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ALPINE AND SUBALPINE WETLAND PLANT COMMUNITIES OF THE UINTA MOUNTAINS, UTAH

George M. Briggs¹ and James A. MacMahon²

ABSTRACT.— Seven wetland areas in the subalpine and alpine regions of the Uinta Mountains are described. Most areas have a mosaic vegetation structure, comprised of several patches that are usually sharply demarcated from one another. Each patch has a distinct species composition, usually with only one or two species. Water level is associated with some of the vegetation patterns found in these sites. Standing crop varied from 28 to 360 g/m². Sites show considerable variation in standing crop that could not be explained by elevation differences between sites. Sites with water flowing over them have substantially greater standing crops than sites where water stagnates. Seasonal patterns in shoot density and standing crop indicate one late summer peak in standing crop and little recruitment of shoots over the summer. On stagnant sites, the average stem weight shows a strong relationship to stem density. This pattern did not appear to be caused by thinning mortality and did not follow a "3/2 power law" pattern.

A conspicuous aspect of many of the western North American mountain ranges is their wetlands. The Uinta Mountains of northeastern Utah have an abundance of wetland areas, from the lower elevations (around streams in sagebrush slopes) to areas near springs at high elevations in the alpine zone. The majority of wetlands are found at the heads of glaciated valleys in a zone just above and below treeline. The vegetation in these areas is dominated by members of the Cyperaceae (sedges), as is much of the upland region in the alpine zone of the Uintas. Although both wetland and upland regions are dominated by *Carex* spp., the structure of the two regions is markedly different (Briggs and MacMahon 1982). In this study we describe a variety of sedge-dominated wetlands, detail some of their structural attributes, and discuss some of the factors that we think are important in determining their patterns of occurrence.

STUDY SITES AND METHODS

All sites are in the Uinta Mountains of northeastern Utah (40°45'N, 110°–111°W), the largest east-west trending mountain range in North America. Bedrock throughout the upper elevations of the range is quartzite. The range was heavily glaciated in Pleistocene time (Hansen 1975) and is dominated by numerous large U-shaped valleys ending abruptly in steep-walled cirques.

No attempt was made to describe or catalog all the wetland areas of the Uintas. Instead, we chose to study a variety of wetland regions that varied in their species composition and standing crop. Most of these regions had a patchwork appearance because they were composed of regions (2–100 m²) of distinct species composition, often monotypic, which abruptly gave way to regions of a different species mixture. In sampling these areas, we first made a rough map that demarcated the "patches" found in them. Each

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patch was then sampled by the methods outlined below. We refer to each patch as a site and present figures representing the species composition and standing crop of each of these. The larger units of vegetation (the entire meadow composed of several patches) are not quantitatively described in this paper. Each site was given a two-letter code that represented the area from which it came and a number that indicated the specific patch sampled (e.g., SC-1 is patch 1 in area SC).

The boundaries to each site were subjectively demarcated and a point was picked within the stand. A 20 × 50 cm frame was placed at that point and all vegetation (except bryophytes) was clipped at ground level. Nine additional samples were taken at regular intervals from the first point. These samples were sorted to species in the field, returned to the lab, air dried for at least two months, and oven dried at 40 C for at least 24 h. Sorting to species was quite easy, even when based on vegetative characters, since there were rarely more than two species per sample. For larger species, the number of stems was directly counted and the average weight per stem calculated. For the smaller species, the average weight per stem was determined by weighing three replicates of 100 stems. The total number of stems was obtained by dividing the total weight of that species in the sample by the weight/stem. All sites were sampled in August, when the fruits of the dominant species were mature. Seasonal changes in aboveground standing crop, number of shoots, and number of fruiting shoots were determined in three of the sites by sampling three or four times during the summer. In addition, several individual plants were observed. The length of each leaf and the length and condition of the fruiting culm (if present) were measured at each sampling time.

At each site, soil samples were dug and pH of the soil was determined. All these sites were submerged at least part of the summer, and notes were made of both the length of time the site was submerged and the degree of water movement over the site.

Site Descriptions

Seven wetland areas were mapped and 21 sites were sampled within these areas. Each

wetland area contains between one and five sites. Table 1 lists the dominant species, elevation, and standing crop of all 21 sites. Figure 1 maps the vegetational patterns found in the more complex areas.

The highest wetland found was at an elevation of 3,768 m, in an area adjacent to the steep, rocky talus pile that makes up the northeast side of King's Peak in the east central section of the Uinta range. Springs moisten the site all summer and feed a small stream that traverses the site. Large rocks are scattered throughout. The wetlands of this region consist of a series of small irregularly shaped pools containing 1–10 cm of water at the end of the summer. The emergent vegetation consists solely of *Eriophorum scheuchzeri* Hoppe. These pools were sampled as site ER-1.

To the north of King's Peak lies Henry's Fork Basin. The head of this basin has large expanses of sedge meadows and willow thickets interrupted by upland regions. In spite of a homogeneity in species composition (much of the area is dominated by *Carex aquatilis*), there is considerable variation in stature and standing crop of wet meadows within upper Henry's Fork Basin. We sampled two sites that represent extremes in *Carex aquatilis* meadows. HF-1 is a border to a small (20 m diameter) pond at an elevation of 3,278 m. Vegetation consisted of robust individuals of *Carex aquatilis* and *Caltha leptosepala*. Water stands at least 10 cm deep throughout the year, draining off the site to the north. HF-2 is a very different *Carex aquatilis* region, with a more dense stand of much smaller plants. There is no proximate open water and the ground surface was dry at the end of the summer although the ground was saturated with water at a depth of 2–5 cm.

The remaining five areas are within four miles of Mirror Lake on the west end of the Uintas. Area TL is part of a circular meadow approximately 200 m in diameter. The meadow has a small stream meandering through it and has numerous small "oxbow lakes" and "kettleholes." The vegetation displays a pattern commonly found in moist subalpine meadows of the Uintas: monotypic stands of *Carex aquatilis* and *Eleocharis pauciflora*, areas of *Carex aquatilis* and *Eleocharis pauciflora* mixed, and sections of bare ground, all

surrounded by an upland that has soil with less organic matter and a vegetation of *Carex illota* L. H. Bailey, *Deschampsia cespitosa*, and *Ligusticum filicinum* var. *tenuifolium* (S. Wats.) Mathias & Constance. A large portion of this area has standing water year around. This area was sampled in five sites (Fig. 1).

Areas FT and SE are small meadows in *Picea engelmannii*-dominated forests. The

vegetation in them is similar to that in TL and is mapped in Figure 1. Both areas were sampled as four sites. Area SC is a meadow in a *Picea engelmannii*-*Pinus contorta*-dominated forest. The meadow has a stream flowing through it and is kept moist by two large seepage areas. The vegetation presents a complex patterning, with part of the area exhibiting the mix described at the TL site.

TABLE 1. Elevation, standing crop, and species found on the sites.

Site	Elevation (m)	Standing crop (g/m ²)	Dominant species (> 10 percent standing crop)	Other species
ER	3,768	28	<i>Eriophorum scheuchzeri</i> Hoppe.	None
HF-1	3,278	360	<i>Carex aquatilis</i> Wahl. <i>Caltha leptosepala</i> DC.	None
HF-2	3,278	103	<i>Carex aquatilis</i>	<i>Eleocharis pauciflora</i> (Lightf.) Link, <i>Pedicularis groenlandica</i> Retz.
SE-1	3,260	172	<i>Carex aquatilis</i> <i>Carex canescens</i> L.	None
SE-2	3,260	234	<i>Carex aquatilis</i>	None
SE-3	3,260	264	<i>Carex aquatilis</i>	None
SE-4	3,260	106	<i>Eleocharis pauciflora</i> <i>Carex aquatilis</i>	<i>Pedicularis groenlandica</i>
FT-1	3,256	152	<i>Eleocharis pauciflora</i> <i>Carex aquatilis</i>	<i>Caltha leptosepala</i> , <i>Pedicularis groenlandica</i> , <i>Dodecatheon pulchellum</i> (Ref.) Merrill, <i>Epilobium alpinum</i> L., <i>Agrostis alba</i> L.
FT-2	3,256	104	<i>Carex aquatilis</i>	<i>Eleocharis pauciflora</i>
FT-3	3,256	78	<i>Eleocharis pauciflora</i>	<i>Carex aquatilis</i>
FT-4	3,256	114	<i>Carex illota</i> L. H. Bailey <i>Ligusticum filicinum</i> (S. Wats.) Mathias and Constance	<i>Carex aquatilis</i> , <i>Eleocharis pauciflora</i> , <i>Caltha leptosepala</i> , <i>Pedicularis groenlandica</i> , <i>Veronica wormskjoldii</i> Roem. and Schult.
TL-1	3,110	86	<i>Carex aquatilis</i>	<i>Deschampsia cespitosa</i> (L.) Beauv.
TL-2	3,110	96	<i>Carex illota</i> <i>Deschampsia cespitosa</i>	<i>Eleocharis pauciflora</i> , <i>Caltha leptosepala</i> , <i>Ligusticum filicinum</i> , <i>Pedicularis groenlandica</i> , <i>Veronica wormskjoldii</i>
TL-3	3,110	139	<i>Eleocharis pauciflora</i>	None
TL-4	3,110	97	<i>Carex aquatilis</i> <i>Eleocharis pauciflora</i>	None
TL-5	3,110	92	<i>Carex aquatilis</i>	None
AQ	3,085	141	<i>Carex aquatilis</i>	None
SC-1	3,073	194	<i>Scirpus cespitosus</i> L. <i>Caltha leptosepala</i>	<i>Carex nigricans</i> A. Meyer, <i>Pedicularis groenlandica</i> , <i>Veronica wormskjoldii</i>
SC-2	3,073	109	<i>Scirpus cespitosus</i> <i>Carex aquatilis</i> <i>Eleocharis pauciflora</i>	<i>Caltha leptosepala</i> , <i>Ligusticum filicinum</i> , <i>Pedicularis groenlandica</i> , <i>Veronica wormskjoldii</i>
SC-3	3,073	83	<i>Carex aquatilis</i> <i>Eleocharis pauciflora</i>	None
SC-4	3,073	251	<i>Carex illota</i> <i>Carex rostrata</i> Stokes <i>Carex aquatilis</i> <i>Caltha leptosepala</i>	<i>Agrostis alba</i> , <i>Carex canescens</i> , <i>Ligusticum filicinum</i>

Other parts of the meadow have a dense turf of *Scirpus cespitosus* L. associated with *Carex aquatilis*, *Eleocharis pauciflora*, and *Caltha leptosepala*. A final portion of the meadow

contains a mix of *Carex illota* and *C. aquatilis*. The whole meadow has standing water throughout the year. SC was divided into four sites (Fig. 1).

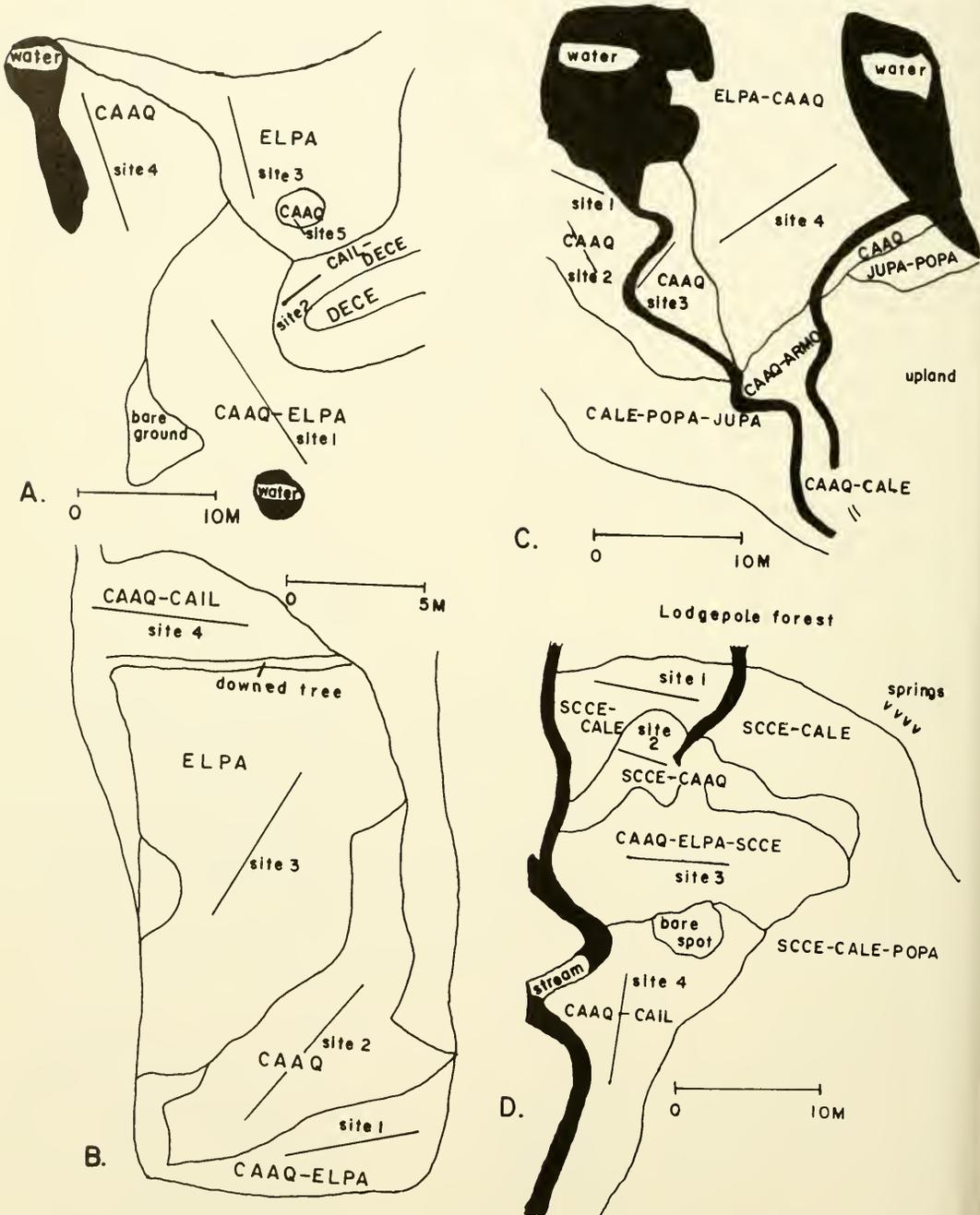


Fig. 1. Maps of four of the wetland areas: A, Area SE. B, Area TL. C, Area SC. D, Area FT. ARMO = *Arnica mollis*, CAAQ = *Carex aquatilis*, CAIL = *Carex illota*, CALE = *Caltha leptosepala*, DECE = *Deschampsia cespitosa*, ELPA = *Eleocharis pauciflora*, JUPA = *Juncus parryi*, POPA = *Poa pratensis*, SCCE = *Scirpus cespitosus*.

Area AQ is on the margin of a small pond that narrows into a stream at one end. It is surrounded by a *Picea engelmannii*-*Pinus contorta*-dominated forest. This area is at least 30 cm under water in the spring. Standing water is present to a depth of 10 cm in the fall. One site was sampled in this area, a region of nearly pure *Carex aquatilis*.

RESULTS AND DISCUSSION

Vegetation

The number of species sampled on each of the 21 sites (Table 1) varied from one to seven. Most of the species present in the wetland sites are common species of the western United States. The *Carex* species collected can be separated, phytogeographically, into two groups: western cordilleran species (*Carex nigricans*, *C. illota*) and circumboreal species (*C. rostrata*, *C. aquatilis*, and *C. canescens*).

One of the striking features of these wetlands is the dominance by plants that are capable of extensive spread by rhizomes. The mosaic structure (Fig. 1) of these communities is a function of the strongly rhizomatous nature of the dominant plants and some, perhaps most, of the "patches" seen represent single plants (genets, Harper 1977) formed by growth from a single propagule. The patterns seen in these wetlands are probably dependent on both the history of propagule arrival and on variations in environmental conditions affecting the success of particular species. A complicating factor results from the "inertia" of these sites—a resistance to vegetational change resulting from both the harsh nature of the climate and the vigorous mode of wetland plant growth. Both these factors could make established vegetation patterns difficult to disrupt. Although seedling establishment is common in some wetlands (Lieffers and Shay 1982), both Costello (1936) and Bernard (1975) noted that seedling establishment was rare in some *Carex* wetlands. Our sites included areas where the dominant was in very poor condition (e.g., HF-2) or had died off completely, leaving areas of bare ground (e.g., part of TL). Both biotic and abiotic factors at these sites may change with time. These changes

will sometimes be to the detriment of the species that has been dominant. But, because of the difficulty in establishing additional species, the dominant may continue to exist in a depauperate condition and may even die back completely before another species is able to invade the area. Thus, the species present today may not reflect present conditions but may represent conditions of an earlier time.

One environmental variable that we found associated with community structure is water level. In TL and FT the *Carex illota* section was always upland relative to the *Carex aquatilis*-*Eleocharis pauciflora* sections. In SC the part of the plot containing *Scirpus cespitosus* was on higher ground than those regions containing *C. aquatilis* and *Eleocharis pauciflora*. Some species distributions could not be associated consistently with water level. *Carex aquatilis* could be found in areas with both more and less standing water than the often adjacent *E. pauciflora* areas (areas TL, FT). *Carex illota*, although usually restricted to areas with no standing water (FT-4, TL-2), sometimes was found in areas 5 cm deep in running water (SC-4).

It is generally thought that the influence of water level in wetland regions is based on variations in waterlogging and aeration. Soil aeration may influence plants either by affecting root respiration (Mendelssohn et al. 1981), which could affect water and nutrient flow through roots, or by affecting soil nutrient status. The influence on soil nutrition can occur directly, by influencing the chemical forms available and their solubilities (Jones 1971, 1972), or indirectly, by affecting soil microbial activity.

The importance of aeration on species distribution is represented in our observations on *Carex illota*, which is intolerant of waterlogged soils if the water is stagnant (and presumably poorly aerated), yet grows quite well under 5 cm of water when it is flowing over the site (and probably better aerated). Further evidence for the importance of aeration in these sites is shown in standing crop data presented below. If aeration does influence the structure of these communities, the complex nature of some of these subalpine sites could be due to underground water flow patterns and resultant aeration patterns. These flow patterns may be due to

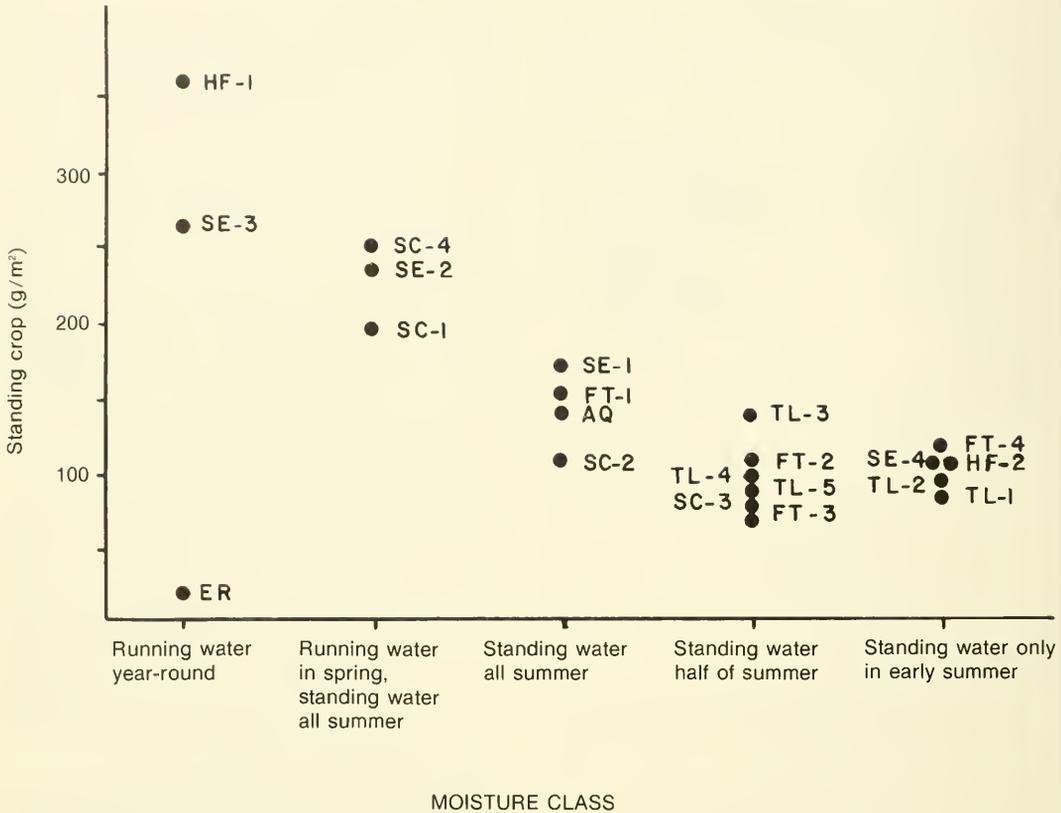


Fig. 2. Graph showing the relationship between standing crop on a site and a measure of water movement over that site.

springs and may not be readily discernable without measurement of soil conditions.

The peak aboveground standing crop values (Table 1) varied considerably, both between areas and also between adjacent sites in one area (e.g., area SC). The very low standing crop value for site ER was undoubtedly due to the short growing season and low temperatures associated with this, the highest site. However, aside from site ER, there is very little relationship between elevation and peak aboveground standing crop. Gorham (1974) derived a regression equation relating standing crop of *Carex* meadows to the highest monthly mean temperature of the year. His data on 11 pure *Carex* stands (on both rich and poor soils) fit the regression line well ($r = 0.84$). The data of Auclair et al. (1976) on wetland stands that were not pure *Carex* also fit this regression. Using weather data for areas in Colorado that are comparable to ours, Gorham's equation predicts a standing

crop of 292 g/m² for a site at 3,109 m (10,200 ft) and 235 g/m² for a site at an elevation of 3,566 m (11,200 ft). The standing crop values that we found are both above and below these values, with most sites below. Gorham's equation is most appropriate for those sites where water is not stagnant (HF-1, SE-2, SE-3, SC-4). The sites with less water movement have less standing crop than predicted by Gorham. The reduced growth on sites where water stagnates is shown in Figure 2, where standing crop is plotted against a gradient in the amount of water movement through the site. Reduced growth on the stagnant sites is probably due to low oxygen levels that may be disturbing root respiration, mineral uptake, or soil nutrient status.

An oxygen-limited situation in *Carex* meadows might explain the timing of nutrient uptake in wetlands. Boyd (1970) and Bernard and Solsky (1977) note considerable

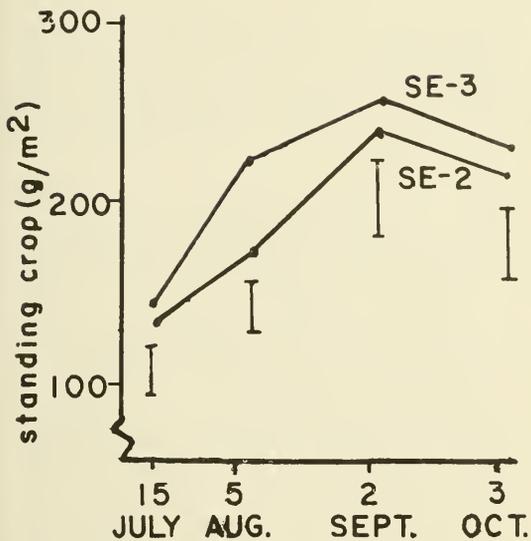


Fig. 3. Seasonal trends in aboveground standing crop for two of the pure *Carex aquatilis* sites, SE-2 and SE-3.

mineral uptake by wetland plants in the early spring. Boyd hypothesized that this early mineral uptake (preceding the growth period) was an adaptation to allow certain species to procure nutrients before other species. Another possible reason for mineral uptake early in the spring could be related to oxygen concentrations. In the early spring, oxygen in wetland soils may be at its highest levels because of well-oxygenated runoff waters and because low temperatures increase the amount of oxygen that water can hold. Thus, plants may take up nutrients in the early spring because that is the most favorable time for root respiration.

In several of the *Carex aquatilis*-dominated sites, we observed the variation in standing crop during the summer. The typical pattern in these subalpine meadows (Fig. 3) includes a single peak in aboveground standing crop which occurs in late summer. Gorham and Somers (1973) and Bernard and MacDonald (1974) also found such a pattern for wetlands composed of *C. aquatilis* and *C. lacustris*, respectively. On our sites there was relatively little new shoot production over the course of the summer (Fig. 4), and the changes in aboveground standing crop were being caused by the growth of individual shoots. Some *Carex* species (e.g., *C. rostrata*) have biannual periods of shoot production and

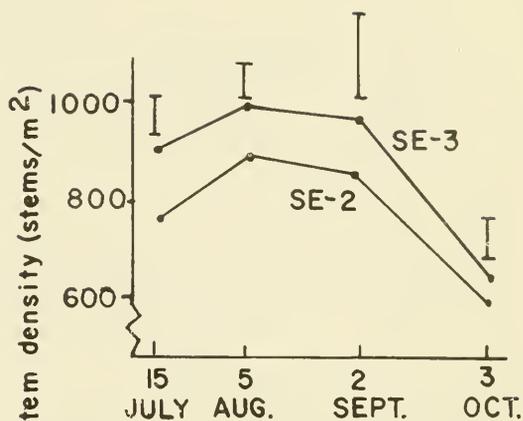


Fig. 4. Seasonal trends in stem density (stems/m²) for *Carex aquatilis* on SE-2 and SE-3.

these may be responsible for bimodal patterns in biomass (Gorham and Somers 1973), although other factors may cause bimodal patterns. The pattern in shoot production that we observed for *C. aquatilis* had been found previously for this species (Gorham and Somers 1973), as well as for *C. lacustris* (Bernard and MacDonald 1974), and would be expected in regions with short growing seasons such as the one we studied.

Based on our observations, the life history of *C. aquatilis* is initiated by growth of a new shoot sometime during the winter or spring. The shoots grow throughout the summer and then overwinter. The following spring the old shoots are distinguishable from shoots of the current year by their large size and old leaves. One or two of these old leaves may undergo additional growth in the spring. At least some and possibly all of the shoots undergo two or possibly more seasons of growth before they flower or die. Many shoots may not flower. Floral initiation is evident very early in the spring; floral parts are visible less than two weeks after growth initiation. During the growing season leaves are initiated, grow quickly to a maximum length, and remain green until early September.

There was considerable variation in plant density in the *C. aquatilis* stands. On the stagnant sites (those where water was not flowing), the variation in density was related to stem weight. If a plot is made of the natural logarithm of plant density vs. the natural logarithm of plant weight (Fig. 5), it can be seen that the stagnant sites fall on a line

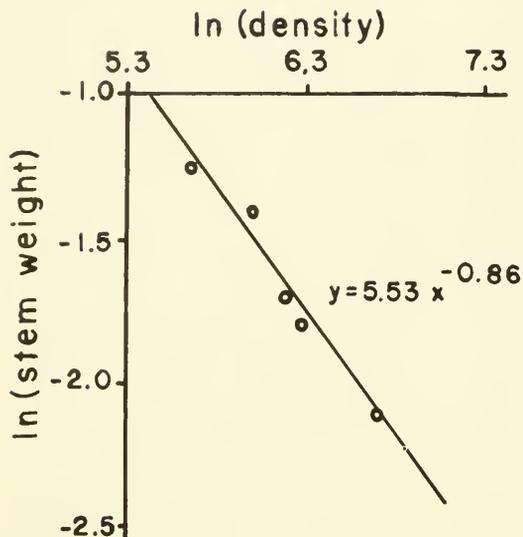


Fig. 5. Graph showing the relationship between stem density and average stem weight for five *Carex aquatilis* stands where water was stagnant.

($r^2 = 0.98$). Sites with flowing water do not fall on this line and have substantially greater plant weights at a particular density than those on stagnant sites. The regression line of Figure 5 describes the following equation:

$$[1] \quad w = 5.53\rho^{-0.86}$$

where w = individual plant weight; ρ = plant density

The form of this equation is characteristic of monotypic stands and an exponential value of $-3/2$ has been found for a wide variety of species of differing life forms and habitats (Gorham 1979, White 1981). The equation has been labeled the "3/2's thinning law" because it describes the changes in density and plant weight that occur in stands during self-thinning. On our plots it is likely that the pattern of density and plant weight is not being caused by mortality (thinning) but rather by recruitment (see Fig. 4). Gorham (1979) cites studies with uncrowded conditions, and therefore little self-thinning, where the exponent value in equation (1) is closer to -1 . Our stagnant sites appear to be similar areas. With an exponent of -1 , standing crop ($w \cdot \rho$) remains constant regardless of density. Such sites may represent areas where standing crop is limited by factors (such as fertility?) that prevent densities to reach levels

where self-thinning in the typical 3/2's fashion can occur. The precise factors that dictate the 3/2's thinning law are still not elucidated (White 1981). Perhaps studies on such areas as these, where the "law" does not hold, may help to clear up the problem.

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