Tussock meadows are diverse in plant species

The defining characteristic of tussock meadows is the presence of tussocks, which are “built” by the tussock sedge (Carex stricta).

Observing tussock meadows over the seasons reveals a diversity of plants. Mosses (and sometimes liverworts) are obvious in winter, apparently photosynthesizing under the snow. In early spring, the stiff leaves of *C. stricta* emerge upright, followed by rapid extension to form a lush and graceful canopy more than a meter tall. By early summer, the tussock meadow looks like a monotype of *C. stricta*. However, in August *C. stricta* leaves senesce, and asters and goldenrods become conspicuous, overtopping the browning sedge leaves that bend or collapse and blanket the tussock. By late fall it is often difficult to see the sedges under dense growth of forbs.

Tussocks foster diversity by increasing soil surface area

Tussocks, which average 15-25 cm tall, can increase the surface area of a flat plot by 45%. Where tussocks are present, species richness is positively correlated with the surface area, height and circumference of tussocks (Werner and Zedler, 2002; Peach 2005). A single *C. stricta* tussock can support up to 16 additional species.

Does the increased surface area explain the abundance of species that occur in tussock meadows? We argue that there is more to it…

Tussocks foster diversity by creating multiple micro-habitats

Michelle Peach (2005) compared three sites (and a total of 191 tussocks) near Madison, WI (Loose Pond, South Cherokee Marsh, and Waubesa Wetland). She found that where water was deepest, tussocks were tallest and tussock height was the best predictor of species richness. Tussocks averaged 24.7 cm (± 1.42 cm standard error) tall at Loose Pond (with 60 species in total), and 15.7 ± .58 cm at South Cherokee and 14.4 ± .32 cm at Waubesa Wetland (both with 25 species). Tussocks added 1.1-3.1 m² of surface area to her 4-m² plots, i.e., up to 45% more surface area than a flat plot.

Greater species richness with taller tussocks suggests that, by raising the topography well above water, tussocks add micro-habitats that contribute to species richness. In fact, tops, sides and bases all differed in environmental conditions and species composition. Tussock tops had the most light, the most litter, and the widest temperature range. Did they also support the most species?
**Tussock tops supported the most species**

Peach (2005) painstakingly sampled 50 tussocks at Loose Pond using contiguous 10 x 10-cm quadrats, starting on top and proceeding down the north and south sides, for up to 13 positions per tussock (depending on tussock height and water level). Comparing tussock tops, upper sides, bases, and off-tussock areas, Peach found that the tops supported an average of 5.5 species per 100 cm² — more than any other micro-habitat.

**Species favored different micro-habitats**

Because some micro-habitats were encountered more often than others (e.g., tussock bases were not exposed until late summer, when water levels receded—the September drawdown), we standardized species per unit area using species-accumulation curves (species-area curves generated by adding data from quadrats in random sequence). The differences in richness by micro-habitat were still clear. New species were added to tussock tops and upper sides more rapidly than bases and areas off-tussock.

Thus, there are differences in species richness among micro-habitats sampled at the 10 x 10-cm scale. Furthermore, many of the species on tops were different from those in the wetter micro-habitats. Of the 80 taxa found at Loose Pond, 34 were associated with one or two micro-habitats. Tops favored 20 species, including 4 “tussock-top specialists” and 16 that preferred tops plus upper sides (see illustration below; from Peach 2004). In contrast, off-tussock areas favored only 7 taxa (*Sium suave*, *Lemna minor*, *Bidens cernuus*, *Equisetum arvense*, *Sagittaria latifolia*, *Alisma subcordatum*, *Schoenoplectus tabernaemontani*, and *Typha spp.*), all of which have aquatic affinities. We conclude that micro-habitats influence both species richness and composition. But wait—there’s more…

**Tussocks foster diversity by changing with the seasons**

By resampling the same 50 tussocks in May, July and September, Peach (2005) documented the temporal dynamics of the numbers and types of species in each micro-habitat. Overall, species richness increased through time, from 35 species in May to 56 in September 2004. Nine species were found only during September. The “aquatic” species became more conspicuous off-tussock as the September drawdown exposed that micro-habitat. Changes in existing micro-habitats and availability of new micro-habitats enhanced species diversity.
We conclude that tussocks increase diversity and structure sedge meadow vegetation by:

1. adding surface area
2. adding micro-habitats that support different species
3. allowing a seasonal progression of species during spring warm-up and late-summer drawdown.

How do tussocks form?

*C. stricta* has a caespitose growth form whereby many culms emerge from a single rootstock. Over time, soil, litter, roots, and live shoots accumulate to form tussocks up to 1 m tall and 1 m in diameter (Costello, 1936). Even where *C. stricta* makes up >90% of the plant cover, its tussocks can still support many co-occurring plant species.

Contributions to ecological theory

Our findings support Hutchinson’s (1961) explanation of high diversity in a very different ecosystem (open water plankton): Because the environment is diverse, many species can co-exist, and because conditions change with season, no species can outcompete others to the point of exclusion. Our results also illustrate emerging theory about topographic heterogeneity that, all else being equal, areas with more heterogeneous topography will have greater surface space, more environmental variability, and more fractal dimensions (Larkin et al. in press).

Recommendations

**RESOURCE PROTECTION** Tussock meadows are valuable and unusual because of their ability to support many native plant species. However, tussocks are known to be vulnerable to disturbances such as grazing and sedimentation (Middleton 2002; Werner and Zedler 2002).

We recommend increased protection of areas where large tussocks are found, by excluding trails and trampling, and including invasive plant control, especially careful removal of reed canary grass (*Phalaris arundinacea*).

**SAMPLING** In order to capture the diversity of tussock meadow vegetation, we recommend sampling in both July and September. Repeated sampling will encounter more species.

**RESTORATION** Because tussock meadows are diverse, we recommend restoring them by:

1. planting *Carex stricta* to form the matrix of the community, using seedling transplants, as recommended by Budelsky and Galatowitsch (2004)
2. adding co-dominant species (*C. lacustris, Calamagrostis canadensis*)
3. introducing several of the less-common associates (cf. Peach 2005).

Because restored sedge meadows often have fewer species than ideal targets/reference sites (Ashworth, 1997; Galatowitsch and van der Valk, 1996), we also recommend adding topographic heterogeneity to sedge meadow restorations to facilitate the establishment of a species-rich plant community. Artificial micro-topography could also enhance the water-quality-improvement and flood-control functions of restored wetlands (Tweedy and Evans 2001).

If cost-effective methods of mimicking tussocks can be found, the addition of surface area and multiple micro-habitats could increase diversity. We recommend experimentation in restoration sites. In one such site (below) we used hands and shovels to form ~200 dirt mounds (artificial tussocks). Plots with mounds had twice as many species as plots without mounds (Hall 2005; Peach 2005; photo by M. Peach).
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Kandis Elliot, UW-Botany Multimedia Facility, transformed our scribbles into artwork.

References


Learn more about restoration research

For additional information about restoration research, attend the Arboretum’s Annual Science Day. Details about the May 16, 2005, program will be posted on the Arboretum web site.