

# Midsummer Standing Crops of Wetland Sedge Meadows Along a Transect from Forest to Prairie

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**ABSTRACT** — Midsummer standing crops of wetland sedges have been measured along a transect from forest to prairie in northwestern Minnesota. The eight forest stands, all but one on waterlogged fibrous peats, are dominated by *Carex lacustris* (4 stands), *C. lasiocarpa* (2), *C. rostrata* (1) and *C. atherodes* (1). They exhibit above-ground standing crops ranging from 425 to 738 g dry wt/m<sup>2</sup>, with a mean of 606 g/m<sup>2</sup>. The five prairie stands on well-drained silty peats are all dominated by *Carex atherodes*, and their standing crops range from 679 to 1248 g dry wt/m<sup>2</sup>, with a mean of 941 g/m<sup>2</sup>. Above-ground standing crop in the prairie sites is therefore 55% greater than in the forest sites.

We have recently begun studies of the standing crop and productivity of wetland sedge meadows, which are widely distributed in north temperate latitudes (Bernard 1973, 1974; Bernard and MacDonald, 1974; Gorham and Somers, 1973; Gorham, 1974), and this paper examines above-ground biomass in midsummer on a 135 km transect from forest to prairie along Highways 200, 71 and 113 in northwestern Minnesota. This vegetation sequence has been the focus for several diverse investigations (e.g., Buell and Cantlon, 1951; Buell and Facey, 1960; Iverson, Seabloom and Hnatiuk, 1967; McAndrews, 1966; Kingsbury, 1970). The eastern forest sites are located in pine-hardwood forest, and grade westward through narrow bands of mesic deciduous forest, oak-aspens forest and oak savanna into prairie (McAndrews, 1966).

Four of the eight sedge meadows in forest sites are dominated by *Carex lacustris* Willd., and one each by *C. rostrata* Stokes, *C. lasiocarpa* Ehrh. and *C. atherodes* Spreng. One has *C. lasiocarpa* codominant with *Scheuchzeria palustris* L., *Eleocharis* sp. and *Dulichium arundinaceum* (L.) Britt. The stands occur generally on fibrous brown peats which were beneath 5-10 cm of water at the time of sampling, except for the mixed stand on a floating mat beneath about 20 cm of water, and the stand of *C. atherodes* where the water-table was 25-30 cm beneath 30 cm of dark brown, sandy and well decayed peat.

All of the five prairie sedge meadows are dominated by *Carex atherodes*, with an appreciable admixture of grasses in three sites and of moss in one site. The stands occupy well decayed and largely amorphous, silty peats, with the water-table more than 25 cm beneath the peat surface.

## Sampling during August

Stands were sampled during 3-8 August, 1973. A linear series of 5 contiguous 25x25cm quadrats (Pearsall and Gorham, 1956) was laid out in the purest part of each sedge stand and where shoot growth and density appeared normal. Shoots were pulled by hand, counted, placed in paper bags, sorted into green and brown components, and air-dried for 5 months at about 20-21°C. Tests of four representative air-

dry samples indicated that 48 hours in a forced-air oven at 80°C led to a loss of 1.60 percent (range 1.52-1.65 percent) in weight; whereas the same period at 105°C led to a loss of 4.80 percent (range 4.53-4.97 percent) of the original air-dry weight.

Newly emergent shoots were rare. Bernard (1975) has observed new shoots of *Carex lacustris* beginning emergence in New York in late July or early August, in a milder climate which may allow earlier emergence than in Minnesota. Flowering shoots were also very scarce in both forest and prairie stands, and at the time of sampling most perigynia had dropped.

## Results

The data are presented in Table 1, which shows that total standing crops are 55 percent higher in the prairie sites, which average 941 g green + brown dry wt/m<sup>2</sup> as compared with 606 g/m<sup>2</sup> in the forest sites. This difference is significant at the 1 percent level. Green material comprises 89 percent of the total in the forest stands and 92 percent in the prairie stands. For those stands in which sedges make up more than 90 percent of total green biomass, the characteristic prairie species *Carex atherodes* averages a standing crop of 862 g green dry wt/m<sup>2</sup>, 78 percent greater than the common forest species *C. lacustris* at 485 g/m<sup>2</sup> (Table 2). The greater biomass for the prairie species is partly owing to greater density and partly to greater shoot weight. *Carex atherodes* exhibits a density of 248 shoots per m<sup>2</sup> as compared with only 189 per m<sup>2</sup> for *C. lacustris*, and a green shoot weight of 3.5 g as compared with 2.6 g. The lowest biomass among the stands dominated by *Carex lacustris* (390 g total dry wt/m<sup>2</sup>) occurs in its most westward site in the zone transitional to prairie, whereas the lowest biomass among the stands dominated by *C. atherodes* (675 g/m<sup>2</sup>) occurs in its most eastward site in the forest zone. There is however a similarly low biomass (679 g/m<sup>2</sup>) in the middle of its range. The smallest shoot weight for the forest species *Carex lacustris* (2.1 g) also occurs in its most westward site at the edge of the prairie. Surprisingly, the two stands of the prairie species *Carex atherodes* which exhibit the lowest shoot weight (2.3 and 2.9 g) are also the most westward. The highest shoot weights (4.7 and 4.8 g) come from nearest the border of the prairie with the transitional zone, where two sloughs exhibit higher salinities (specific conductance 628 and 931 micromhos at 20°C) than do sloughs and ponds either eastward (117-374

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micromhos in seven sites) or westward (157-486 micromhos in three sites).

### Discussion

Table 2, which brings together our North American data with comparable data from southern Sweden (Mörnsjö, 1969), indicates that the green standing crop of *Carex atherodes* in the prairies of northwestern Minnesota (862 g/m<sup>2</sup>) is the second highest yet recorded for this genus, but well below the 1270 g/m<sup>2</sup> recorded for *C. lanuginosa* Michx. in western New York (Bernard and Howick, unpublished). Another notable feature of Table 2 is the wide range of shoot weights exhibited by *Carex lacustris* (2.6 to 5.5 g) and *C. rostrata* (1.0-4.8 g).

Among the fifteen stands recorded in Table 2, there is a marked inverse correlation ( $\log_{10} r = -0.87$ ) between shoot size and shoot number. The solid curve in Fig. 1., drawn as the reduced major axis (Imbrie 1956) because neither variable is dependent, demonstrates a decline in shoot size from 5.25 g dry wt at a density of 150 shoots per m<sup>2</sup> to 0.51 g dry wt at a density of 800 shoots per m<sup>2</sup>. It follows from this relationship that there is a drop in standing crop from 790 g/m<sup>2</sup> at a density of 150 shoots/m<sup>2</sup> to 410 g/m<sup>2</sup> at a density of 800 shoots/m<sup>2</sup>, as shown by the dashed curve in Fig. 1. The les-

ser biomass of the denser stands is probably owing partly to a decline in shoot height with increasing density. Mörnsjö (1969) gives some measurements of mean shoot height, which follow for stands in which *Carex* accounts for at least 90 percent of green biomass: *Carex acuta* L. 144 cm, *C. lacustris* 118 cm, *C. elata* All. 111 cm, *C. lasiocarpa* 98 cm, *C. rostrata* 79 cm, and *C. vesicaria* L. 75 cm. There is a distinct tendency among these species for shoot height to fall with increasing density and to rise with increasing standing crop. If the two species differing most in height (*Carex acuta* and *C. vesicaria*) are compared, then the difference in standing crop is almost matched by the difference in height. However, in no other species comparison can the height difference account for nearly such a large part of the difference in standing crop.

Table 2 does not include estimates of the below-ground material in wetland sedge meadows. However, midsummer data are available for some of the stands. At the end of July in 1972 and 1973 *Carex lacustris* in western New York averaged 43 percent as much dry matter below ground as was harvested green above ground (Bernard and MacDonald, 1974, and Bernard and Howick, unpublished). Also at the end of July, the percentage for *Carex rostrata* in central Minnesota (Bernard, 1974) is 22 percent, and in western New

TABLE I. Midsummer Standing Crops of Sedge Meadows in Northwestern Minnesota

Site No.	Carex Species	Approx. km from Origin <sup>1</sup>	Shoot no/m <sup>2</sup>	Carex shoots			Total standing crop		
				Green dry wt/m <sup>2</sup>	Green dry wt/shoot	% Total green dry wt.	Green % total dry wt.	Green dry wt/m <sup>2</sup>	Total dry $\pm$ S.D. wt/m <sup>2</sup>
FOREST									
1.	<i>C. lacustris</i>	47.0 E	221	672	3.0	100	91	672	738 $\pm$ 277
2.	<i>C. rostrata</i>	15.8 E	195	434	2.2	99.3	85	437	514 $\pm$ 199
3.	<i>C. lacustris</i>	4.2 W	166	363	2.2	93	92	391	425 $\pm$ 134
4.	<i>C. lasiocarpa</i>	9.0 W	992	612	0.62	99.8	83	613	735 $\pm$ 211
5.	<i>C. lasiocarpa</i> <sup>2</sup>	14.6 W	448	221	0.49	40	90	546	604 $\pm$ 174
6.	<i>C. lacustris</i>	19.6 W	150	388	2.6	97	85	402	471 $\pm$ 178
7.	<i>C. atherodes</i>	34.3 W	186	624	3.4	100	92	624	675 $\pm$ 313
8.	<i>C. lacustris</i>	43.0 W	230	636	2.8	99	93	643	689 $\pm$ 354
	Mean						89	541	606
TRANSITION									
		49.6 W							
9.	<i>C. atherodes</i>	50.2 W	266	1060	4.0	99.6	91	1061	1160 $\pm$ 476
10.	<i>C. lacustris</i>	57.8 W	176	364	2.1	100	93	364	390 $\pm$ 166
PRAIRIE									
		59.2 W							
11.	<i>C. atherodes</i> <sup>3</sup>	60.8 W	224	1055	4.7	91	93	1162	1248 $\pm$ 516
12.	<i>C. atherodes</i> <sup>3</sup>	69.7 W	131	624	4.8	72	91	867	950 $\pm$ 349
13.	<i>C. atherodes</i> <sup>3</sup>	73.7 W	134	527	3.9	85	92	622	679 $\pm$ 291
14.	<i>C. atherodes</i>	78.0 W	314	709	2.3	100	89	709	796 $\pm$ 439
15.	<i>C. atherodes</i> <sup>4</sup>	87.9 W	278	797	2.9	82	93	965	1033 $\pm$ 268
	Mean						92	865	941

<sup>1</sup>Origin is the junction of Hwy. 113 with Hwy. 71, SE corner of Itasca State Park

<sup>2</sup>Codominant with *Scheuchzeria palustris*, *Eleocharis* sp. and *Dulichium arundinaceum*.

<sup>3</sup>Other species chiefly grasses.

<sup>4</sup>Other species a pleurocarpous moss.

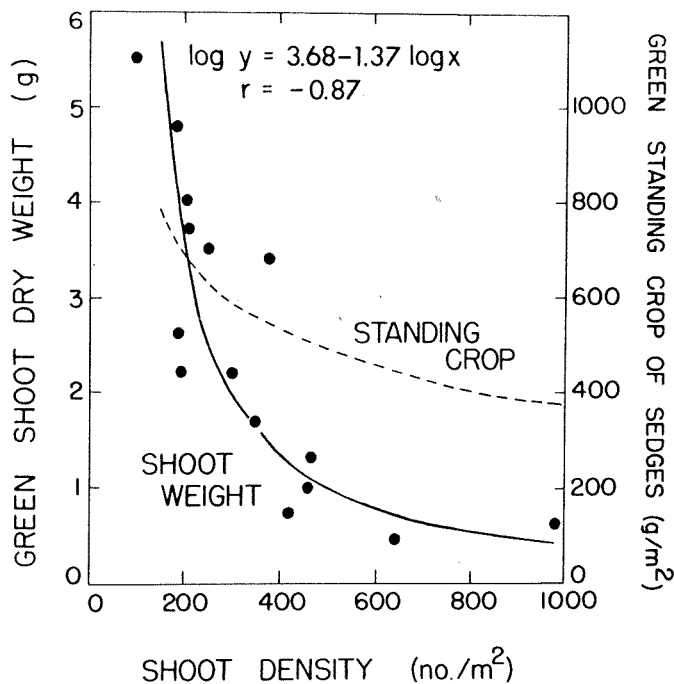


FIGURE 1. — Shoot weights and green standing crops in fifteen stands of eight sedges, in relation to shoot density.

York (Bernard and Howick, unpublished) it is 46 percent. For *Carex lanuginosa* in western New York (Bernard and Howick, unpublished) the percentage at the end of July is 93 percent. For a sparse stand of *Carex lasiocarpa* in a south Swedish fen with a dense mat of *Sphagnum teres* Angstr. (Mörnsjö, 1969) below-ground material is 33 percent of above-ground green standing crop. In contrast, the extremely tussocky *Carex elata* in south Sweden (Mörnsjö, 1969) yields a below-ground biomass in midsummer of 3.8 times the above-ground green biomass.

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#### References

- BERNARD, J. M. 1973. Production Ecology of Wetland Sedges: the Genus *Carex*. *Pol. Arch. Hydrobiol.*, 20.
- BERNARD, J. M. 1974. Seasonal Changes in Standing Crop and Primary Production in a Sedge Wetland and an Adjacent Dry Old-Field in Central Minnesota. *Ecology*, 55.
- BERNARD, J. M. 1975. The life history of shoots of *Carex lacustris* Willd. *Can. J. Bot.*, 53.
- BERNARD, J. M., and MACDONALD, J. G., JR. 1974. Primary Production and Life History of *Carex lacustris* Willd. *Can. J. Bot.*, 52.
- BUELL, M. F., and CANTLON, J. E. 1951. A Study of Two Forest Stands in Minnesota with an Interpretation of the Prairie-Forest Margin. *Ecology*, 32.
- BUELL, M. F., and FACEY, V. 1960. Forest-Prairie Transition West of Itasca Park, Minnesota. *Bull. Torrey Bot. Club*, 87.

- GORHAM, E. 1974. The Relationship between Standing Crop in Sedge Meadows and Summer Temperature. *J. Ecol.*, 62.
- GORHAM, E., and SOMERS, M. G. 1973. Seasonal Changes in the Standing Crop of Two Montane Sedges. *Can. J. Bot.*, 51.
- IMBRIE, J. 1956. Biometrical Methods in the Study of Invertebrate Fossils. *Bull. Amer. Mus. Natur. History*, 108.
- IVERSON, S. L., SEABLOOM, R. W., and HNATIUK, J. M. 1967. Small-Mammal Distribution Across the Prairie-Forest Transition of Minnesota and North Dakota. *Amer. Midl. Nat.*, 78.
- KINGSBURY, P. J. 1970. Calanoid Copepods from the Forest to Prairie Transition in the Itasca Park Region of Minnesota. *Iowa Acad. Sci.*, 77.
- MCANDREWS, J. H. 1966. Postglacial History of Prairie, Savanna, and Forest in Northwestern Minnesota. *Mem. Torrey Bot. Club*, 22.
- MÖRNSJÖ, T. 1969. Studies on Vegetation and Development of a Peatland in Scania, South Sweden. *Opera Botanica*, No. 24.
- PEARSALL, W. H., and GORHAM, E. 1956. Production Ecology I. Standing Crops of Natural Vegetation. *Oikos*, 7.

<i>Carex</i> species	Location	Shoot no/m <sup>2</sup>	Sedge		Total green dry wt/m <sup>2</sup>
			Green dry wt/shoot	Green dry wt/m <sup>2</sup>	
<i>C. lanuginosa</i>	W New York <sup>1</sup>	379	3.4	1270	1283
<i>C. atherodes</i>	N W Minnesota	248	3.5	862	890
<i>C. rostrata</i>	W New York <sup>1</sup>	187	4.8	894	905
	Central Minnesota <sup>2</sup>	204	3.7	750	760
	S W Alberta <sup>3</sup>	301	2.2	669	669
	S Sweden <sup>4</sup>	455	1.0	452	472
	N W Minnesota	195	2.2	435	438
Mean		268	2.4 <sup>6</sup>	640	649
<i>C. acuta</i>	S Sweden <sup>4</sup>	350	1.7	605	635
<i>C. lacustris</i>	W New York 1972 & 1973 <sup>1,5</sup>	203	4.0	829	831
	S Sweden <sup>4</sup>	105	5.5	575	580
	N W Minnesota	189	2.6	485	495
	Mean	166	3.8 <sup>6</sup>	630	635
<i>C. elata</i>	S Sweden <sup>4</sup>	466	1.3	604	616
<i>C. lasiocarpa</i>	N W Minnesota	992	0.62	611	614
	S Sweden <sup>4</sup>	643	0.46	297	313
	Mean	818	0.56 <sup>6</sup>	454	464
<i>C. vesicaria</i>	S Sweden <sup>4</sup>	420	0.69	290	305

<sup>1</sup>Bernard and Howick (unpublished)

<sup>2</sup>Bernard (1974)

<sup>3</sup>Gorham and Somers (1973)

<sup>4</sup>Mörnsjö (1969)

<sup>5</sup>Bernard and MacDonald (1974)

<sup>6</sup>Mean calculated by dividing mean dry weight by mean shoot number.

TABLE 2 — A comparison of four *Carex* species in northwestern Minnesota with species elsewhere (*Carex* ≥ 90 percent total green dry weight).