Site 3 ($n = 15$), 0.242 ± 0.093 m² at Site 4 ($n = 14$), and 0.200 ± 0.066 m² at Site 5 ($n = 15$).

At our field experiment sites, the average species richness per tussock was 0.9 ± 0.8 species per tussock at Site A, 2.0 ± 1.3 at Site B, and 2.8 ± 1.6 at Site C prior to the manipulations. Eleven colonist species were sampled each at Sites A and B, and 19 species were sampled at Site C prior to the manipulations. The average tussock area at each site was 0.081 ± 0.044 m² at Site A, 0.127 ± 0.084 m² at Site B, and 0.186 ± 0.114 m² at Site C.

The treatments explained 40% of the variation in ΔS , with all of the two-way interactions among the factors significant (Table 2, Fig. 3). "Site" and tussock area were not significant. Among treatment cells, the highest

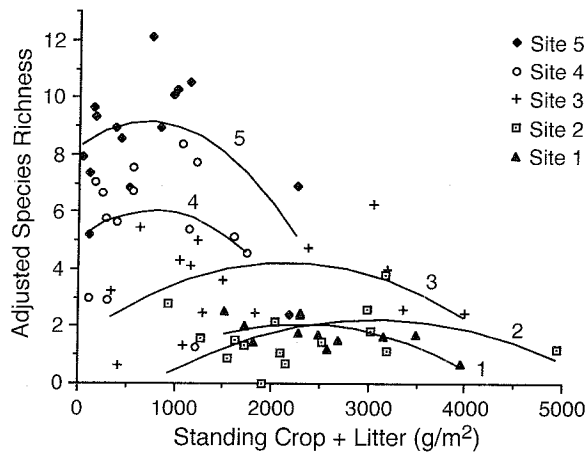


FIG. 2. The relationship between maximum seasonal standing crop + leaf litter and species richness of individual *Carex stricta* tussocks. Tussocks were sampled from five New Hampshire wetlands representing a broad range of average species richness per tussock ($N = 71$ tussocks). Tussock area ranged from 0.033 to 0.441 m^2 , but each datum was standardized to the average tussock area (0.165 m^2). Regressions were constructed using the ANCOVA coefficients with variation due to tussock area removed. Numbers adjacent to the regression lines indicate the associated sites.

mean ΔS was for the clipping + litter removal + seed addition treatment (4.6 ± 1.9 species). The next highest mean was for litter removal + seed addition (2.2 ± 1.3 species). These two means were significantly different from each other and were the only two cell means that were significantly different from the control mean (0.8 ± 1.2 species) using Tukey's multiple comparison test at $P < 0.05$ (Fig. 3).

DISCUSSION

The patterns in our 1992 correlational study were consistent with Grime's model. The humped shapes and variation in the peaks of the species richness–biomass relationships (Fig. 2) closely resemble Grime's model of species richness with variation in propagule availability (Fig. 1). Given the variability in the distributions and the damped shape of the regressions, however, the curvilinear relationships for Sites 1–3 may explain rel-

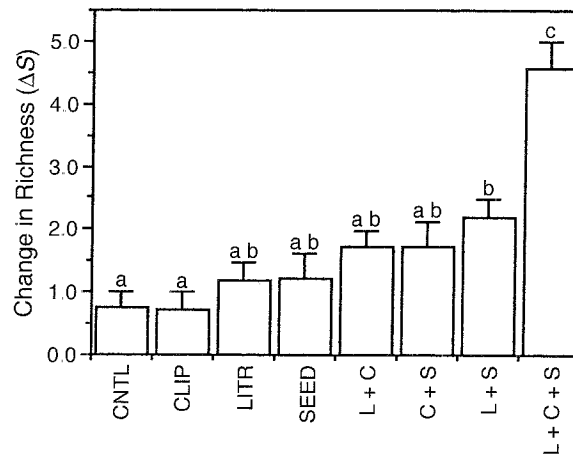


FIG. 3. Means and standard errors by treatment cell for the change in plant species richness (ΔS). Lowercase letters indicate significant differences. CNTL = control; CLIP (C) = *Carex stricta* leaves clipped; LITR (L) = leaf litter removed; SEED (S) = seeds added.

atively little variation. Lord (1996) later documented that the pattern of variation in average species richness per tussock among sites was related to variation in both within-wetland species pools and dispersing propagule densities.

Recent work by Cade et al. (1999) demonstrated that regression quantiles may sometimes be more appropriate for describing limiting ecological relationships than the traditional least squares methods that we employed. This is because least squares methods reflect relationships at the center of response distributions where unmeasured limiting factors may dampen the perceived effect. Regression quantiles, on the other hand, reflect the maxima of response distributions where there may be less interference between a limiting factor and its associated response. We elected to use least squares as a more conservative approach to explore species richness–biomass relationships against the natural background of unmeasured variables operating in these systems. Further support for this approach is that 81% of the variation was explained in

TABLE 2. Effects of treatments on the change in plant species richness (ΔS) on individual *Carex stricta* tussocks over one year (1994–1995) with tussock area as a covariate.

Source	ss	df	ms	F	P
Site	11.694	2	5.847	2.520	0.084
Litter removal	75.532	1	75.532	32.549	0.000
Clipping <i>C. stricta</i>	29.373	1	29.373	12.657	0.000
Seed addition	77.595	1	77.595	33.438	0.000
Tussock area	3.939	1	3.939	1.697	0.195
Litter \times clipping	17.164	1	17.164	7.396	0.007
Litter \times seed	13.903	1	13.903	5.991	0.015
Clipping \times seed	13.176	1	13.176	5.678	0.018
Litter \times clipping \times seed	4.043	1	4.043	1.742	0.189
Error	362.012	156	2.321		

Notes: Sites were selected with relatively high biomass. $N = 167$, $r^2 = 0.403$.

our analysis, indicating a relatively low influence of unmeasured limiting factors.

The 1994 field experiment supports our first hypothesis that *Carex stricta* standing crop production, leaf litter accumulation, and propagule availability all limit species richness on *Carex stricta* tussocks. When the limitations by all three factors were reduced on tussocks in populations with relatively high biomass levels, the increase in species richness that occurred was at least twice as great as when the limitations associated with only two of the factors were reduced (Fig. 3). This indicates that standing crop, leaf litter, and propagule availability were all important influences on species richness. The experimental data also support our second hypothesis that the *magnitudes* of species richness limitations by *Carex stricta* standing crop and leaf litter were each affected by propagule availability, with greater effects occurring where propagules from more species were present. Clipping or litter removal alone had little effect on species richness, but when seeds were added in conjunction with either of these manipulations, there was a substantial increase in species richness. These results indicate that standing crop, leaf litter, and propagule availability all influence species richness, and the slope of the species richness–biomass relationships is dependent on propagule availability, which is consistent with Grime's model (Fig. 1).

No hypothesis was made as to whether there would be a significant interaction between clipping and litter removal; nevertheless, the significant clipping \times litter interaction that was found (Table 2) is also consistent with Grime's model. Since we were reducing competition of the dominant, the portion of Grime's model of interest is to the right of the peak in species richness (Fig. 1). If our manipulations resulted in a bitonic species richness–biomass relationship as depicted in this portion of Grime's model, then reductions in both standing crop and litter could result in greater increases in species richness than would come about by the reduction of either factor alone.

As the results of this experiment were somewhat limited due to the short duration, we repeated the analyses with the change in richness calculated using only new colonizers that had reached a reproductive stage (ΔS_r , presented in Lord 1996). While limited to those species able to reach reproductive maturity in a single year, these analyses were conducted to help support the ΔS results because reproductive individuals could clearly be considered "established" and could give rise to persistent populations. The patterns from the ΔS_r analyses were similar to those found for ΔS .

In addition to supporting Grime's model, our results imply that the effects of standing crop, leaf litter, and dispersal on species richness should not be studied in isolation. For example, many researchers have examined the effects of competition by suppressing dominant species or manipulating leaf litter, but the results

of these experiments have not been consistent. A number of studies found that these manipulations increased species richness (Abul-Fatih and Bazzaz 1979, Monk and Gabrielson 1985, Gurevitch and Unnasch 1989, Cowie et al. 1992, Foster and Gross 1998). In other cases, however, the manipulations had mixed results or did not result in increased richness (Penfound 1964, Pinder 1975, Allen and Forman 1976, Hils and Vankat 1982, Armesto and Pickett 1985, van der Valk 1986, Carson and Peterson 1990, Weiher and Keddy 1995). It is likely that the lack of consistent results is at least partly due to interactions with propagule availability, which can vary widely, both spatially and temporally.

Specific examinations of Grime's model have generally been 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 + leaf litter. While negative or unimodal relationships were revealed in most of these studies (e.g., Al-Mufti et al. 1977, Wheeler and Giller 1982, Vermeer and Berendse 1983, Wilson and Keddy 1988, Moore and Keddy 1989, Shipley et al. 1991, Wheeler and Shaw 1991, Garcia et al. 1993, Tilman 1993, Gough et al. 1994, Guo and Berry 1998), the relationships were often weak, with much scatter in the data. In some studies, no significant relationships were detected (e.g., Vermeer and Verhoeven 1987, Day et al. 1988).

Where Grime (1979) had encountered weak relationships, he attributed them to erratic, nonequilibrium stress or disturbance. A second, equally important explanation is that the observations came from communities that vary in their levels of propagule limitation (e.g., Huston 1999). One example of this was found in a correlational study by Gough et al. (1994) in which species richness was sampled in coastal marshes along gradients of salinity and elevation. The higher salinity sites had smaller species pools (closely related to propagule availability) and also appeared to have a more shallow slope to the species richness–biomass relationship (Gough et al. 1994: Fig. 1 vs. Fig. 6). Unfortunately, the species pool \times biomass interaction was not included in the statistical analyses; however the authors did conclude that species pools should be considered in addition to biomass in the prediction of species richness. The data from Gough et al. support our findings that biomass effects become more important with increased propagule availability—a conclusion consistent with Grime's model.

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