

Tiller organization within the tussock grass *Schizachyrium scoparium*: a field assessment of competition–cooperation tradeoffs

Justin D. Derner, David D. Briske, and H. Wayne Polley

Abstract: Tussock grasses are characterized by a compact spatial arrangement of tillers that contributes to intense intratussock competition. This investigation was designed to directly assess the magnitude of competition among autonomous subunits of tillers within individual tussocks (i.e., integrated physiological units) to further define the mechanisms of tiller organization within this successful growth form. Experimentally constructed tussocks of *Schizachyrium scoparium* (Michx. Nash) were grown in the field in central Texas, USA, for 2 years with 1, 4, 8, or 12 autonomous subunits to span the range observed in naturally occurring local populations. Increasing numbers of subunits per tussock did not affect tiller density or the mean mass of individual vegetative or reproductive tillers, but it did intensify intratussock competition as evidenced by a large reduction in total tiller mass and number per subunit. This pattern of tiller organization is indicative of a division of labor within the tussock that is manifested as a tradeoff between competition among autonomous subunits and cooperation among tillers within these physiologically integrated subunits. We conclude that an increasing number of autonomous subunits associated with tussock basal expansion contributes to coarse-scale resource preemption and competitive ability, while resource sharing among tillers within subunits supports new tiller establishment and growth within this highly competitive microenvironment.

Key words: bunchgrass, integrated physiological unit, little bluestem, physiological integration, resource sharing, sectoriality.

Résumé : Les herbes en touffes se caractérisent par un arrangement spatial compact de talles contribuant à une forte compétition dans la touffe. Cette recherche a été conçue pour évaluer directement l'amplitude de la compétition parmi des sous unités autonomes de talles à l'intérieur d'une touffe individuelle (c.-à-d., unité physiologique intégrée) afin de mieux définir les mécanismes d'organisation des talles sous cette forme efficace de croissance. Les auteurs ont construit des touffes de *Schizachyrium scoparium* (Michx. Nash) au champ, dans le centre du Texas aux États-Unis, au cours de deux années et comprenant 1, 4, 8, ou 12 sous unités autonomes et ainsi couvrir l'amplitude des situations survenant dans les populations naturelles locales. L'augmentation du nombre de sous unités par touffe n'affecte pas la densité des talles ou la masse moyenne des talles végétatifs ou reproductifs individuels, mais intensifie la compétition dans la touffe comme le montre la forte réduction de la masse totale des touffes et du nombre par sous unité. Ce patron d'organisation des talles traduit une division du travail à l'intérieur de la touffe se manifestant par une contre partie entre la compétition entre les sous unités autonomes et la coopération entre les talles dans ces unités physiologiques intégrées. Les auteurs concluent qu'une augmentation du nombre de sous unités autonomes, associée avec l'expansion basale de la touffe, contribue à la capacité de préemption et de compétitivité à grande échelle, alors que le partage des ressources entre les talles dans les sous unités supporte l'établissement des talles et la croissance dans ce microenvironnement fortement compétitif.

Mots-clés : graminées cespitueuses, unité physiologique intégrée, petit andropogon, intégration physiologique, partage des ressources, sectorialité.

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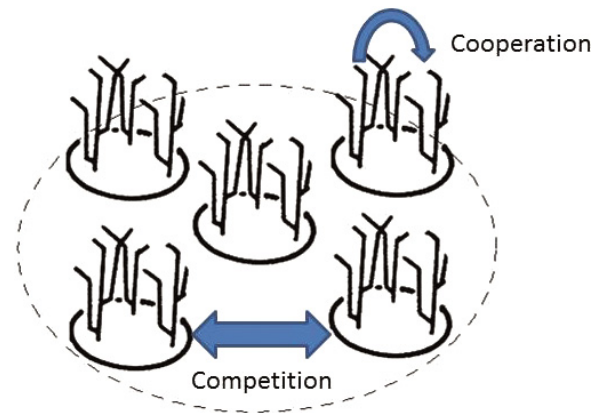
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Introduction

Tussock (also known as caespitose, bunchgrass, or phalanx) grasses represent a dominant herbaceous growth form that occurs on all continents from the high Arctic to the sub-Antarctic and they are especially well represented within the grassland biome (Leith 1978; Walter 1979). The wide distribution and dominance of tussock grasses are somewhat surprising given that the majority of modern monocot families are rhizomatous (Tiffney and Niklas 1985). Tiller development in tussock grasses occurs within the subtending leaf sheaths of parental tillers resulting in minimal intertiller distances and compact spatial arrangement of tillers (White 1979; Briske 1991). In contrast, tiller development in rhizomatous and stoloniferous grasses occurs horizontally through leaf sheaths of parental tillers to disperse tillers in patterns established by various branching angles and internode lengths (White 1979; Harper 1981). These patterns of architectural variation characterized by the spatial distribution of tillers further influence the capacity of these growth forms to exploit resources within their environment and interact with neighbors (Harper 1981).

The compact pattern of tiller organization in tussock grasses contributes to intratussock competition for resources (Briske and Butler 1989; Cheplick and Salvadori 1991; de Kroon and Kwant 1991) and poses the question, how do tussock grasses remain a dominant growth form with widespread distribution despite the occurrence of within-plant competition? Resource sharing among anatomically connected tillers, produced from successive tiller recruitment and characteristic of all clonal plants, provides a partial answer. Resources are allocated from older tiller generations to support juvenile tiller establishment (Welker et al. 1991; Williams and Briske 1991). However, only those tillers located within anatomically connected subunits termed integrated physiological units (IPUs) (*sensu* Watson and Casper 1984; Watson 1986) possess this ability, such that individual IPUs appear to function autonomously within tussocks (Fig. 1; Welker et al. 1987, 1991; Williams and Briske 1991; Derner and Briske 1998). These IPUs develop within 2 years of tussock establishment when the common progenitor of the tussock (initial tiller originating from seed) dies and decomposes resulting in a loss of vascular continuity within the tussock (Gatsuk et al. 1980). As a result, the number of tillers per IPU and IPUs per tussock define the size and architectural configuration of tussocks. Wilhalm (1995) reported a range of 2–35 IPUs per tussock for 24 perennial tussock species in Europe. An increasing number of IPUs may be an inevitable consequence of basal tussock expansion in this growth form (Gatsuk et al. 1980). With increasing tussock size and age, IPUs become physically separated as the initial tiller generations die and decompose (Gatsuk et al. 1980; Olson and Richards 1988). This physical separation of IPUs leads to fragmentation of the tussock, which is a common characteristic of tussock grasses (Gatsuk et al. 1980; Wilhalm 1995). The distances of physical separation between IPUs are quite short (mm) in tussock grasses, which prevents visual differentiation of IPUs in most tussock grasses, especially those with compact arrangement of tillers. A greater understanding of the function and dynamics of IPUs is required because they may represent the most relevant level at which to investigate the ecology of clonal plants (Cain 1990).

Fig. 1. Tillers within a tussock grass (dashed circle) are envisioned to be organized within multiple integrated physiological units (IPUs; solid circles) that are assumed to function autonomously within the tussock and compete for resources. Each IPU consists of several anatomically connected tiller generations that possess the capacity for resource sharing. Modified from Briske and Derner 1998.



Several models have been developed to simulate the patterns and ecological consequences of physiological integration within clonal plants, but they have limited applicability to tussock grasses because they include rhizomes in their model structure (e.g., Herben and Suzuki 2002; Herben 2004). Models combining elements of clonal architecture and patterns of resource allocation (i.e., integration) are required to more fully explore the ecological success of tussock grasses (Tomlinson et al. 2007).

Cooperation within IPUs results from resource sharing among anatomically connected tiller generations (Watson 1986). Integration among these tiller generations has been documented for several tussock grasses using a number of methodologies, including isotopic labeling (Welker et al. 1991; Price et al. 1992; Derner and Briske 1998), severing of vascular connections (Williams and Briske 1991; Hartnett 1993), and morphological assessments of plant architecture (Gatsuk et al. 1980; Wilhalm 1995; Derner and Briske 1999). For example, IPUs in *Schizachyrium scoparium* (Michx. Nash), a widely distributed tussock grass in North America, are comprised of three tiller generations (Fig. 1; Welker et al. 1991). For this species IPUs are restricted to three generations because the oldest tiller generation dies and decomposes prior to development of the quaternary tiller generation. Photosynthetic carbon, nitrogen, and water are primarily allocated from older to younger tiller generations, but these patterns can be temporarily reversed by increasing sink strengths of older tiller generations (Welker et al. 1987, 1991; Bullock et al. 1994; Derner and Briske 1998). Physiological integration supports establishment and growth of juvenile tillers within the competitive microhabitat created by numerous IPUs within the compact basal area of individual tussocks (Williams and Briske 1991).

In contrast, competition among IPUs has been less thoroughly investigated. Evidence indicates that the intensity of competition among IPUs within tussocks may be similar to that of intraspecific competition between tussocks (Briske and Butler 1989; Cheplick and Salvadori 1991; de Kroon

and Kwant 1991). Intratussock competition among IPU occurs both above and belowground, but it appears that soil resources are most important in mediating intratussock competition and therefore density-dependent regulation of tiller organization within tussocks (Derner and Briske 1999). It has been hypothesized that the balance between competition among IPU and cooperation within IPU represents the primary mechanism of tiller organization within the tussock growth form (Briske and Butler 1989; de Kroon and Kwant 1991).

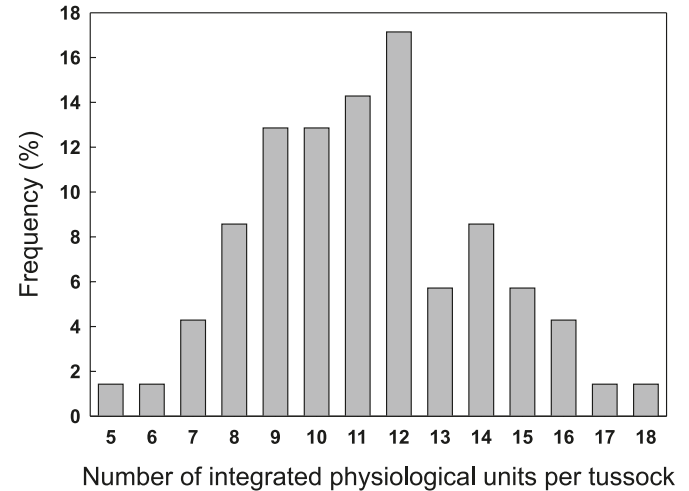
A field experiment was designed to directly assess the magnitude of competition among individual IPU and to indirectly infer the consequences of cooperation among tillers within IPU of tussocks of the C4 perennial grass *S. scoparium*. Experimental tussocks were constructed in the field with various numbers of IPU that spanned the range observed in naturally occurring populations of this species (see below). Responses variables were evaluated at the individual tiller (mass), IPU (mass and numbers of reproductive and vegetative tillers), and entire tussock (total mass and numbers of reproductive and vegetative tillers, tiller density, basal area, canopy volume, and height) for 2 successive years. This unique experimental design enabled us to test the prevailing hypothesis of tiller organization within the tussock growth form by determining if an increasing number of IPU decreases performance of individual tussocks, while growth of individual tillers within IPU is buffered from these competitive effects by the capacity for resource sharing among tillers within these subunits.

Materials and methods

The field experiment was conducted at the United States Department of Agriculture-Agricultural Research Service Grassland, Soil & Water Research Laboratory near Riesel, Texas (31°28'N, 96°52'W). Soils on the site are the Heiden series (fine, smectitic thermic Udic Haplusterts) and are well-drained and very slowly permeable with a 1% slope. Clay content of the soil is 40%–60%. Both inter- and intra-annual precipitation variability are high (Harmel et al. 2003). Long-term (1938–1999) mean annual precipitation is 871 ± 228 mm (mean ± 1 SD) with wet springs (April–June) and dry summer and winter months (Harmel et al. 2003). For 1999, 2000, and 2001 total annual precipitation was 58%, 126%, and 129% of the long-term mean, respectively. Mean long-term precipitation for the primary growth period of C4 grasses, from May to July, is 250 mm (Harmel et al. 2003). During 1999, 2000, and 2001, rainfall for this period was 77%, 122%, and 95% of the 62-year mean, respectively.

Schizachyrium scoparium is a widely distributed C4 perennial tussock grass that occurs throughout the central and eastern United States (Gould 1975). Seventy randomly chosen tussocks of *S. scoparium* were destructively harvested on 30 June 1998 from a relict tallgrass prairie located immediately adjacent to the field plots where the constructed tussocks were grown. These tussocks were excavated and root systems soaked in water to remove soil and facilitate separation of IPU to determine the frequency distribution of IPU in natural tussocks. Mean basal area of these tussocks was 97.5 cm² (range 67–132 cm²), and the number of IPU per tussock ranged from 5 to 18 with a maximum frequency

Fig. 2. Frequency histogram of the number of integrated physiological units per tussock derived from destructively sampling 70 randomly selected tussocks of the perennial grass *Schizachyrium scoparium* in a native Texas prairie on 30 June 1998.



(17%) of 12 (Fig. 2). Seeds of *S. scoparium* (ecotype 9029926-91) were obtained from the USDA-Plant Materials Center in Knox City, Texas, USA, and planted 11 February 1999 into 125 cm³ pots (5 cm × 5 cm × 5 cm) containing a 50:50 mix of commercial potting soil and topsoil from the field plots. Following emergence, plants were thinned to one per pot, watered three times weekly and grown in a greenhouse. Intact, uniform-sized plants, consisting of 6 (±0.2, 1 SD) connected tillers (i.e., the IPU), were transplanted into the field plots with the mix of potting soil and topsoil, but without pots, on 12 April 1999. Height and biomass of transplants were not measured.

These individual plants were arranged to establish constructed tussocks with 1, 4, 8, or 12 IPU per tussock (Fig. 1). Constructed tussocks all initially had a circular basal circumference of 35 cm (97.5 cm² basal area) with a radius of 5.5 cm from the tussock center to the individual transplants. For example, in tussocks consisting of four IPU, individual transplants were arranged in cardinal directions from the tussock center, and in tussocks with 12 IPU, transplants were arranged at the 12 locations on a clock. Sixty tussocks with each of the four numbers of IPU ($n = 240$ total tussocks) were randomly located on 2 m diameter spacings to minimize interplant competition (Tilman 1989) in a completely randomized design. Experimental tussocks were hand watered weekly from transplanting to mid-May (five watering events) with application rates approximating a 2.5 cm precipitation event because of the dry conditions during the spring of 1999. The field had previously been used for a long-term rotation of cultivated crops of *Avena sativa* L. and *Triticum aestivum* L. Weeds were removed from the plots by hand weekly. All constructed tussocks were defoliated to a height of 10 cm following senescence (early December) each year to facilitate sampling of vegetation attributes the following year.

We constructed tussocks using IPU that likely differed genetically owing to their origin from individual seed; whereas, tussocks in nature are composed of IPU derived from a single genotype. Although less than ideal, we adopted this ap-

proach to avoid potential errors associated with the identification of IPUs in natural tussocks and the invasive procedure of severing vascular connections within individual tussocks. By using a tilled field, removing weeds, and spacing constructed tussocks on 2 m intervals, we also reduced intertussock competition from that experienced by tussocks in the nearby native tallgrass prairie. Therefore, we acknowledge that results obtained are specific to this experiment and methodology used, but that the general inferences derived are applicable to the competition–cooperation tradeoffs influencing tiller organization in tussock grasses.

We measured basal area, canopy height, and canopy volume each year on 10 randomly chosen tussocks with each number of IPUs. These tussocks were destructively harvested in early August in 2000 and 2001. Each constructed tussock was excavated. Roots were soaked in water to facilitate soil removal and separation into IPUs. Tillers in each IPU were separated into vegetative (no elongation of culm internodes) or reproductive (culm elongation evident) categories to determine if the number of IPUs per tussock differently affected resource allocation patterns. Individual tillers were counted and aboveground biomass was weighed following drying to a constant mass at 60 °C. Because the circumference of tussock canopies increased from the base to the top (inverted frustum of a cone), canopy volume of tussocks was calculated using the equation: $V = 1/3\pi h(r^2 + rR + R^2)$ where V is volume, h is distance from soil surface to top of tussock canopy (canopy height), r is radius of basal area occupied by tussock, and R is radius of area at top of tussock canopy (canopy radius) (Derner and Briske 1999).

Analysis of variance (ANOVA) was conducted to determine if the number of IPUs affected tussock variables. Data were tested for normality (Shapiro–Wilk test) and residuals plotted and examined for outliers. We assessed the correlations between tiller density and tiller number and mass variables, and between entire tussock variables of height and canopy volume. These correlations were conducted to determine the influence of tiller density independent of the number of IPUs on tiller and tussock response variables. Linear, polynomial, hyperbolic, and power functions were used to determine relationships between tiller numbers and mass among tussocks comprised of various numbers of IPUs. The model with the greatest r^2 value was considered the best fit (Derner et al. 2004). Statistical significance was assumed at $P < 0.05$ in all cases.

Results

Tussock responses

Tiller density per tussock was not affected by the number of IPUs per tussock, year, or the interaction of these variables (1.34, 1.33, 1.23, and 1.28 tillers/cm² for 1, 4, 8, and 12 IPUs per tussock, respectively). Tiller density was, however, positively ($r = 0.34$ – 0.40) correlated (Pearson correlation coefficient) with the total mass of vegetative tillers per tussock, number of vegetative tillers per tussock, and total number of tillers per tussock (Fig. 3). Tiller density was not significantly correlated with the total mass of reproductive tillers per tussock, total mass of tillers per tussock, or number of reproductive tillers per tussock. The ratio of the number of vegetative to reproductive tillers per tussock was positively correlated

($r = 0.34$) with tiller density; whereas, the ratio of the mass of vegetative to reproductive tillers per tussock, canopy volume, and tussock height was not (data not shown). Total tiller number per tussock and basal area per tussock were lowest in tussocks composed of a single IPU, but did not significantly differ among tussocks composed of 4–12 IPUs (Fig. 4). Relationships between the number of IPUs and both total tiller number and basal area per tussock were similar in both years.

IPU responses

The mean mass per individual vegetative and reproductive tiller did not differ as a function of the number of IPUs per tussock (Fig. 5). The number of vegetative and reproductive tillers and total mass of tillers per IPU, however, significantly decreased as the number of IPUs per tussock was increased, as illustrated by inverse first order polynomial regressions for both years ($r^2 > 0.97$) (Fig. 6).

Discussion

Construction of experimental tussocks with various numbers of IPUs provided a unique opportunity to assess tradeoffs between competition and cooperation on tussock organization. The main findings from this field experiment were that increasing the number of IPUs from 1 to 12 within tussocks (*i*) did not affect the mass per individual tiller of either vegetative or reproductive tillers, tiller density, or the height of tussocks; but (*ii*) significantly reduced total tiller mass and number within individual IPUs. Total tiller number per tussock and basal area of entire tussocks were lowest when tussocks were constructed with only a single IPU (Fig. 4). This likely occurred because these tussocks initially contained the smallest number of tillers that restricted the subsequent rate of total tiller recruitment and basal area expansion. However, these variables did not differ among tussocks constructed with 4–12 IPUs. Occurrence of intense competition among IPUs within individual tussocks (i.e., intratussock competition) is supported by reduced tiller numbers and total tiller mass per IPU (Fig. 6). In contrast, beneficial effects of resource sharing within IPUs are supported by the absence of a detrimental effect on individual tiller mass or height (Fig. 5).

Negative consequences of competition among IPUs were demonstrated by inverse first order polynomial relationships between tiller number and total tiller mass per IPU and the number of IPUs per tussock for both years (Fig. 6). The explanatory power of these relationships was high ($r^2 > 0.97$). This competition among IPUs, as indicated by the decrease in tiller number and total mass per IPU, increased rapidly from one to four IPUs per tussock. Intratussock competition continued to increase to the maximum number of 12 IPUs per tussock as indicated by the increasing suppression of these variables. Mass per individual tiller of both vegetative and reproductive tillers remained constant within IPUs regardless of the number of IPUs per tussock (Fig. 5). These results imply that cooperation among tillers within IPUs (e.g., Williams and Briske 1991; Derner and Briske 1998) offset, at least partially, the detrimental consequences of competition among IPUs within tussocks, which is between identical tiller genotypes. Competition among IPUs in this species

Fig. 3. Pearson's correlation coefficients of tiller density per tussock with (a) vegetative tiller mass per tussock, (b) vegetative tiller numbers per tussock, (c) reproductive tiller mass per tussock, (d) reproductive tiller numbers per tussock, (e) total tiller mass (vegetative + reproductive) per tussock, and (f) total tiller (vegetative + reproductive) numbers per tussock for constructed tussocks ($n = 80$) of the perennial grass *Schizachyrium scoparium* grown in the field.

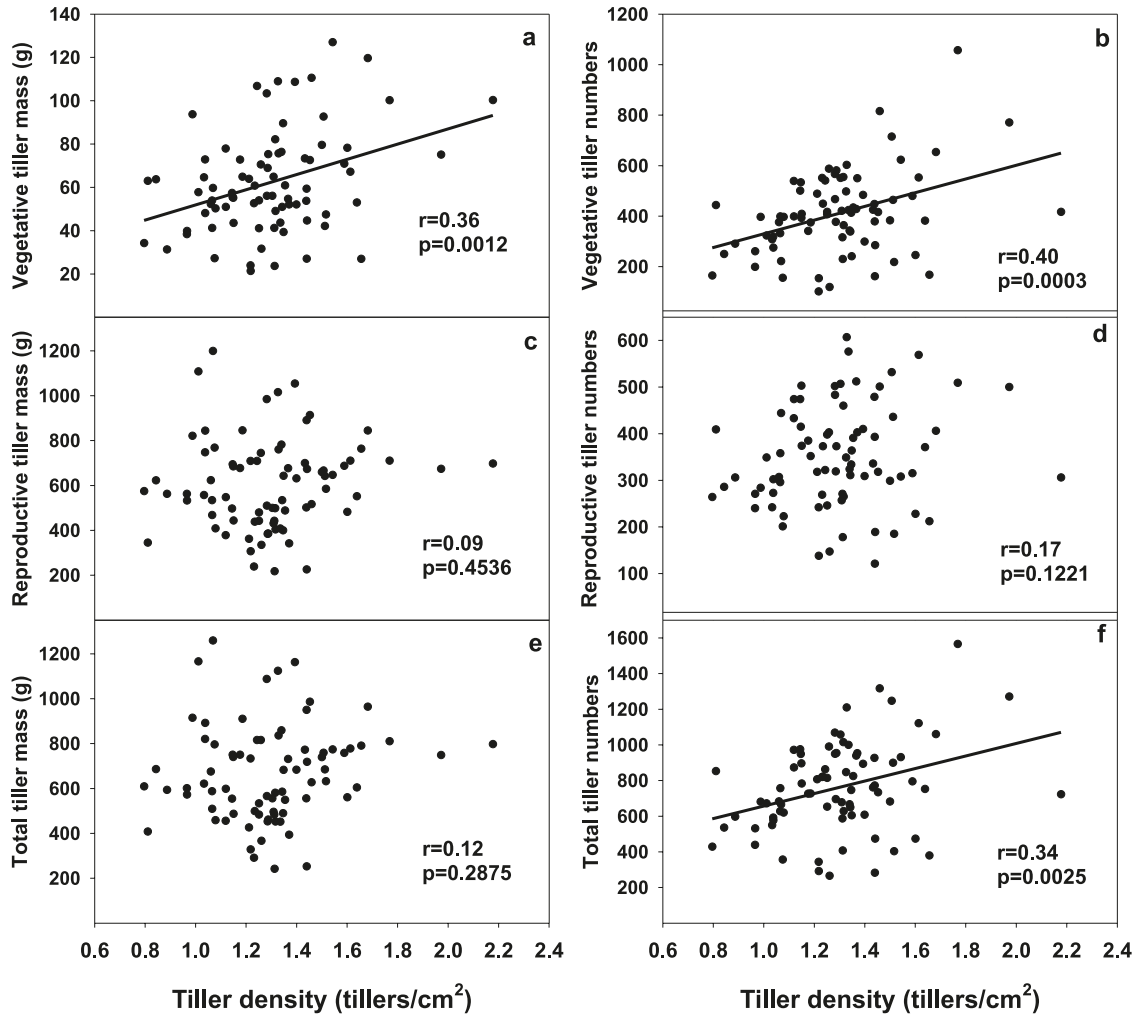
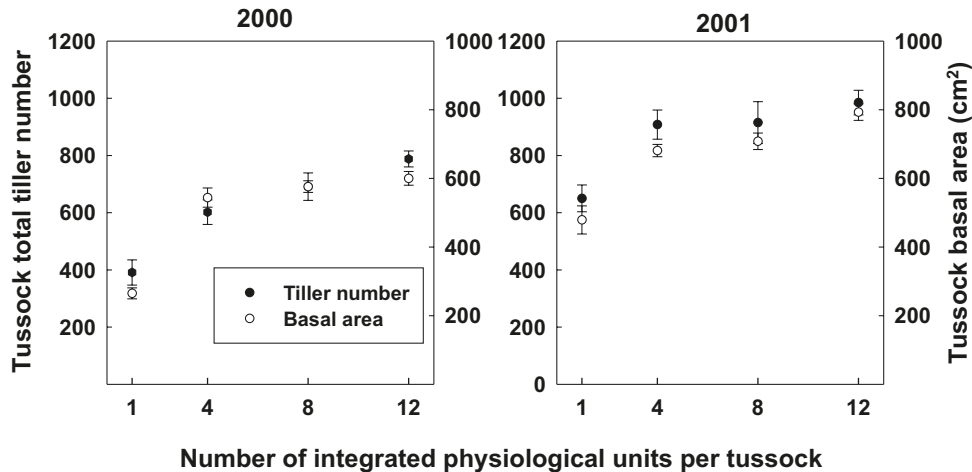


Fig. 4. Mean values (\pm SE, $n = 10$) for total tiller number per tussock and basal area of constructed tussocks of the perennial grass *Schizachyrium scoparium* grown in the field with 1, 4, 8, or 12 integrated physiological units (IPUs) per tussock and destructively harvested in 2000 and 2001. Total tiller number per tussock and basal area were lower with constructed tussocks composed of a single integrated physiological unit, but did not significantly differ as the number of IPUs increased from 4 to 12.



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Fig. 5. Mean values (\pm SE, $n = 10$) for tiller mass of individual vegetative and reproductive tillers of constructed tussocks of the perennial grass *Schizachyrium scoparium* grown in the field with 1, 4, 8, or 12 integrated physiological units (IPUs) per tussock and destructively harvested in 2000 and 2001. The number of IPUs per tussock did not significantly affect either individual vegetative or reproductive tiller mass in 2000 or 2001.

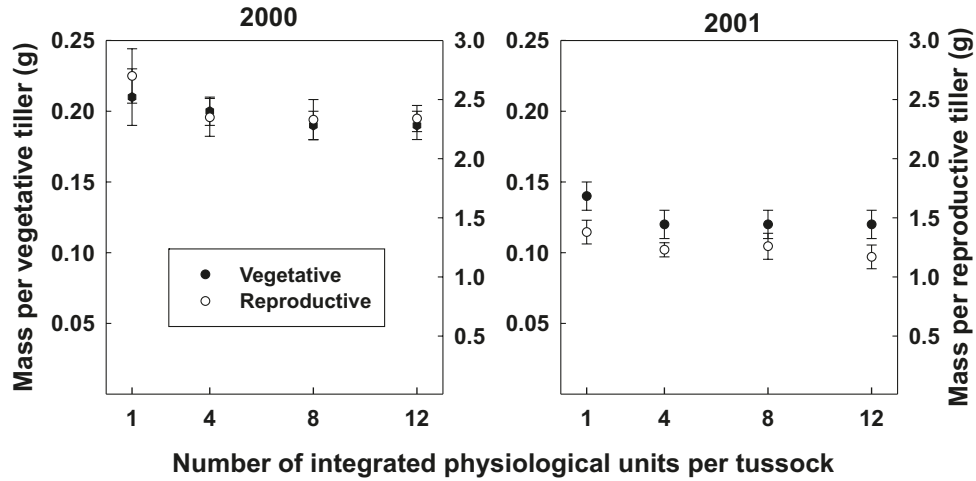
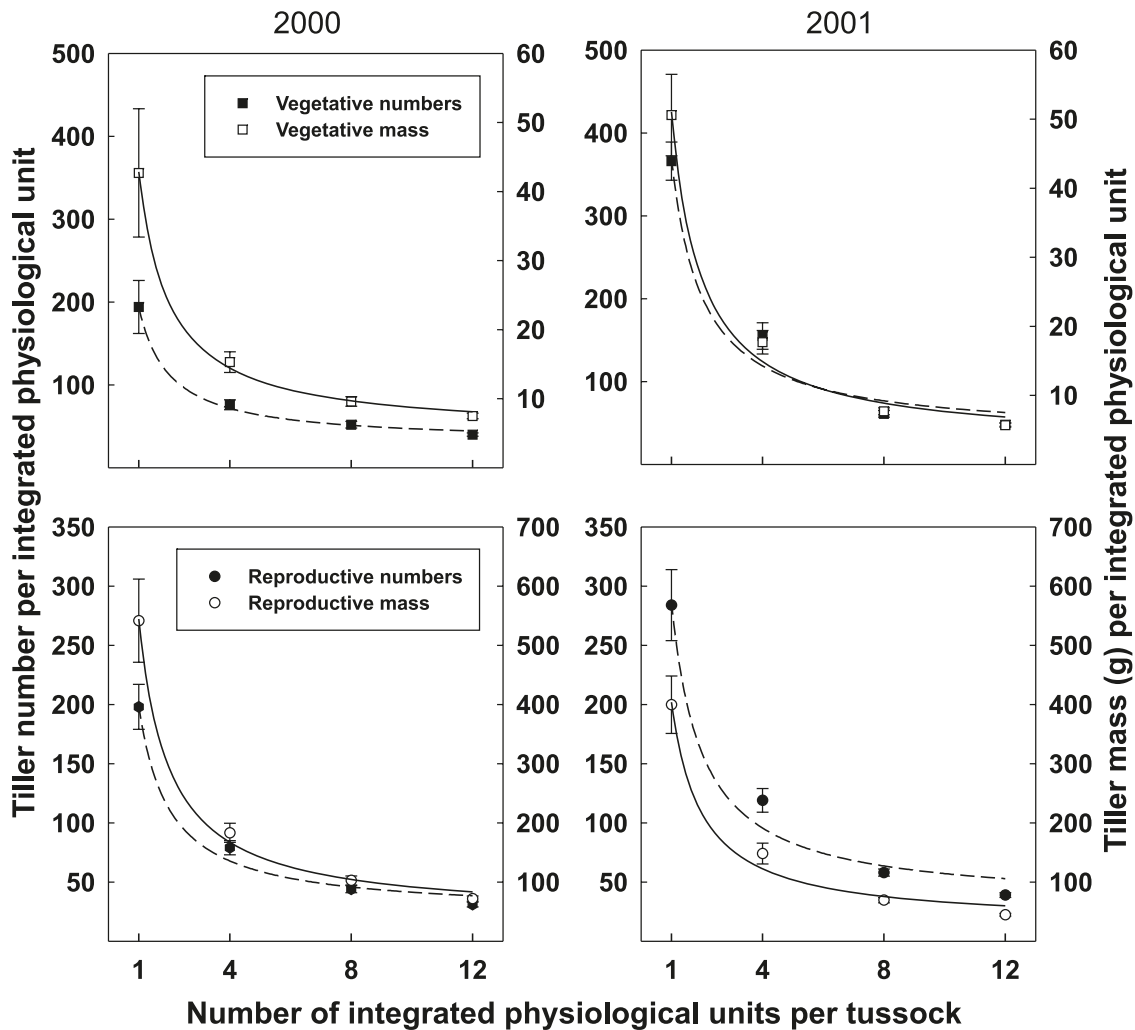


Fig. 6. Relationships of mean (\pm SE, $n = 10$) total tiller number and tiller mass (g) per integrated physiological unit of constructed tussocks of the perennial grass *Schizachyrium scoparium* grown in the field with 1, 4, 8, or 12 integrated physiological units per tussock and destructively harvested in 2000 and 2001. Regression lines shown are all inverse first order polynomial equations and all r^2 values exceed 0.97.



appears to be primarily centered on belowground, rather than aboveground resources. Tiller recruitment and aboveground growth have been shown to exhibit a proportional increase with increasing soil volume, while shading to approximately 50% of ambient radiation did not negatively affect these variables in the same tussock grass (Derner and Briske 1999).

Constant mass of individual vegetative and reproductive tillers over a wide range of IPU's per tussock (Fig. 5) supports the ecological benefit of resource sharing among tillers (i.e., cooperation) within IPU's (Welker et al. 1987, 1991; Bullock et al. 1994; Derner and Briske 1998). These data corroborate previous interpretations that recruitment of new tillers, rather than plasticity of either vegetative or reproductive tiller mass, is the primary mechanism organizing growth of tussock grasses in response to resource variability (Watson et al. 1997; Derner and Briske 1999). Unfortunately, the specific resources and physiological mechanisms contributing to axillary bud activation and tiller recruitment are only partially understood (Cline 1991; Coenen and Lomax 1997; McIntyre 2001; Sachs 2008). Regulation of tiller outgrowth is likely a multivariable process controlled by several interacting physiological and environmental variables within individual tillers, and perhaps IPU's, but not within entire tussocks (Tomlinson and O'Connor 2004; Tomlinson et al. 2007). Physiological integration in this species has been demonstrated to support juvenile tiller establishment by allocating water, nutrients, and photosynthetic carbon from the two older tiller generations to the younger third generation (Welker et al. 1991; Williams and Briske 1991; Derner and Briske 1998). Successful establishment of juvenile tillers is essential to the perennation of individual tussocks and sustainable production of grasslands because individual tillers have a short longevity (<2 years, Briske and Richards 1995) and therefore must be replaced on a near annual basis from axillary buds located near the base of established tillers (Hendrickson and Briske 1997; Dalgleish and Hartnett 2006).

The occurrence of intratussock competition with as few as four IPU's poses the question why do such a large number of physiological units frequently occur in tussock grasses? We observed a maximum of 18 IPU's per tussock (range 5–18; mode 12) in native populations of this species that is near the center of the range (2–35) reported for 24 perennial tussock species in Europe (Wilhelm 1995). An increasing number of IPU's may be an inevitable consequence of basal tussock expansion in this growth form (Gatsuk et al. 1980). Although tiller number per tussock and basal area per tussock increase proportionately to maintain a constant tiller density in the early stages of tussock growth, as was the case in this experiment, tiller recruitment eventually becomes disproportionately higher at the tussock periphery resulting in declining tiller densities in the tussock interior as basal area increases (Briske and Derner 1998; Wikberg and Svensson 2003). At this point, tussocks consist of an assemblage of independent IPU's and further basal expansion will result in the production of additional IPU's. This interpretation suggests that the hollow centers and eventual fragmentation of large tussocks are a consequence of meristematic limitations that restrict tiller recruitment in this region of the tussock rather than due to resource depletion (Wan and Sosebee 2000), or a detrimental consequence of intratussock competition (Gatsuk et al. 1980; Wikberg and Svensson 2003). Alternative bi-

ophysical hypotheses for tussock fragmentation include intense competition for soil water (Sheffer et al. 2007) and interaction with abiotic processes, especially in arid environments (Ravi et al. 2008).

This pattern of tiller organization is indicative of a division of labor characterized by a specialization of function between two distinct levels of tussock organization to form a cooperative system within entire tussocks (Vuorisalo and Hutchings 1996). Tussock expansion associated with an increasing number of IPU's contributes to coarse-scale resource preemption and competitive ability (de Kroon and Schieving 1990), while cooperation among tiller generations within IPU's promotes fine-scale resource acquisition and juvenile tiller establishment and growth. Individual tillers appear to encounter a comparatively consistent competitive background within these tussocks based on the relatively constant tiller density and mass expressed by this species. This suggests that competition among IPU's may be symmetrical due to belowground competition being size symmetric (Bartelheimer et al. 2008), even with heterogeneous soils (Blair 2001), and therefore capable of contributing to size equalization among tillers and the regulation of tiller recruitment within tussocks (Hutchings and Barkham 1976; Ekstam 1995). Intratussock competition among genetically identical IPU's may have provided the selective agent for evolution of effective resource sharing among tillers to increase the success of juvenile tiller establishment and enhance fitness of perennial tussock grasses whereas intraspecific competition between tussocks is likely among unique tiller genotypes.

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