

Phenology of *Carex stricta*: It pays to be tall!

Joy Zedler, Botany Department and Arboretum, University of Wisconsin-Madison

INTRODUCTION

Southern Wisconsin tussock meadows are greatly diminished in area relative to pre-settlement times (Zedler and Potter 2008; Figure 1), and restoration is warranted. The geographically-widespread sedge, *Carex stricta*, is considered a “superplant” for restoring southern Wisconsin’s wet meadows because it is readily grown from both ramets (vegetative propagules) and seeds (Leaflet 22; see arboretum.wisc.edu/leaflets). Young plants can be tailored to different restoration sites by manipulating water and nitrogen (Gallagher 2009). Also, the species is easy to outplant in restoration sites, and canopies rapidly expand to create dense cover (Gallagher 2009, Lawrence and Zedler 2011, Doherty and Zedler 2015).



FIGURE 1.

A wet meadows dominated by *C. stricta* tussocks reveals their distinctive microtopography in winter, after canopies have collapsed but not decayed. This tussock meadow is an unplowed remnant in the University of Wisconsin-Madison Arboretum.

Once established, *C. stricta* provides valued ecosystem services, including carbon storage. Most graminoids store carbon belowground, but tussocks do so both above- and belowground (Lawrence and Zedler 2011, 2013; Lawrence et al. 2013). In seven Wisconsin *C. stricta* meadows, the number of tussocks averaged 4.9/m², with a mean volume of 1160 cm³ and height of 15 cm; tussocks were predominantly organic (74–94% of total dry mass) and composed of leaf bases (46–59%), fine roots (10–31%), and duff (5–13%) (Lawrence and Zedler 2011). Five Upper Midwest remnant tussock meadows had tall (17 cm), large (4,113 cm³) tussocks consisting of up to 95% carbon and comprising 41–62% of total biomass carbon; the tussocks in three reference sedge meadows contained 843–1,697 g C/m² making them second only to soil in C storage (Lawrence and Zedler 2013).

Carex stricta supports biodiversity, including several associates recommended for introduction after the *C. stricta* matrix is well established in restoration sites (Johnston and Zedler 2012). Tussocks add surface area (40% more with 15-25 cm-tall tussocks; Werner and Zedler 2002), provide topographic heterogeneity, and grow early in spring, allowing temporal segregation (Peach and Zedler 2006; this study). Other wetland dominants suppress and exclude subordinate species (Lord and Lee 2001; Werner and Zedler 2002; Peach and Zedler 2006; Frieswyk et al. 2007; Johnston et al. 2008).

With few remnant *C. stricta* meadows, there are limited data on phenology. Does interannual variability exceed that of tussock size? A warm year might increase *C. stricta* growth, but so might a tall tussock. Monitoring and nondestructive sampling were called for. An obvious trait to monitor would be tussock height. However, tussocks accumulate mass slowly, beginning with loosely-organized mats of adventitious roots (apparent within 2 yrs of continuous flooding) leading to dense, solid mass, as found in an 11-yr-old restoration site with 15-20-cm tall tussocks (Lawrence and Zedler 2011, 2013). An early report of 1.2-m-tall tussocks (Costello 1936) does not state whether that was just the pedestal (tussock, herein), or if it included the canopy (plant height, herein). I have seen 50-cm tussocks in mature sedge meadows, but none over a

meter. Estimates from ^{14}C dating indicated that 16-18-cm tall tussocks in three remnant sedge meadows were ~52 years old in the 1960s (peak ^{14}C emissions from atomic bomb tests; Lawrence and Zedler 2013). Tussocks grow too slowly to measure annual rates.

Ramets and leaves are difficult to count, but the tallest leaves can characterize herbaceous wetland plants (Vernescu and Ryser 2009). Maximum leaf length (MLL) on a tussock is easily measured for *C. stricta*, and when the leaves curve, the resulting canopy height can be assessed. Flowering and the abundance of inflorescences are also readily recorded, as are heights of co-existing forb species.

My aim in monitoring *C. stricta* heights and flowering was to track growth over time, relative to forbs, and to compare interannual variation with differences among tall and short tussocks.

METHODS

Several areas with groundwater seepage support *C. stricta* tussock meadows near headwater springs in Dunn Township, Dane County, Wisconsin. One tussock meadow (~0.1 ha) is adjacent to a shallow, 4-m wide, perennial cold-water spring (42.9° N, -89.4° W.) and readily accessible. It receives continuous groundwater discharge (visibly wet soil) of constant temperature (54°F). Rainfall is unnecessary for growth, and there is no watershed to supply surface water runoff. The study site is not pristine as remnants of rusty barbed wire fencing indicate past grazing, probably by cattle.

I established an 8-m-long trail within the tussock meadow and added five short (~1-m) planks to stabilize the wet soil and mark the path. My path connected eight taller *Carex stricta* tussocks and six that were shorter (Figure 2).

I measured tussock height by placing a meter stick vertically on the side away from my path. Nearly every Sunday during 11 growing seasons (late April through early Nov., 2005-2015), I assessed the same 14 tussocks, placing the m stick on top of each, stretching the handful of leaves, and recording the longest leaf (in cm). I counted the number of inflorescences when present, then measured canopy height (to the nearest 5 cm above the pedestal). When a canopy had split (part decumbent, part taller), I recorded both heights and used the average. This aspect of variation was not anticipated and, although uncommon, it and the 5-cm intervals make canopy height an imprecise attribute. As leaves began to senesce, I tried measuring maximum tip necrosis, necrosis of the longest leaf, and then

selected the maximum extent of green leaf tissue as the most repeatable measure, because dry dead tips broke easily. I recorded the identity and height of the tallest forb that was shading a tussock (measuring from the tussock top, as for canopy height).

The dataset generates new hypotheses and quantifies earlier observations, e.g., the temporal shift from sedge dominance in spring toward forbs in fall (Peach and Zedler 2006). I avoided statistical tests, because the path and its 14 tussocks were not chosen randomly. While this limited analysis, it was clear that confining my sample to a single, short transect also confined trampling effects. Weekly walking compressed the organic soil, affected tussock height measurements, and appeared to encourage wildlife to use the same path and bed down on top of some shorter tussocks. As in the Heisenberg principle, I changed the ecosystem by trying to describe it. Random sampling would have spread the damage, but would not eliminate disturbance.

I consulted weather data for Madison (www.usclimate-data.com/climate/madison) to explore variations in mean monthly high and low temperatures and total precipitation, including the last spring snowfall >1 inch. Gorham (1974) suggested that a site's highest monthly mean temperature (in his example, 9-22°C) was a reliable predictor of its productivity, based on 11 *Carex* meadows from 41° to 52° N. Latitude in North America and Europe, with 170 to 1470 g/m² canopy biomass. However, Curtis Prairie's canopy biomass (354 g/m² in August 2008, Doherty and Zedler 2014) and Madison's highest monthly mean temperature of 28°C do not fit Gorham's curve. Still, Gorham's findings suggest that unusually warm or cold air temperatures in March or

FIGURE 2.

Study site in mid-May 2005. The log was a useful landmark after canopy closure obscured the trail.



April months could accelerate vegetative resprouting of *C. stricta*, and unusual weather in April and May could affect flowering. Snowfall >1" continued into April only in 2007 (5.3" on 11Apr) and 2011 (1.3" on 19Apr). Mean monthly minimum temperatures were near normal in both of those years, so there was little evidence to support a late-snowfall effect.

RESULTS AND DISCUSSION

Data are for 294 Sundays (mean 27/yr; range: 19 in 2005 to 37 in 2010), with over 4,000 MLL and 4,000 canopy measures, plus counts of inflorescences in May-June and heights of adjacent forbs into November. Means are presented as \pm standard errors.

Tussock heights. Measures of tussock height were imprecise, because both the soil base and tussock top (with leaves and attached litter) were compressible. The 2005 heights included litter, so I assessed litter in 2012 by measuring tussock height with and without applying moderate pressure with a meter stick. I then recalculated the 2005

tussock heights (mean without litter = 32 ± 5.7 cm). Still, re-measures in 2012 (mean 22 ± 4.6 cm, range 2-45) and 2015 (mean 21 ± 4.4 cm, range 0-42) documented substantial decline since 2005. Two tussocks (T#6, T#11) near the path were no longer present in 2015, following disturbances that included my trampling and probable deer bedding.

I used the average of the 2012 and 2015 measurements (19.8 cm) as a criterion to separate tussocks into two subgroups. Thus, six above-average tussocks (20-42 cm) were considered tall, leaving eight in the short subgroup (Table 1).

The ratio of largest to smallest mean MLL was 1.1, both between height subgroups (Table 1) and years (Table 2). However, the other ratios of trait means were greater for height subgroups than for years: canopy height (1.5 vs. 1.2), flowering tussocks (3.6 vs. 1.8) and total inflorescences (9.7 vs. 3.5). On average, the six tall tussocks produced longer leaves, taller canopies (without considering tussocks, not just when added to tussock heights), and more inflorescences. Just how widely these differences might

TABLE 1.

Attributes of tall vs. short tussocks (data are ranges and means for 6 tall and 8 short tussocks). T = tussock; # = number from south to north along an 8-m path; ht = height; max = maximum; MLL = maximum leaf length; spikes were also noted on 1Nov2015. MLL and canopy heights are summed to yield plant heights only for 2015, when tussock heights were last measured.

Height subgroup	T# from tall to short	Tussock height in 2015 (cm)	Max height of spikes 9Nov2014 (cm)	MLL on 17May 2015 (cm)	MLL in all of 2015 (cm)	Max canopy height 2015 (cm)	Plant ht (tussock + its canopy) (cm)	# yrs a tussock flowered (of 11)	11-yr total inflorescences produced
Tall	9, 7, 13, 12, 3, 2	18-42	2-3	40-60	138-158	65-80	88-115	8-10	53-153
Mean		30.5	2.5	51.3	150.8	71.7	102.2	9.0	102.8
+ s.e.		3.2	0.3	3.5	3.6	2.1	3.7	0.4	17.3
Short	1, 14, 4, 10, 8, 6, 11, 5	0-15	1-3	0-60	0-160	0-65	0-80	0-6	1-41
Mean		8.6	1.7	41.5	113.8	46.6	55.3	2.5	10.6
+ s.e.		2.1	0.2	6.5	18.5	8.0	9.1	0.8	5.1

TABLE 2.

Attributes of *C. stricta* over 11 years of monitoring (n = 14 tussocks). Abbreviations as in Table 1. Grand means (N = 11 yrs) \pm s.e. were: MLL = 137.0 ± 1.3 cm; canopy height (excluding the tussock) = 68.0 ± 1.3 cm; inflorescences per tussock = 6.6 ± 0.4 , and total inflorescences produced annually by all 14 tussocks = 64.7 ± 6.5 .

Attribute	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Mean MLL (cm)	135.1	136.6	136.6	133.7	135.7	138.9	141.2	128.4	142.0	144.2	134.5
Standard error	2.1	3.3	3.3	3.9	3.7	5.3	5.5	5.2	5.1	3.6	6.5
Mean canopy height (cm)	77.1	70.1	66.1	65.0	63.8	64.3	66.6	63.6	68.4	74.2	68.3
Standard error	1.7	1.5	2.8	3.0	1.8	1.7	4.1	3.8	3.4	3.4	3.0
Number that flowered	7	7	9	8	7	8	6	5	5	5	6
Total inflorescences	26	80	63	92	89	69	44	91	48	53	57

be generalized awaits data suitable for statistical analysis. These 14 tussocks support a light-limitation hypothesis, i.e., leaves higher in the canopy absorb light first and produce more biomass. In 2015, tall plants (tall tussocks + tall canopies; mean = 102.2 ± 3.7 cm) averaged 1.8 times taller than short plants (short tussocks + short canopies; mean = 55.3 ± 9.1 cm). Leaves of the shortest plants were often shaded by taller *C. stricta* canopies.

Overwintering spikes. As early as October, tussock tops had produced short, sharp shoots that overwintered and grew early in spring. Their triangular shoot base made them sturdy, and while they were difficult to see, they felt like nails (“spikes” hereafter). Spike MLL was 1-3 cm on 9 November 2014 (Table 1). The spikes often have a white powdery coating that persists when the shoots begin elongating (Figure 3). Overwintering spikes could confer an advantage by responding early to snow melt or warm days. A late frost, however, could override any early-melt advantage. According to Bernard and Solsky (1997) and Bernard et al. (1988), many other *Carex* species also have overwintering spikes, and their high concentrations of N, P, and K, allow an early-growth advantage that leads to flowering. Photographic evidence indicates that *C. stricta* inflorescences can elongate nearly as fast as green shoots (Figure 4). A 2016 study will focus on overwintering shoots and their role in flowering.

Leaf elongation. Despite emerging early in the season, shoots of *C. stricta* grow slowly for the first 6-7 weeks when nights are still cold. Once leaves reach about 25 cm in May, they elongate at a near-linear rate of ~ 15 cm/week, then slow to reach maximum leaf length (grand mean 137 cm) near the summer solstice (Figure 5). Because the leaf tips are often at the bottom of the canopy, their necrosis is understandable. By lifting and measuring leaves to obtain MLL, I likely affected rates of tip necrosis.

The leaves senesced gradually as measured by maximum green leaf (Figure 6). Mean MLL increased from 8 March through 5 July and mean maximum green leaf length decreased from 5 July through 1 November. Often, a single leaf retained some green tissue, so this trait overestimates whole-plant condition.

Mean monthly high and low temperatures identified 2012 as unusually warm throughout the growing season, and 2003 and 2014 had unusually cold weather in March. The mean high temperature for March 2012 was 40.4°F compared to normal (25°F). April was just 2°F above the 57°F norm, but May had the highest mean temperature in 11 years at 51.6°F (norm = 46°F). That year, *C. stricta* shoots exceeded 15 cm MLL on 25 March (one month “ahead of schedule”), and inflorescences were abundant in early April.

This early advantage (early height growth to 15 cm) was lost for the stand as whole, however. Shading by skunk cabbage (*Symplocarpus foetida*) occurred by 20 May when it was the tallest forb with leaves extending to 30-75 cm above nearby short tussocks, including T#11. By June 10, T#11 was reduced to a single stem; later it was covered by *S. foetida*'s large dead leaves. I also caused damage by adding planks that I stepped on weekly, by removing Canada thistle (*Cirsium arvense*) within easy reach, and even by lifting sedge leaves to select and measure the longest ones changed their position relative to adjacent canopies. I blame deer, however, for other damages. I saw browsed leaves on T#10 on 6 May (my only observation of consumption) and a flattened canopy on T#14 on 13 May. On 7 February 2016, I happened to observe four deer romping in my study site; their hoof-prints in recent snow showed that they followed my path and avoided tall tussocks but not necessarily short ones. My direct and indirect impacts could explain tussock height declines from 2005-2015.



FIGURE 3. Whitish-green shoots (here, ~ 10 cm tall) emerge from overwintering spikes (1-3-cm tall) that are easier to feel than see among the tussock-top litter (12 April 2005 photo).



FIGURE 4. On 8 May 2005, black inflorescences were visible on tussocks with mean MLL = 34 cm). An equally tall leaf of reed canary grass (*Phalaris arundinacea*) is also visible, along with its litter from 2004.

Given multiple disturbances, the mean MLL for 2012 (128 cm) was well below the 11-year mean of 137 cm, despite potential for extraordinary growth that year, with the highest mean maximum temperatures of 11 years in June, July and August. Still, a few undisturbed tussocks appear to have experienced a “year effect.” Four tussocks grew leaves >140 cm by 1 July, and growth continued to a record 160 cm. Increased growth under high temperature is consistent with the findings of He and Holaday (2011), who compared *C. stricta* photosynthetic rates with temperature

treatments administered in spring, summer and autumn. Their greenhouse data are relevant; they used seed from my Wisconsin population to grow their experimental plants.

The two “cool years” had below-average March monthly mean high temperatures (2013 = 18.4; 2014 = 18.3; “normal” = 25°F) and below-average monthly mean low temperatures of 34.7°F and 37.4°F, respectively (normal = 43°F). Subsequent months were near normal, yet both years achieved above-average mean MLL (142 and 144, respectively). In 2014, leaves exceeded the grand-mean MLL a

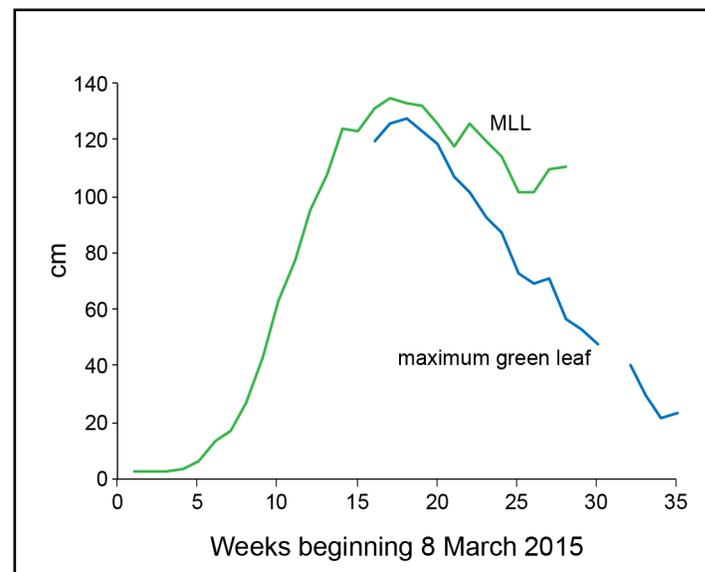
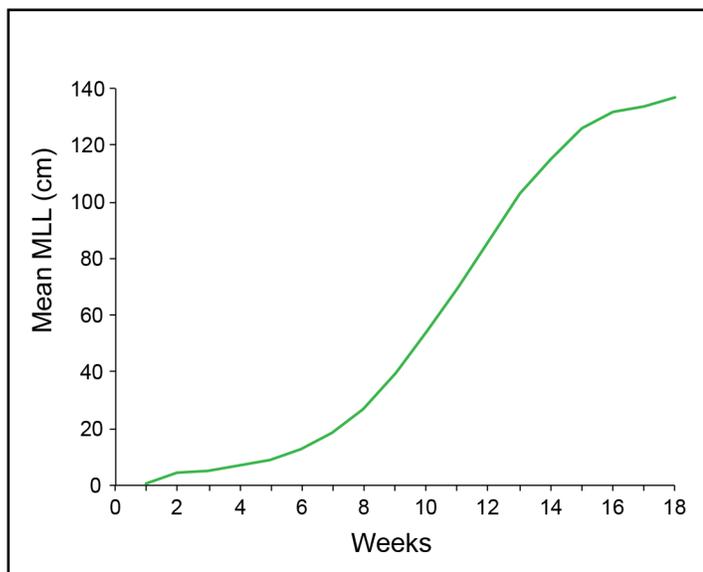


FIGURE 5. Maximum leaf lengths (MLL, in cm, N = 11 years) aligned on their greatest value (mean±s.e. = 137.0±1.3, at week 18). Thereafter, leaf tips experienced necrosis and it became easier to measure maximum green leaf (Figure 6).

FIGURE 6. Data from 2015 show that MLL (including necrotic tips) extends beyond the maximum green leaf tissue on a tussock (lower curve). No green remained on 15 November (T#5 and T#11 were absent in 2015 and T#6 and T#14 lost all live leaves mid-season). Break in curve = no data.

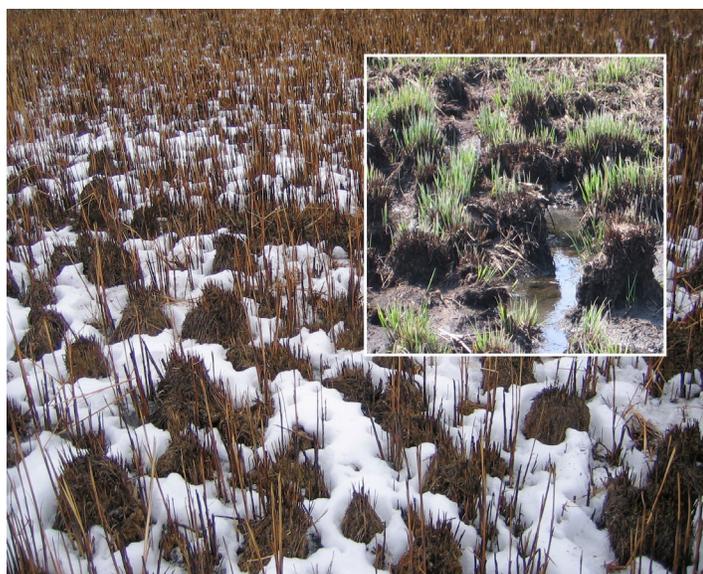


FIGURE 7. Bare black tussocks in Cherokee Marsh in winter 2008 after a controlled burn (to manage shrub invasion) in fall 2007. Inset shows young shoots after snow melt. This sedge meadow is one of Madison’s Conservation Parks (www.cityofmadison.com/parks/cherokeenorth/).

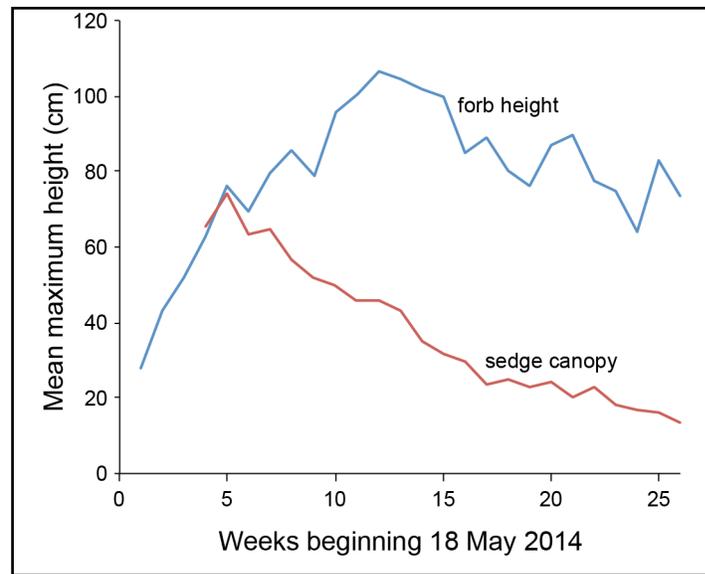


FIGURE 8. Forbs (upper line) overtop the *C. stricta* canopy (lower line) in summer. Sedge data are for 14 tussocks and forb data are for the tallest forb that shaded a tussock (N ≤ 14, since some tussocks were not always shaded by forbs). Plots are heights above tussock tops.

month before their peak MLL, but not in 2013. These early high MLL data were not consistent with warmer temperatures, seen in 2012. Monthly temperature data did not explain high MLLs in cool years.

Inflorescences. *C. stricta* flowered (i.e., produced at least one inflorescence) in May and released seed in June. Flowering occurred in all 11 years, and all but one tussock flowered at least once (Table 2). I counted 712 inflorescences for 14 tussocks over 11 years. On average, a tussock flowered 5.3 times in 11 years and those that flowered averaged of 9.6 ± 1.1 inflorescences per flowering event ($N = 74$) or 4.6 ± 3.1 per year, including zeroes ($N = 154$). The largest number of inflorescences for a single tussock was 38 in 2008; that tussock (#9, in the tall subgroup) skipped two years, then produced 16 and then 34 inflorescences (the 2nd highest number per tussock). Tussock #9 was the top reproducer, based on total inflorescences. The top year for number of flowering tussocks was 2007 with nine plants producing inflorescences—but the top year for the number of inflorescences was 2008 with a total of 92. As observed by Post et al. (2008), not all life history events are equally responsive to environmental variation. Frequency of flowering and inflorescence production were correlated ($R = 0.77$) and both were less predictable than leaf elongation.

Tussock flowering did not display a boom-and-bust pattern; rather, high- and low-production was associated with height subgroups (Table 2). The six tall tussocks produced the most inflorescences over 11 years and flowered most often. Reproductive advantages of a tall tussock should include improved chances of widespread wind pollination and potential for long-range seed dispersal.

Other factors known to correlate with *C. stricta* flowering are hydroperiod and nutrients. In 72 outdoor mesocosms, 91% of 3-yr-old *C. stricta* seedlings produced inflorescences; more were produced under wetter hydroperiods and 40% more when N and P were added (Lawrence & Zedler 2011). In contrast, Costello (1936) stated “Examination of thousands of tussocks over a period of more than six years in the Milwaukee region has yielded comparatively few fruiting specimens. Seedlings of *Carex stricta* were never found during this period.”

C. stricta seeds might be adapted to germinate on dark substrates, which I observed in a small sedge meadow where tussocks were bulldozed to divert agricultural runoff. The bare black soil produced many volunteer seedlings. Also, in trays of seeds given shallow water and full sun, *C. stricta* germinated in black but not white trays. Both of these observations are explained by experimental results that *C. stricta* seeds need high temperatures to germinate (Kettenring and Galatowitsch 2007). The sun’s warming of disturbed, black soil likely stimulates both germination and

seedling growth. The same might be true of fire-scorched tussocks (Figure 7).

Canopy height. Canopies exhibit temporal segregation during the growing season. Canopies measured above the tussock (ignoring differential tussock heights) achieved peak height in July and gradually declined thereafter (Figure 8, lower curve). The seasonal sequence of dominant green cover thus begins with mosses in early spring, at least where there are openings in the litter layer (Figure 3), followed by closure of the sedge canopy in June, and then overtopping of sedges by tall, conspicuous forbs.

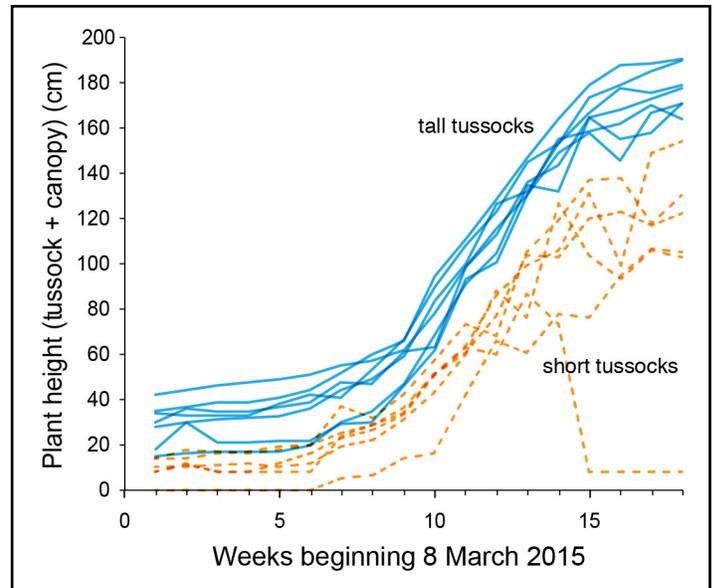


FIGURE 9.

Plant heights (tussocks + canopies) for tall (left) vs short (right) tussocks. In 2015, the intermediate T#1 resembled tall tussocks and is included in the left graph.



FIGURE 10.

Photo of the study on 24 June 2006. The *C. stricta* canopy is continuous and intermittent forbs overtop.

Whole plants (tussocks + canopies). The six tall tussocks were about 0.5-1.3 m apart, and their canopies rarely overlapped. They did, however, shade the shorter plants. The combined *C. stricta* canopies expanded to ~100% cover soon after the summer solstice (Figures 9-10).

Forbs on or near the 14 tussocks. Forbs grew rapidly from late May to over a meter above tussock tops by early July (Figure 10). The most common tall forbs were goldenrod (*Solidago canadensis*) and New England aster (*Symphotrichum novae-angliae*). Usually, an unbranched forb stem with leaves <10 cm long provided <20% cover. Forb stems remained upright through October, either live or as standing dead.

Forb heights increased with stem growth but decreased with several variables, e.g., wilting, heavy dew (as on 24 May 2015), senescence, leaning or breakage, and occasional insect damage. Heights could increase again with short-term recovery or with the appearance of a different forb leaning over a tussock. Although the tussock canopy declined (Figure 7), tall forbs were not likely the cause, because they never cast heavy shade. Instead, the *C. stricta* canopy collapsed as its leaves senesced (maximum green leaf shortened; Figure 5). An exception was *S. foetidus* which has large leaves on upright petioles (Figure 11). In May 2013, its leaves extended to 85 cm tall and overtopped short tussocks (T#4, 5, 10, 11), which “went missing” in 2014. *S. foetidus* leaves sometimes inhibited short, but not tall, tussock sedges.

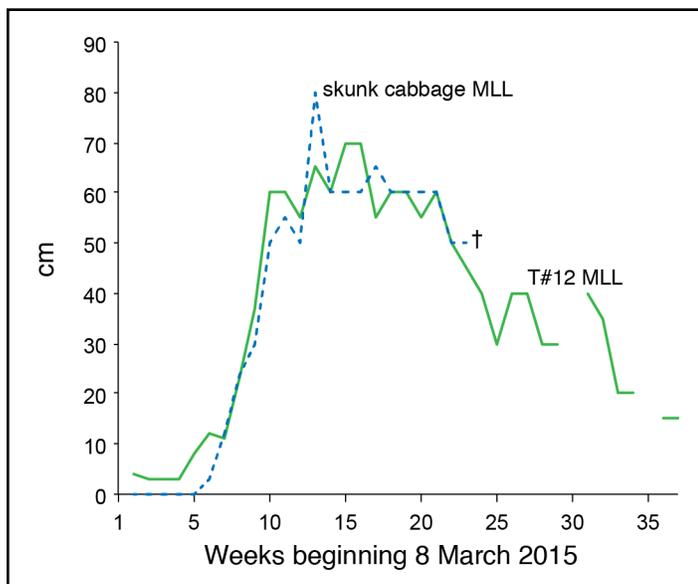


FIGURE 11.

Height in 2015 of the tallest leaf of *Symplocarpus foetidus* that cast significant shade on *C. stricta* T#12 until that leaf senesced (16 August 2014) and collapsed. Both data sets are for heights above the 14-cm *C. stricta* tussock. Figure 2 shows *S. foetidus* among *C. stricta* at the study site in mid-May 2006.

CONCLUSIONS, HYPOTHESES AND RECOMMENDATIONS

The phenology of *C. stricta* was consistent for 14 tussocks over 11 years of weekly monitoring. Shoots overwintered and began elongating in March-April, then lengthened ~16 cm/week from mid-May to mid-June. Leaves > 43 cm long curved and formed a canopy (mean = 64-77 cm) above tussock tops from June 9-24. After the summer solstice, leaves achieved maximum length (grand mean = 137 cm; range = 128-144 cm). Leaves senesced from leaf tips to bases, from mid-May to early November. Dead leaves remained attached to tussocks and persisted through the next growing season. Flowering occurred in late April-May, with seed rain in June. From 2005 through 2015, tussocks that flowered produced 9.6 ± 1.08 inflorescences on average (N = 74).

Results support two hypotheses: H_1 - interannual variation of flowering and canopy heights is less than differences between tall vs. short plants and H_2 - flowering varied more than vegetative traits. Inflorescences ranged from 0-38/tussock, but six tall tussocks (> 22 cm) reproduced the most dependably and produced 11-yr totals of 52-153 inflorescences, while eight shorter tussocks produced 0-41. Six tall tussocks remained tall for 11 years, while shorter tussocks and their canopies were vulnerable to trampling and wildlife, e.g., deer bedding.

It pays to be tall. The advantages likely include greater productivity, ability to shade subordinates, and resistance to being trampled. A positive feedback might be that tall tussocks with long leaves and high canopies accumulate biomass readily, adding height and storing reserves for seed production.

Monitoring can degrade the ecosystems we try to conserve. Further research is needed to identify effects of direct (trampling) and indirect human impacts (creating paths that deer follow). To reduce effects of monitoring, sampling can shift to targeted dates, based on a year of weekly data on overwintering spikes, linear leaf elongation, flowering time, peak canopy height and declining length of green tissue on leaves. Critical times are mid-May (for MLL and # inflorescences per tussock), 2 weeks in mid-June (for MLL to calculate elongation rate) and canopy height in early July and September to document tall forbs.

Further research is needed to quantify overwintering spikes (presence, nutrient content, production of inflorescences), the effects of late-winter frosts on photosynthesis, and local stressors (e.g., frost on tussock tops) as weather becomes more variable. ■

ACKNOWLEDGMENTS

I thank Ralph Tiner for encouraging this submission, and the Town of Dunn, Wisconsin, for protecting tussock meadows using conservation easements on private lands.

REFERENCES

- Bernard, J.M., D. Solander, and J. Kvet. 1988. Production and nutrient dynamics in *Carex* wetlands. *Aquatic Botany* 30: 125-147.
- Bernard, J.M., and B.A. Solsky. 1977. Nutrient cycling in a *Carex lacustris* wetland. *Canadian Journal of Botany* 55: 630-638.
- Costello, D.R. 1936. Tussock meadows in southeastern Wisconsin. *Botanical Gazette* 97: 610-648.
- Doherty, J.M. and J.B. Zedler. 2015. Increasing substrate heterogeneity as a bet-hedging strategy for restoring wetland vegetation. *Restoration Ecology* 23: 15-25. doi: 10.1111/rec.12154
- Doherty, J.M. and J.B. Zedler. 2014. Dominant graminoids support restoration of productivity but not diversity in urban wetlands. *Ecological Engineering* 65:101-111.
- Frieswyk, C.B., C.A. Johnston, and J.B. Zedler. 2007. Identifying and characterizing dominant plants as an indicator of community condition. *Journal of Great Lakes Research* 33- SI3: 125-135.
- Gallagher, S.K. 2009. Use of nitrogen and water treatments to manipulate *Carex stricta* Lam. propagules. MS Thesis, University of Wisconsin-Madison.
- Gorham, E. 1974. The relationship between standing crop in sedge meadows and summer temperature. *Journal of Ecology* 62: 487-491.
- He, Z., L.P. Bentley, and A.S. Holaday. 2011. Greater seasonal carbon gain across a broad temperature range contributes to the invasive potential of *Phalaris arundinacea* (Poaceae; reed canary grass) over the native sedge *Carex stricta* (Cyperaceae). *American Journal of Botany* 98: 1-11.
- Johnston, C.A. and J.B. Zedler. 2012. Identifying preferential associates to initiate restoration plantings. *Restoration Ecology* 20: 764-772.
- Kost, M.A. and D. De Steven. 2000. Plant community responses to prescribed burning in Wisconsin sedge meadows. *Natural Areas Journal* 20: 36-49.
- Kettenring, K.M. and S.M. Galatowitsch. 2007. Temperature requirements for dormancy break and seed germination vary greatly among 14 wetland *Carex* species. *Aquatic Botany* 87: 209-220.
- Lawrence, B.A. and J.B. Zedler. 2011. Formation of tussocks in sedges: effects of hydroperiod and nutrients. *Ecological Applications* 21: 1745-1759.
- Lawrence, B.A. and J.B. Zedler. 2013. Carbon storage by *Carex stricta* tussocks: A restorable ecosystem service? *Wetlands* 33: 483-493.
- Lawrence, B.A., T. Fahey, and J.B. Zedler. 2013. Root dynamics of *Carex stricta*-dominated tussock meadows. *Plant and Soil* 364: 325-339. doi: 10.1007/s11104-012-1360-y
- Lord, L.A. and T.D. Lee. 2001. Interactions of local and regional processes: Species richness in tussock sedge communities. *Ecology* 82: 313-318.
- Middleton, B.A. 2002a. Nonequilibrium dynamics of sedge meadows grazed by cattle in southern Wisconsin: *Plant Ecology* 161: 89-110.
- Middleton, B.A. 2002b. Winter burning and the reduction of *Cornus sericea* in sedge meadows in southern Wisconsin. *Restoration Ecology* 10: 723-730
- Peach, M.A. and J.B. Zedler. 2006. How tussocks structure sedge meadow vegetation. *Wetlands* 26: 322-335.
- Post, E., C. Pedersen, C.C. Wilmers, and M.C. Forchhammer. 2008. Phenological sequences reveal aggregate life history response to climatic warming. *Ecology* 89: 363-370.
- Vernescu, C. and P. Ryser. 2009. Constraints on leaf structural traits in wetland plants. *Am. J. Botany* 96:1068-1074.
- Werner, K.J. and J.B. Zedler. 2002. How sedge meadow soils, microtopography, and vegetation respond to sedimentation. *Wetlands* 22:451-466.
- Zedler, J.B. and K. Potter. 2008. Southern Wisconsin's herbaceous wetlands: Their recent history and precarious future. Pages 193-210 in *The Vanishing Present*. D. Waller and T. Rooney (eds.) University of Chicago Press.