Seasonal control over allocation to reproduction in a tussock-forming and a rhizomatous species of *Eriophorum* in central Alaska

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Summary. The evergreen tussock-forming *Eriophorum vaginatum* revealed consistently earlier (c. 1 month) phenology and greater biomass per tiller than the summergreen rhizomatous *E. scheuchzeri* in all four components measured (vegetative and reproductive shoots and stems) under the same climatic regime in central Alaska over one growing season. Greatest allocation to vegetative shoot growth occurred in mid-summer in both species. The tussock growth form of *E. vaginatum* raised shoot meristems 25-30 cm above the soil surface, where temperatures were warmer, permitting shoot growth to begin earlier in spring and continue longer in autumn than in *E. scheuchzeri*. Consequently, *E. vaginatum* was able to allocate reserves to reproductive tillers primarily in autumn and early spring, times when minimal reserves were required for vegetative growth. By contrast, the rhizomatous *E. scheuchzeri* had a more constrained growing season, and allocation to reproduction coincided with allocation to vegetative growth. For this reason, reserves were drawn down more fully in mid-summer in *E. scheuchzeri* than in *E. vaginatum*. The more conservative use of nutrient stores in *E. vaginatum* may relate to its great longevity, reduced allocation to reproduction (including low seedling recruitment), and relatively stable habitats. The mid-seasonal pulse of allocation to reproduction in *E. scheuchzeri* appears viable only in relatively fertile disturbed sites, where the soil nutrient supply is sufficient to support simultaneous allocation to vegetative growth and reproduction.

Key words: *Eriophorum vaginatum* – *E. scheuchzeri* – Growth – Flowering – Phenology

Recent studies have demonstrated that there is much greater reproductive allocation in arctic tundra species (e.g., Chester and Shaver 1982) than was previously thought (Bliss 1962; Billings and Mooney 1968). However, nothing is known about the reserve requirements for reproduction in arctic plants. Control over reproduction seems particularly complex in those clonal species where both vegetative and reproductive ramets are physiologically attached (Mattheis et al. 1976). There have been many experimental studies examining the effects of defoliation and severing of inter-

ramet connections (e.g., Hartnett and Bazzaz 1983; Welker et al. 1985; Slade and Hutchings 1987). However, we are not aware of any study that follows the detailed seasonal patterns of reserves in interconnected vegetative and reproductive ramets. Such studies are important in understanding the basis of physiological integration in clonal species (Hartnett and Bazzaz 1983).

This study was undertaken to examine the role that reserve stores play in supporting reproduction in two strongly clonal, widespread species of the cotton sedge genus, *Eriophorum*, with contrasting life forms, ecological roles and allocations to reproduction. The evergreen tussock-forming *E. vaginatum* L. characterizes nutrient-poor permanently wet mostly stable habitats – muskegs and moist tussock tundra of the low arctic (Bliss 1981), which it dominates extensively throughout the circumboreal region (Sjors 1965; Britton 1966; Hulten 1968; Polozova 1979; Wein 1973; Wein and Bliss 1974). By contrast, *E. scheuchzeri* is a summergreen, strongly rhizomatous species which, although circumboreal in permanently wet often peaty sites (Raup 1965; Crawford 1983), is often more restricted to areas of recent disturbance (Webber and Ives 1978) that often contain mineral as distinct from largely organic soil.

A comparative ecological study of the two species on nearby representative sites in central Alaska examined their respective phenologies and allocations of biomass, energy and certain macronutrients to vegetative and reproductive components in an attempt to understand the basis for their contrasting habitat-strategy relationships.

Methods

Sites

The study population of *E. vaginatum* ssp. *spissum* (Fern.) Hult. in the muskeg adjacent to Smith Lake (c. 160 m elevation; 64° 48′ N; 148° W), close to the University of Alaska is characterized by permafrost, a thick organic mat and a high water table (Kummerow et al. 1983). At approximately two-week intervals throughout the 1983 growing season, depth of the active layer was measured between tussocks at 5 points. Using a thermister, temperature was measured at 5 cm (vertical) intervals within the caudex of a marked tussock, at 5, 10, and 15 cm below ground level beneath the tussock, and at 10 cm below ground level in

the intertussock area. Ambient air temperature was measured at 1.2 m in the shade.

A small population of *E. scheuchzeri* growing on mineral soil in a damp roadside ditch along the Steese Highway was studied 30 km north of Fairbanks at *c.* 360 m elevation adjacent to the Washington Creek black spruce ecosystem study site (Van Cleve et al. 1986). Air and soil temperatures were measured at three depths (-3, -5, -10 cm) at each time of sampling.

Growth and development

In each of six full-sized tussocks of *E. vaginatum* at the Smith Lake muskeg, five mature vegetative tillers were randomly selected near the center of the tussock crown and identified with small jewellers' labels in early-May 1983. Flowering tillers, being obvious at this time, were avoided. Total and green-leaf lengths were measured on all leaves of each monitored tiller, as described in Mark (1965). The outermost dead leaves were cut to a common base level, to serve as a reference, at the time of the first measurement, soon after the season's growth had begun. Each of the measured leaves was identified by severing its dead tip so that newly emerged leaves could be recognized and measured as they appeared. The seasonal patterns of leaf elongation and new leaf emergence were obtained with twice-monthly measurements until late September by which time growth had ceased.

For *E. scheuchzeri*, five tillers were randomly selected from each of six separate clones and were labelled, as for *E. vaginatum*, on May 11, soon after new-season's leaves emerged from the soil. Tillers and leaves were identified as for *E. vaginatum*, but since all leaves were elongating, a small plastic toothpick, firmly inserted into the soil alongside the emerging tiller, served as a basal reference for measuring elongation of each leaf in the tiller. Measurements were usually made within one day of those in *E. vaginatum* at the muskeg site. When culm elongation in some *E. scheuchzeri* tillers in early-June signalled inflorescence development, other vegetative tillers were substituted for them to maintain a constant sample size for phenological measurements of vegetative tillers. Measurements continued until leaf growth ceased and die-back was completed in late-September.

Information on flowering phenology and material for carbohydrate and nutrient analyses were obtained from the *E. vaginatum* population by removing about one-tenth of a tussock as a wedge from each of five tussocks adjacent to those being measured and selected at random from among those that had at least 10 inflorescences. No tussock was sampled more than once. The stage of development was noted in 10 inflorescences from each sampled plant, and both culm length and panicle width were measured. These parts, with attached leaves, were retained as one component (reproductive shoot), together with the basal stem sections (reproductive stems), which were separated from them. Twenty vegetative tillers were also removed from each sampled plant and separated into live leaf including sheath (i.e., vegetative shoot) and stem (vegetative stem). These four components from each tussock were freeze-dried for at least 48 h, weighed, ground to 0.5 mm in a Wiley mill, and refrigerated until analysed.

Comparable material of *E. scheuchzeri* was obtained by excavating a 20 × 20 cm turf from the periphery of each study clone at the time of sampling. The stage of inflorescence development was noted and culm and panicle dimensions measured in 10 inflorescences from each sample. These were retained (as reproductive shoots) for future analyses, as were samples of vegetative shoots (live leaves including sheaths) and their associated buried rhizomatous stems. The rhizomes were separated into two groups, vegetative and reproductive stems, based on their association with either vegetative or flowering tillers. The four components were rinsed in distilled water, freeze dried, weighed, ground, refrigerated and analysed as for *E. vaginatum*.

Chemical analyses

Determinations of carbohydrate (sugars and starch), phosphate (inorganic, soluble organic and total) and nitrogen (cold-soluble and total) were conducted on the ground material according to the procedures described by Kedrowski (1983). The values were assessed in terms of both concentrations (% dry weight) and pool sizes based on the mean dry weights of the respective components.

Statistical analyses

Biomass values for each of four components (vegetative shoots and stems plus reproductive shoots and stems) for each species, together with values for each chemical compound in each component, were analysed for each species singly as well as comparatively (ANOVA, Duncan's New Multiple Range Test), using the Teddybear computer program (Wilson 1979) so as to provide interspecific comparisons throughout the growing season. Analyses were performed on both raw an $\log_e$ – transformed data for biomass values and pool sizes of the various chemicals, and with arcsine transformations for concentrations. With the reproductive components, separate analyses were made to compare the species on the basis of standard calendar time as well as on phenological time – here the periods were adjusted so that the reproductive phenologies of the two species coincided.

Terminology

Use of the term rhizome to describe the underground stems of *E. scheuchzeri* is appropriate, but it is inaccurate to apply the term to the stems of *E. vaginatum* which are situated in the crown of a caudex and elevated 9–32 cm above the ground surface according to site (Mark et al. 1985). Nevertheless, much of the ecological literature on *E. vaginatum* refers to its currently active stems not only as rhizomes but even as below-ground components (Wein and Bliss 1974; Chapin et al. 1979). Rhizomes are generally defined as "more or less horizontal underground stems " (Raven et al. 1986). The caudex or trunk, of *E. vaginatum*, consists of the dead proximal regions of tillers, including their leaf bases, plus several seasons' complements of annually produced adventitious roots (Chapin et al. 1979). This is more appropriately interpreted as an above-ground component, together with the currently active stems which surmount it, reserving the term rhizome for truly below-ground stems as occur in *E. scheuchzeri*. The relevance of this distinction to the comparative ecology of these two species of *Eriophorum* will be discussed later, in the light of results from this study. The term tiller refers to a combined shoot-stem unit of both species.
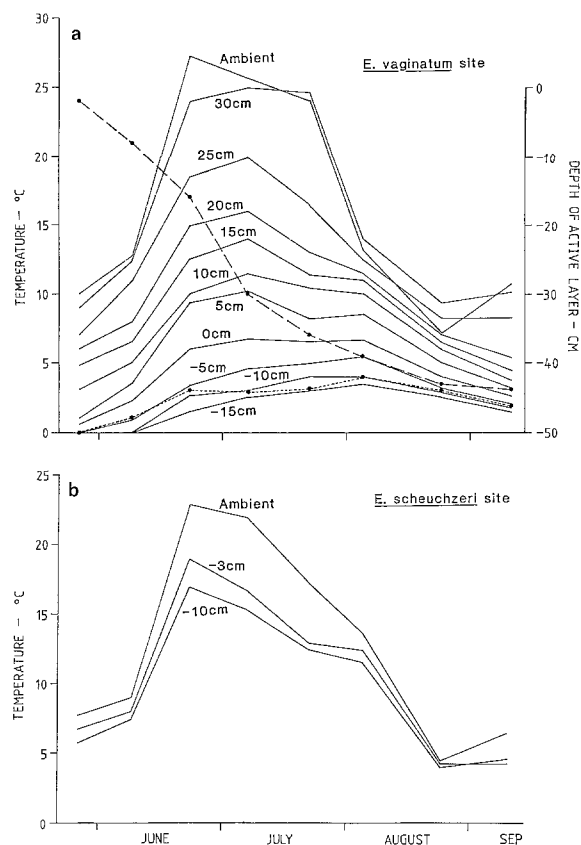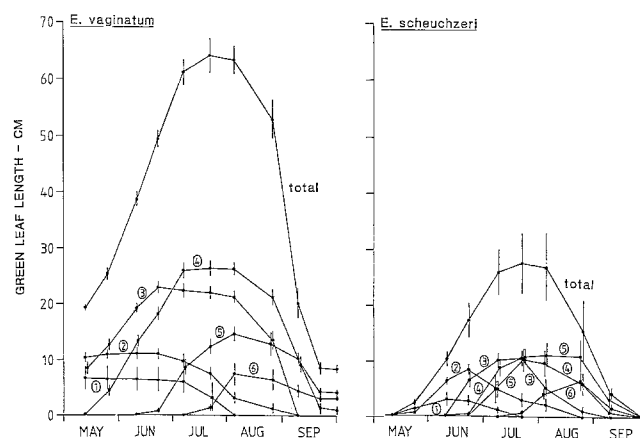
Fig. 1. a Temperatures recorded periodically within (30 cm to ground level) and beneath (−5, −10, −15 cm) a tussock of *Eriophorum vaginatum* throughout the 1983 growing season (*solid lines*) together with simultaneous values for ambient air and at 10 cm depth in the intertussock area (*dotted line*). Depth of the active layer of thawed soil (*dashed line*) is also shown. b Comparable values for two soil depths plus ambient air at the *E. scheuchzeri* site

Fig. 2. Seasonal pattern of leaf emergence and of mean length of green leaf for each cohort (numbered 1 to 6 in order of emergence) and for total leaves in a tiller in two species of *Eriophorum*. Data are means ± SE; $n = 30$

Results

Temperature

Soils at depths of 0 to −10 cm warmed more rapidly and to a higher temperature (by c. 10° C) at the *E. scheuchzeri* site than at the *E. vaginatum* site, despite somewhat lower ambient air temperatures at the former site (Fig. 1). The depth of the active layer (i.e., depth of thawed soil) between tussocks of *E. vaginatum* advanced steadily from −2 cm on 24 May to −44 cm on 9 September. Permafrost was absent from the *E. scheuchzeri* site. Despite lower soil temperatures at the *E. vaginatum* site, there was a pronounced vertical temperature gradient within the tussock caudex, so that the crown of the tussock close to the meristematic region experienced temperatures within 3° C of the ambient air. These temperatures were considerably higher than those of the meristematic regions of *E. scheuchzeri* plants at −3 cm. Moreover, meristem temperatures in excess of 10° C prevailed for about 80 days in *E. vaginatum* (1 June–13 August) but for only about 65 days (11 June–13 August) in *E. scheuchzeri* (Fig. 1).

The 1983 study season was warmer than the long-term average in early- to mid-summer, accumulating 15% more degree-days (1230 degree-days, 5° C base) than the 30-yr mean (1070 degree-days). Thus, it is likely that in normal summers the periods above 10° C would be shorter than we recorded in 1983.

Phenology and biomass

Both species of *Eriophorum* exhibited a sequential pattern of leaf production, with the oldest leaf cohorts beginning to senesce in mid- to late-June and the youngest ones, initiated in July, senescing in early- to mid-August (Fig. 2). At the time of maximum total leaf length (late-July in both species), leaf length was twice as great in *E. vaginatum* as in *E. scheuchzeri*. *E. scheuchzeri* differed from *E. vaginatum* in that no green leaves were present at snow melt, and all leaves senesced by late-September. In *E. vaginatum*, by contrast, all green leaves initiated during the growing season retained green basal portions in late-September (Fig. 2) and throughout the winter (data not shown).

Floral phenology differed strikingly between the two species (Fig. 3). At the first sampling in mid-May, shortly after snow melt, both the culms and panicles of *E. vaginatum* were about half their mature sizes; they had been initiated and made substantial growth during the previous summer. By contrast, culms and panicles of *E. scheuchzeri* remained below ground until June. No floral initials were seen in *E. scheuchzeri* in late summer up to the time of final seasonal sampling on 30 September. Full size of both culms and panicles was achieved by mid-June in *E. vaginatum* but not until late-July – early-August in *E. scheuchzeri*, by which time the former had initiated the following season's inflorescences. Moreover, anthesis was virtually complete in *E. vaginatum* by mid-May, whereas in *E. scheuchzeri* it occurred between 10 June and 6 July. Similarly, shedding of seeds began about one month later in *E. scheuchzeri* (20 July) than in *E. vaginatum* (22 June).

As with leaf production, the seasonal patterns of shoot and stem biomass of vegetative tillers were similar between the two *Eriophorum* species, reaching maximum values in early-August (Fig. 4). In *E. vaginatum*, reproductive shoots were losing biomass in midsummer at the same time that vegetative shoots were growing most rapidly. In *E. scheuchzeri*, by contrast, vegetative and reproductive shoots reached peak biomass at the same time, suggesting a greater potential competition for stored reserves between vegetative and reproductive shoots in *E. scheuchzeri*.
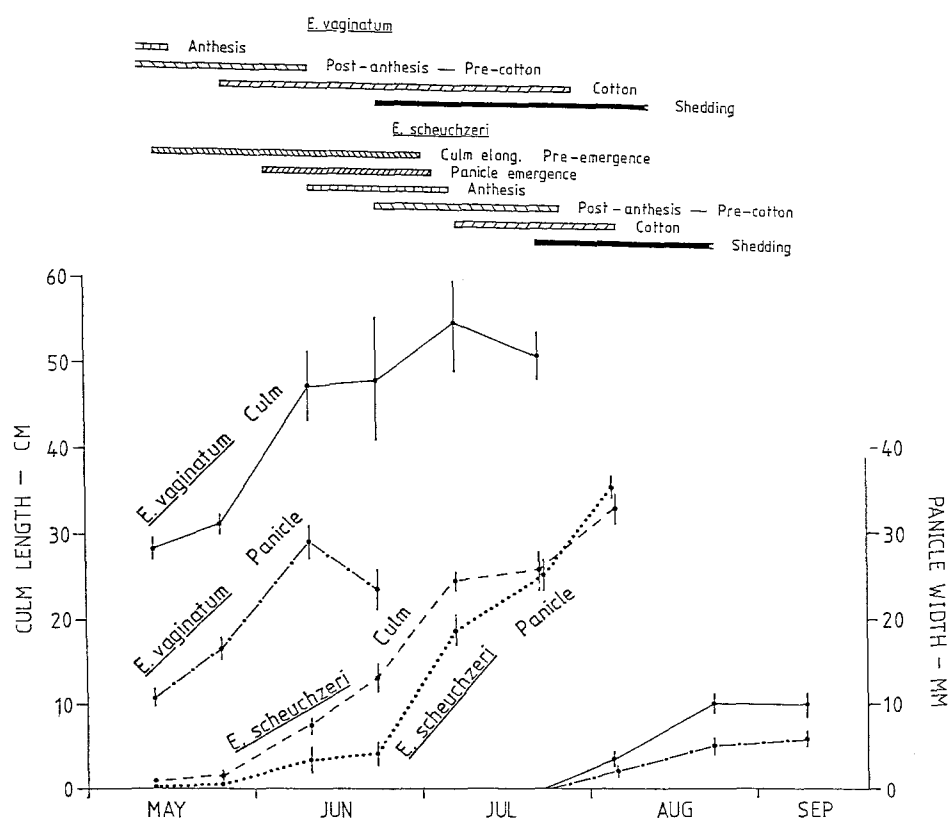
Fig. 3. Patterns of floral phenology and dimensions of panicles and culms in two species of *Eriophorum* through the 1983 season. Note, culm and panicle development in *E. vaginatum* is spread over two seasons, whereas in *E. scheuchzeri* it is completed during a single season. Data are means of ten measurements from each of five plants, ±S.E.
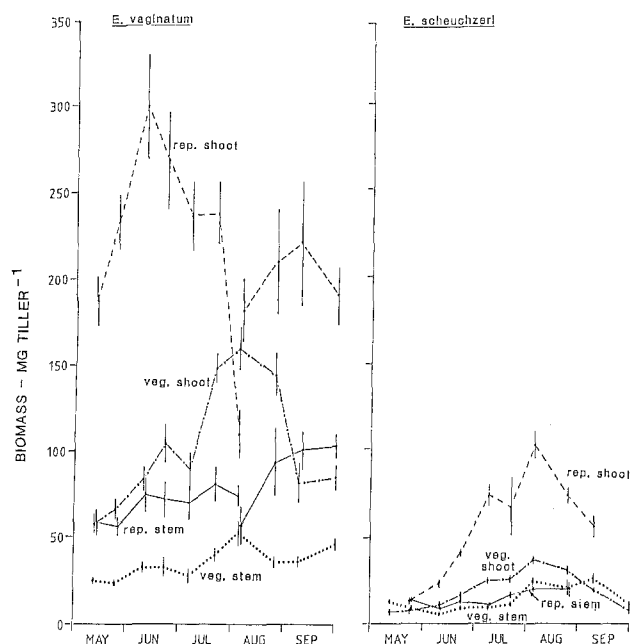
Fig. 4. Biomass values for shoot and stem components of vegetative tillers and shoot (culm + panicle) and stem components of reproductive (flowering) tillers in two species of *Eriophorum*, over the 1983 growing season. Note, values for flowering tillers of *E. vaginatum* beyond early August are for newly formed initials. Data are means ± SE; n = 5

Rhizome weight in *E. scheuchzeri* was minimal on 10 June, coinciding with commencement of rapid shoot and inflorescence growth, and maximal in August–September after fruit ripening and during leaf senescence. Rhizome

lengths (and weights), however, did not differ ($P > 0.05$) between vegetative (3.55 ± 0.37 cm) and reproductive (3.48 ± 0.19 cm) tillers, nor between sampling occasions, suggesting that the greater biomass of reproductive shoots in *E. scheuchzeri* must have been achieved by drawing upon reserves and current photosynthate of the entire tiller system rather than just from rhizomes immediately associated with the reproductive shoots.

In *E. vaginatum* biomass of reproductive shoots (culm + panicle) did not differ ($P > 0.05$) from that of vegetative shoots when they were first detectable in early August (Fig. 4). After this date vegetative shoots declined 50% in biomass, whereas reproductive shoots maintained relatively constant biomass, then increased nearly 2-fold the following spring after snow melt. The striking reduction in biomass of reproductive shoots after mid-June coincided with shedding of seeds (Fig. 3) and general chlorosis. Stems of reproductive tillers differed from those of vegetative tillers in that they doubled in weight between early August and late September and remained twice as heavy as vegetative stems the following season, up to the time of seed shedding. Thus, in contrast to *E. scheuchzeri*, much of the biomass increase in reproductive tillers of *E. vaginatum* occurred in late summer of the year prior to flowering and in early spring in the year of flowering rather than in midsummer.

Chemical constituents

Carbohydrates. In most plant parts of both species sugar concentrations were low in summer, then increased to high levels in late-September (Fig. 5). In *E. vaginatum* reproductive shoots had higher sugar concentrations in early spring and low concentrations in mid-summer when they were largely senescent, but otherwise there were no major differ-
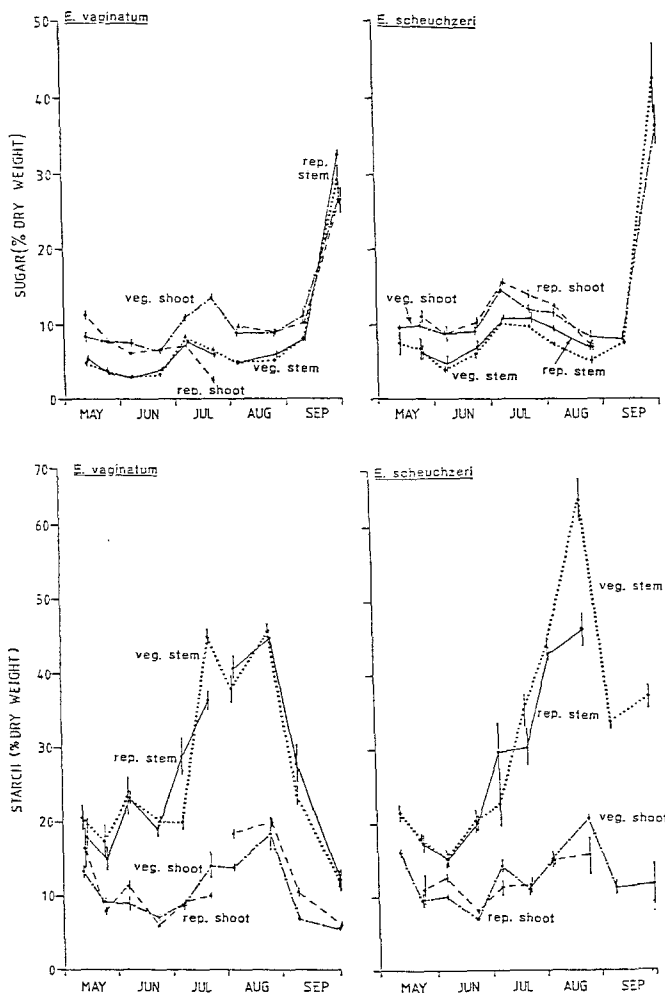
Fig. 5. Carbohydrate concentration (sugar top; starch bottom) for shoot and stem components of both vegetative and reproductive tillers in two species of *Eriophorum* over the 1983 season. Note, values for flowering tillers of *E. vaginatum* beyond early August are for newly formed initials. Data are means ± SE; n = 5

ences in sugar concentrations between reproductive and vegetative tillers. Consequently, reproductive tillers, with their greater biomass of both shoots and stems (Fig. 4), also had greater pool sizes of sugars than did vegetative tillers (data not shown). Sugar pool sizes were maximal in each plant part in late September and were particularly high in reproductive tillers. In *E. scheuchzeri* sugar concentrations were very similar between reproductive and vegetative tillers for both plant parts. Consequently, pool sizes of sugar were greater in reproductive than in vegetative shoots but did not differ between their stems (rhizomes). Sugar pool sizes in reproductive tillers of *E. scheuchzeri* declined somewhat in September from peak values in July, perhaps associated with initiation of new tillers below ground (which were not sampled).

Seasonal patterns of starch concentration differed strikingly from those of sugar: starch was maximal in late-July and early-August (Fig. 5) at the time of maximal shoot biomass in vegetative tillers (Fig. 4) and decreased sharply in autumn. Starch concentration showed no consistent difference between reproductive and vegetative tillers for either plant part of either species.
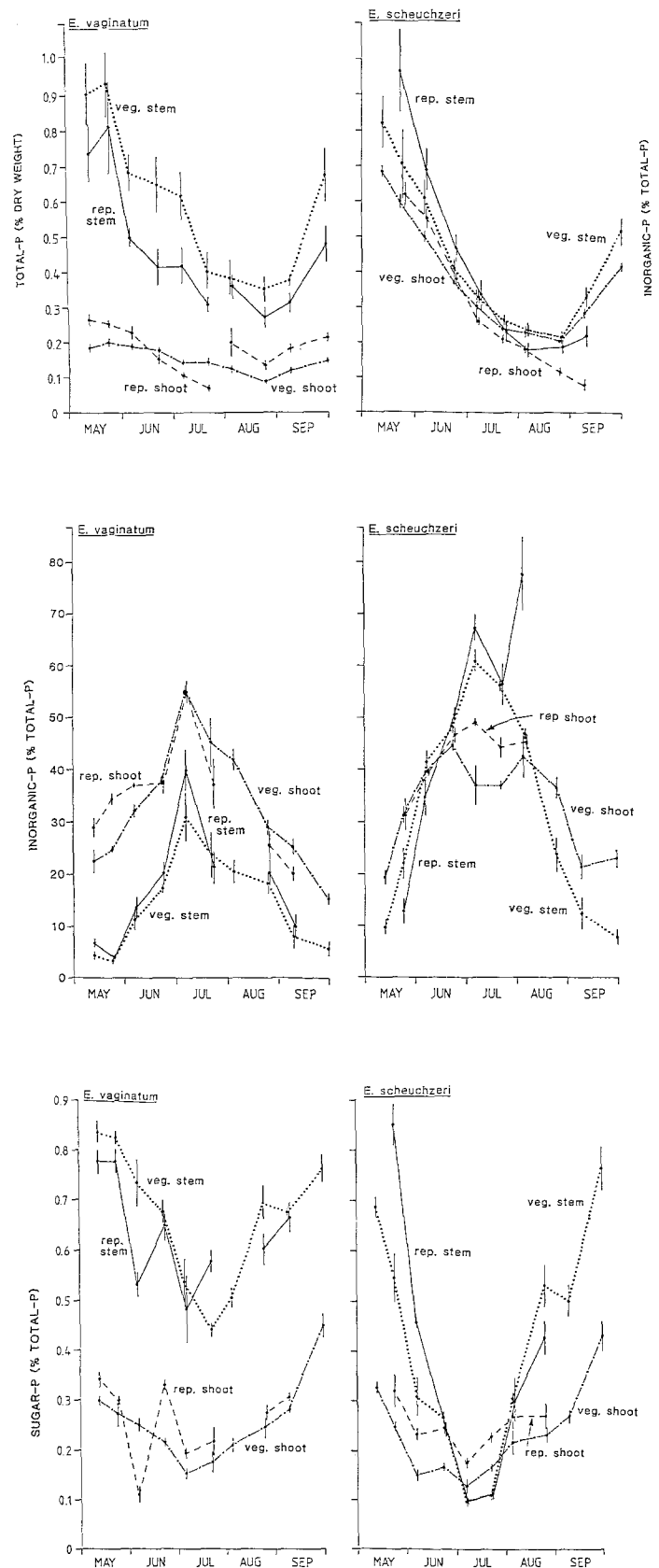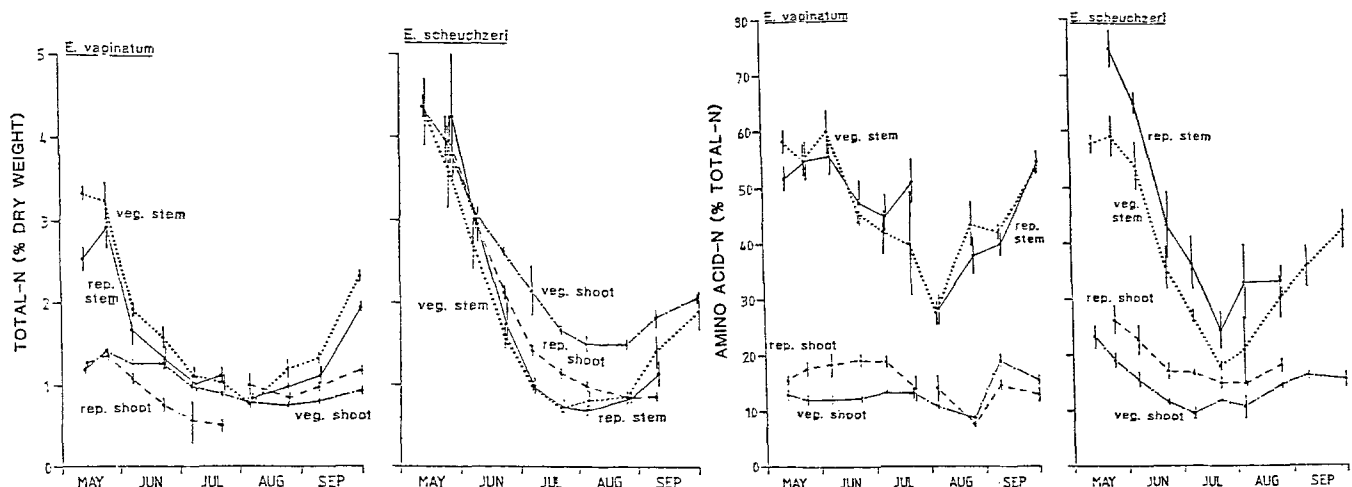

Fig. 6. Total-phosphorus (P) concentration, ratio of inorganic-P to total-P concentration, and ratio of sugar-P to total-P concentration for shoot and stem components of both vegetative and reproductive tillers in two species of *Eriophorum* over the 1983 season. Note, values for flowering tillers of *E. vaginatum* beyond early August are for newly formed initials. Data are means ± SE; n = 5

Fig. 7. Total-nitrogen (N) concentration (left) and ratio of amino acid-N to total-N concentration (right) for shoot and stem components of both vegetative and reproductive tillers in two species of *Eriophorum* over the 1983 season. Note, values for flowering tillers of *E. vaginatum* beyond early-August are for newly formed initials. Data are means ± SE; *n* = 5

Phosphorus. Phosphorus (P) concentrations declined from May until late-August and increased in September in all plant parts sampled except rhizomes of reproductive *E. scheuchzeri* tillers, which showed no September recovery (Fig. 6). In *E. vaginatum*, reproductive tillers differed from vegetative tillers in having lower P concentrations in stems and higher P concentrations in shoots (except in senescing reproductive shoots in July), indicating a preferential allocation of P (relative to biomass) to above-ground reproductive components in this species. The reduction in P concentration of shoots coincided with shedding of seeds and chlorosis of leaves. In *E. scheuchzeri* there were less pronounced differences in P concentration between reproductive and vegetative tillers. In both species, pool sizes of P in stems were high in spring and autumn and low in mid-summer. By contrast, pool sizes of P in shoots were highest in mid-summer, suggesting that P reserves stored in stems were important in supporting shoot growth in spring and were recovered from senescing shoots in autumn. In *E. vaginatum*, P was transported out of reproductive shoots and stems in mid-summer, when the P requirement of vegetative shoots was greatest. By contrast, in *E. scheuchzeri* the P requirements of both reproductive and vegetative shoots were greatest in mid-summer.

Seasonal trends in inorganic-P and sugar-P mirrored each other, with the proportion of inorganic-P generally increasing 2- to 6-fold in both species from early- to mid-season and then declining to early-season values, whereas that for sugar-P followed the reverse trend (Fig. 6). This indicates a conversion to inorganic-P during the season of active growth in all plant parts of both species. Stems (rhizomes) of reproductive tillers of *E. scheuchzeri* had high sugar-P concentrations in early-summer and high inorganic-P concentrations during seed shedding in late-summer, but otherwise there were no striking differences in allocation of P among chemical fractions between reproductive and vegetative tillers of either species.

Nitrogen. Seasonal changes in total-nitrogen (N) were very similar to those described for total-P, for all plant parts of both species (Fig. 7). Thus, concentrations declined in mid-summer and recovered in autumn except in reproduc-

tive shoots of *E. scheuchzeri* which showed no September recovery. As with P, reproductive tillers of *E. vaginatum* were characterised by lower N concentrations in stems and higher concentrations in shoots (late-summer only), suggesting preferential allocation of N above-ground in reproductive tillers. In both species, spring and mid-summer shoots that were actively flowering and setting seed had lower N concentrations than did vegetative shoots. When pool sizes were examined, reproductive shoots and stems of *E. vaginatum* declined in N in mid-summer, at the time of greatest N requirement of vegetative shoots. By contrast, in *E. scheuchzeri* N pool size was greatest in mid-summer in shoots of both vegetative and reproductive tillers. Seasonal patterns of amino acid-N with species and reproductive requirement status were very similar to those for sugar-P.

Discussion and conclusions

The phenological differences between the two species of *Eriophorum* studied are necessary for each to reproduce successfully in its particular habitat. The tussock growth form of *E. vaginatum* allows meristem temperatures close to those of the ambient air during the spring-early summer period of active growth and development, despite cold soils, slow thaw between tussocks, and presence of permafrost (this study, Chapin et al. 1979). These relatively high plant temperatures appear essential if inflorescences initiated the previous summer are to develop as rapidly as we observed. Since mature tussocks of this species are 120–190 years old (Mark et al. 1985), it seems unlikely that a tussock microenvironment could develop in areas of frequent physical disturbance, such as those occupied by *E. scheuchzeri*. By contrast, the disturbed sites typically occupied by this latter species have relatively warm, better drained soils, with higher nutrient availability (McGraw and Chapin 1988), a habitat that permits this species to complete its reproductive development in the season in which it flowers. Bell and Bliss (1978) noted that, in general, those tundra plants with perennating buds and/or major storage organs beneath the soil surface have particularly low growth rates and short growing seasons.

The prolific tillering that characterises *E. scheuchzeri* in late summer and which is required for effective exploitation of disturbed habitats may preclude large allocation of reserves to inflorescence development in late summer. However, *E. vaginatum* is able to support late-season inflorescence development, because (1) it allocates a much smaller proportion of its production to the formation of daughter tillers than does *E. scheuchzeri* (McGraw and Chapin 1988), and (2) its allocation to daughter tillers occurs continuously through the growing season (Shaver et al. 1986). Consequently, the nutrients that are translocated from senescing leaves in *E. vaginatum* in autumn (Jonasson and Chapin 1985) are available to support the reserve accumulation by a developing inflorescence, as we observed. Overwinter storage of nutrients is best developed in infertile habitats such as those occupied by *E. vaginatum* (Chapin and Shaver 1985). This same pattern of autumn translocation of nutrients for storage can also support late-summer development of inflorescences. Thus, the low nutrient availability that characterizes arctic soils may be one factor, along with a short, cold growing season, selecting for early development of inflorescences in the year prior to flowering (Sorensen 1941).

The sequential pattern of leaf production that we observed in *Eriophorum vaginatum* (see also Johnson and Tieszen 1976, Jonasson and Chapin 1985) may be an adaptation for effective retention of nutrients in infertile habitats (Jonasson and Chapin 1985). However, the occurrence of similar sequential development in *E. scheuchzeri*, a species of more fertile sites, suggests it is a trait that may not necessarily be related to habitat fertility.

The overwintering of green leaves in *E. vaginatum* is functionally similar to the habit of evergreen shrubs. This trait may enable evergreens to initiate seasonal activity earlier (Tieszen and Johnson 1968; Chapin et al. 1979; Kummerow et al. 1983), photosynthesize over a longer period (Schulze et al. 1977; Chabot and Hicks 1982), and reduce annual nutrient requirement for leaf production (Chapin 1980). The presence of the evergreen habit in *E. vaginatum* and its absence in *E. scheuchzeri* is consistent with the generalization that evergreen species are more effective in exploiting infertile soils (Small 1972; Chapin 1980).

Among arctic shrubs, deciduous species initiate growth earlier than do evergreen species (Bliss 1956; Johnson and Tieszen 1976; Chapin et al. 1980), a pattern that contrasts with that in *Eriophorum*. Among shrubs, the delayed leaf growth of evergreen species may be a consequence of early-season allocation to root growth in these species (Kummerow et al. 1983). It is unlikely that this tradeoff would exist in *Eriophorum* because 90% of the roots die each autumn (Bliss 1956; Chapin et al. 1979; Shaver et al. 1986), so both species must initiate root growth early in the season to exploit the spring flush of nutrients.

The general similarity of levels and seasonal patterns of reserves between reproductive and vegetative tillers probably reflects their close interconnection in both species. Similarly, carbohydrate concentrations in stems of New Zealand snow tussocks do not differ between vegetative and repoductive tillers until the second half of the growing season, when concentrations increase in stems of vegetative but not reproductive tillers (Payton and Brasch 1978). In clonal plants, interconnections among ramets permit reproductive shoots to draw upon a large pool of stored reserves from nearby vegetative ramets and support reproduction even when resource levels in the environment are quite low (Hartnett and Bazzaz 1983; Slade and Hutchings 1987).

The patterns of carbohydrate, N, and P storage observed in stems of the tussock-forming *E. vaginatum* (see also Chapin et al. 1986) are similar to those of the rhizomatous *E. scheuchzeri* but, in the case of N and P, these reserves were drawn down more fully in mid-summer in *E. scheuchzeri* because of the simultaneous growth of vegetative and reproductive shoots. *E. vaginatum* may be more conservative in its use of nutrient stores because of the long lifespan of individuals (Mark et al. 1985) and the infrequence with which its seedlings successfully establish (Gartner et al. 1986). By contrast, the rhizomatous habit of *E. scheuchzeri* would assist it to occupy sites of ephemeral disturbance. Such sites may exert strong selection for allocation to reproduction, even at the expense of maintaining reserves for other contingencies.

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