The unusual vascular structure of the corm of *Eriophorum vaginatum*: implications for efficient retranslocation of nutrients

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Abstract

*Eriophorum* spp. are abundant perennial graminoids in the Arctic tundra and boreal peatlands. Because ecological studies indicated that some plants are unusually productive on infertile and cold sites, the anatomy of the overwintering corms of *Eriophorum vaginatum* (L.) and *Eriophorum scheuchzeri* (Hoppe) were examined to determine their involvement in nutrient uptake and storage. Components of the long-distance transport pathways were identified within the plants by using histochemical techniques and transport of apoplastic and symplastic dyes. *E. scheuchzeri* produced a rhizome that consisted mainly of storage parenchyma cells within which collateral vascular bundles were centrally located and arranged in a circle. By contrast, *E. vaginatum* developed a ring of horizontally arranged xylem and phloem, in addition to axial amphivasal vascular bundles leading to the leaves, all of which were bordered by transfer cells. As shown by the transport of fluorescein in the phloem and Safranine O in the xylem, each axial bundle and adventitious root contacted the horizontal ring of vascular tissues so that solutes from one vascular bundle were translocated into the vascular ring and circulated to another vascular bundle and/or to the roots. In addition, special groups of sclereids that functioned in both phloem and xylem transport were found at the base of the leaf traces and within junctions of senescing roots. These sclereids were named ‘vascular sclerenchyma’ and it was hypothesized that they provide a moving end for the vascular system because the corm dies progressively from the distal end as it grows upward from the apical meristem. It was concluded that this unusual vascular system of *E. vaginatum* is efficient in recycling nutrients internally, which may account for its competitive advantage in infertile and cold sites.

Key words: Endodermis, *Eriophorum scheuchzeri*, *Eriophorum vaginatum*, exodermis, phloem, sclereid, transfer cell, vascular ring, vascular sclerenchyma, xylem.

Introduction

The cottongrasses *Eriophorum vaginatum* and *E. scheuchzeri* are circumpolar sedges that occupy different ecological niches in arctic and boreal regions. *E. vaginatum* forms tussocks and dominates relatively infertile, permanently wet tundra, whereas *E. scheuchzeri* is rhizomatous and typically inhabits more fertile floodplains and other wet sites characterized by disturbance (Mark and Chapin, 1989; McGraw and Chapin, 1989). In some sites, the productivity of *E. vaginatum* is limited by nitrogen availability (Defoliart et al., 1988), while in other sites the net primary production is limited by low phosphate (Thormann and Bayley, 1997).

A number of traits have been identified that enhance the competitive ability of *E. vaginatum* to dominate sites with low fertility in the Arctic tundra and other peatlands. When grown experimentally in competition with *E. scheuchzeri*, *E. vaginatum* exhibited lower reproduction rates, slower growth rates even when fertilized with nitrogen, higher root:shoot ratios, lower nitrogen uptake, and higher nitrogen use efficiency (McGraw and Chapin, 1989).

The phenology of the two species is also an important factor in their relative competitive abilities. *E. vaginatum* is an evergreen that forms clonal tussocks, which raise the shoot meristems above the soil surface. Because the

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temperatures are warmer above the soil, E. vaginatum initiates new growth earlier in the season and grows later into the autumn compared with E. scheuchzeri (Mark and Chapin, 1989). This growth strategy allows E. vaginatum to flower early in spring and then initiate the season's vegetative growth without requiring a higher level of mineral nutrition at any one time. In fact, flowering takes place with minimal nutrient uptake because the soil is still frozen. Leaf production is also limited in E. vaginatum. In northern Alaska, E. vaginatum produces only 4–6 leaves sequentially during the growing season, with each leaf expanding at the expense of nutrients retranslocated from an older leaf (Defoliart et al., 1988; Shaver and Laundre, 1997). With little nutrient uptake, these growth strategies all rely on effective internal recycling of nutrient elements and on minimal intermediate storage of nutrients in other tissues (Shaver and Laundre, 1997).

By contrast, E. scheuchzeri is a summer-green plant with a rhizomatous growth habit that has a shorter growing season and must support reproductive and vegetative growth simultaneously (Mark and Chapin, 1989). Because more nutrients are required to support growth and development within a limited period of time, E. scheuchzeri is restricted to sites with more fertile soils.

In this study the anatomy of E. vaginatum corms were examined and the pathways of xylem and phloem transport were explored. Evidence is provided that the unusual ability of E. vaginatum to store and retranslocate nutrients is correlated with its uniquely adapted vascular anatomy, which differs from the closely related species E. scheuchzeri.

Materials and methods
Plant material
Eriophorum vaginatum L. plants collected in Fairbanks, Alaska, USA (64°51′ N, 147°43′ W), and E. scheuchzeri Hoppe plants collected in Iqaluit, NU, Canada (63°45′ N, 68°31′ W), were divided and planted in 10 cm pots in Turface (Plant Products, Brampton, ON, Canada) and maintained in 2 cm of standing water in the greenhouse in Waterloo, ON, Canada (42°18′ N, 83°01′ W), under natural lighting supplemented with fluorescent lights to extend the day-length to 21 h.

Histochemistry and microscopy
Freehand sections were stained for lignin and suberin following the procedure of Brundrett et al. (1988). Briefly, sections were stained in 0.1% (w/v) berberine hemisulphate (Sigma Chemical Co., St Louis, MO, USA; Cat. no. 75160) in distilled water for 1 h and rinsed in distilled water for 30 min. Sections were then counterstained by immersion in 0.5% (w/v) aniline blue (Polysciences, Warrington, PA, USA; Cat. no. 42755) in distilled water for 30 min, rinsed as above, and mounted on slides in 0.1% (w/v) FeCl₃ in 50% (v/v) glycerine. When stained in this way, lignin and suberin fluoresced yellow when viewed with ultraviolet light.

The presence of the lignin in the sclerified cells was further confirmed by a positive reaction with phloroglucinol-HCl (Gurr, 1965). Pectin was stained with ruthenium red according to Luft (1971). Calllose, or (1,3)-β-D-glucans, fluoresced yellow upon staining with aniline blue fluorochrome at pH 9.0 (Stone et al., 1984). Starch granules were visualized upon reaction with iodine/potassium iodine (Gurr, 1965). Condensed tannins were visualized by their reaction with 1% (w/v) 2,4-dimethoxybenzaldehyde in 95% (v/v) ethanol mixed with 18% (v/v) HCl on the slide (Mace and Howel, 1974).

All microscopic observations were performed using a Zeiss Axioskop microscope (Carl Zeiss, Don Mills, Ontario, Canada) equipped with an Osram HBO 100 W mercury lamp and optics for epifluorescence. Sections were viewed with white, ultraviolet and blue light. The ultraviolet filter set consisted of the G365 exciter filter, the FT395 chromatic beam splitter, and the OP420 barrier filter. The blue light set of filters included a BPS46 exciter filter, a FT580 chromatic beam splitter, and a LP590 barrier filter. Images were captured on Kodak Ektachrome daylight slide film, ISO 200, then scanned and processed using Adobe Photoshop (Adobe Systems Inc., San Jose, CA, USA).

Phloem loading
Fluorescein, the disodium salt, was dissolved in 5 mM MES buffer, pH 6.3. Loading was performed at the beginning of the light period by cutting the end of a mature source leaf at an oblique angle and inserting it into a fluorescein-filled 100 µl capillary. The plant was illuminated with a tungsten lamp (100 µmol photons m⁻² s⁻¹ PAR) for 3 h. After the loading period, the plant was dissected and sections taken from the leaves and corm were rinsed in distilled water and observed with blue light using the epifluorescent microscope. The distribution of fluorescein was indicative of the presence of functioning phloem and highlighted the long-distance pathway of assimilates transport from leaves to roots (Grignon et al., 1989).

Xylem loading
E. vaginatum corms were separated and their roots washed in running tap water. Roots were cut at the oblique angle under water to prevent air embolism in their xylem elements. Once xylem tension was relieved, roots were immersed in 1% (w/v) Safranine O solution and allowed to transpire from 2–24 h. In some experiments, only roots on one side of the corm were immersed in Safranine O solution, while others were in water. At the end of loading period, plants were removed from the loading solution, rinsed, and sectioned with a dry razor blade to minimize tracer diffusion. Sections were mounted in 50% (v/v) glycerine and observed immediately. Safranine O stained lignified xylem elements and facilitated identification of the pathway of water and solute movement through xylem elements (Sauter, 1984; Cholewa et al., 2001; Schulte and Brooks, 2003).

Results
Anatomy of the corm
After removing all dead and living leaves and roots, the corm of E. vaginatum appeared to be a modified stem with leaf scars forming rings around the corm at the nodes (Fig. 1A). Longitudinal growth arising from the activity of the apical meristem was very slow, as evidenced by the short axis, short internodes and crowding of the appendages. As the plant grew, the end of the old corm died progressively from the bottom, and new secondary corms or cormels (Harris et al., 1992) grew from one or more lateral buds (Fig. 1A, B). All leaves and adventitious roots arose from the corm.

The corm of E. vaginatum was thickened and modified for storage. When sectioned, the major tissues of the corm...
were visible, including the epidermis, cortex, and central vascular cylinder (Fig. 1B–O). Sectioning was difficult because of the presence of many red, thick-walled, lignified cells associated with axial vascular strands within the vascular cylinder (Fig. 1B). Cross-sections through the mature corm with two developing cormels revealed that the vascular cylinders of the mature corm and developing cormels were directly connected (Fig. 1C). The majority of parenchymal cells located within the central cylinder had thin cellulolic primary cell walls that stained with aniline blue (Fig. 1C). The parenchyma in both the cortex and the vascular cylinder (Fig. 1D) stored a substantial amount of starch, as visualized with iodine staining (Fig. 1E).

The outermost layers of the corm’s cortex were modified into a protective, multi-layered exodermis, similar to that found in many roots (Ma and Peterson, 2003). Although Metcalfe (1971) reported that a hypodermis was absent in E. vaginatum, staining with berberine/aniline blue revealed the presence of suberized lamellae and Casparian bands in the cell walls of the exodermis (Fig. 1F). The innermost cell layer of the cortex was bordered by an endodermis, with typical, lignified, U-shaped thickening in its cell walls (Fig. 1G). Within the vascular cylinder enclosed by the endodermis were numerous axial vascular bundles where the phloem tissue was surrounded by a ring of xylem elements. These amphivasal vascular bundles were encircled, in turn, by transfer cells, which were characterized by thickened cell walls containing many pitfields that made them easy to distinguish from the storage parenchyma in the rest of the corm (Fig. 1H).

In addition to the axial vascular bundles, there was a ring of horizontally oriented vascular tissue adjacent to the endodermis (Fig. 1H–L). Aniline blue staining for wound-induced callose revealed that sieve tubes of phloem were present in the vascular ring just inside the endodermis (Fig. 1J). Upon staining with berberine/aniline blue, lignified xylem elements with scalariform thickenings of their cell walls were evident in the vascular ring by their yellow fluorescence and were located to the interior of the phloem (Fig. 1I). Interior to the xylem were several layers of transfer cells.

In some parts of the corm, where the sclereids were present in a plane of the cross-section, a different arrangement of xylem elements of the vascular ring was observed. It appeared that xylem elements were centripetal to the sclereids, with some tracheids in direct contact with the cluster of sclerified cells (Fig. 1M). Such a direct connection implied that both cell types (xylem elements and sclereids) were involved in the apoplastic long-distance transport of solutes. Another connection was observed between the xylem and the transfer cells of the vascular ring and xylem and transfer cells of the axial leaf traces was observed (Fig. 1N), which would ensure continuity of the xylem transport of solutes from vascular ring to the leaf traces for upward delivery of solutes to the leaves. Interestingly, xylem elements of roots were also in direct contact with the vascular ring (Fig. 1O). It seems that the vascular ring plays a central role in xylem transport, being connected on one side to the roots and on the other to the leaf traces.

**Vascular sclerenchyma**

The development and role of the clusters of sclerified cells associated with the leaf traces of the corm of E. vaginatum was puzzling. When compared with the surrounding cells in the corm that were still dividing and elongating, the cell walls of a group of sclereids began to lignify very early in development (Fig. 2A). While the cell walls stained readily for lignin, they did not stain with ruthenium red, thus indicating a low amount of pectin at a stage in development where all the other tissues had primary cell walls that were easily stained with ruthenium red (Fig. 2B). Fully developed sclereids had massively thickened cell walls with a small cell interior and pit canals leading to the plasmodesmal connections between cells (Fig. 2H).

Within the corm, the sclereids were always arranged in a central position with respect to axial bundles, with some of their peripheral cells in contact with a leaf trace (Fig. 2C). In the younger, distal part of the corm, clusters of such sclereids were present in the roots (Fig. 2D). Closer examination of the corm-root junction revealed that sclereids filled the stele at the site of the lateral root connections (Fig. 2E). To the authors’ knowledge, this is the first study reporting the development of sclerified cells in the steles of senescing roots.

In studies of E. vaginatum, Metcalfe (1971) identified structures on the centripetal side of vascular bundles and named them ‘sclerenchyma caps’. Zee (1974) also identified anatomically distinct cells associated with vascular bundles at the nodes of bamboo culms and named them ‘phloem transfer cells’. In cross-sections of bamboo nodes, these phloem transfer cells were grouped together in a structure associated with the vascular tissues that resembled the general structure of the cluster of sclereids in E. vaginatum. However, the sclereids in E. vaginatum were characterized by much thicker cell walls and were active in both apoplastic and symplastic transport (data shown below), so it was decided to name them ‘vascular sclerenchyma’.

**Phloem transport**

The distribution of fluorescein is indicative of the presence of functioning phloem and can be used to highlight the long-distance pathway of symplastic assimilate transport from leaves to roots (Grignon et al., 1989). Movement of fluorescein shows the existence of actively transporting sieve tube connections (Schoning and Kollmann, 1997). Fluorescein is first taken up into the leaf apoplast, then it accumulates in the cytosol by an ion trap mechanism (Teskos et al., 1997) and is transferred symplastically to
the phloem. In these experiments, a fluorescein-filled microcapillary was used to load the dye into the cut surface of a mature, source leaf of *E. vaginatum* (Fig. 3A). Fluorescein was then detected in leaf mesophyll cells (Fig. 3B) and in the leaf traces (Fig. 3C). Fluorescein was transported in the phloem to the vascular cylinder of the corm (Fig. 3D). By observing movement of the dye, phloem connections were detected between axial vascular bundles and the horizontal vascular ring. In addition, vascular sclerenchyma associated with leaf traces retained
fluorescein even after prolonged rinsing. This indicated that the sclerenchymal cells were symplastically connected to the phloem of leaf traces and that the sclereids were still alive at maturity, because only living cells with intact cell membranes retain fluorescein and fluoresce. Although lignified cell walls may autofluoresce under blue light, the intensity of the autofluorescence of unstained vascular bundles shown in Fig. 3E, was very low. From these observations, the pathway of assimilate transport in the phloem could be defined. Once loaded into the phloem in the leaves, assimilates were transported to the corm, redistributed via the vascular ring, and delivered to the roots and growing leaves or to the storage parenchyma.

Xylem transport

Transport of ions and water taken up by roots depends on the dynamic co-ordination between hydraulic conductances of interconnected xylem vessels. Safranine O is frequently used as a reliable tracer for water transport in the xylem (Sauter, 1984; Cholewa et al., 2001; Schulte and Brooks, 2003), so a Safranine O solution was used to determine the pathway of water and solute transport from E. vaginatum roots to the aerial parts of the plant (Fig. 4A–F). When roots were allowed to take up Safranine O, it was transported in the xylem elements of the roots and delivered to the xylem of the vascular ring of the corm. Safranine O was then distributed around the vascular ring and to adjoining leaf traces (Fig. 4A). It appeared that the delivery of water and solutes by the roots to the corm depended on the site of root attachment to the corm. When only some of the roots located on one side of the corm were allowed to take up Safranine O while others were incubated in water, Safranine O distribution was not uniform. Under such conditions, the tracer was only distributed to that part of the vascular ring to which the roots submerged in Safranine O were connected. The remaining part of vascular ring associated with roots submerged in water did not stain with Safranine O (Fig. 4B). Observations of the sections taken from near the apex of the corm revealed that Safranine O was present in discrete patches of the vascular ring from where it was conducted upwards in some of leaf traces adjacent to the vascular ring (Fig. 4C). Immersing roots of a mature corm in Safranine O resulted in dye transport into young cormels (Fig. 4D). Some of the sclereids associated with leaf traces were stained with Safranine O. Such staining might be due to the diffusion of Safranine O in the corm or it may indicate that the cell walls of these sclereids are somehow involved in apoplastic transfer of solutes (Fig. 4E). The endodermis surrounding the vascular cylinder of the corm effectively blocked outward diffusion of the solutes. Even after a 24 h incubation of the roots in Safranine O, the corm’s cortex remained unstained, while Safranine O diffused throughout the entire vascular cylinder (Fig. 4F). These results demonstrate that the vascular ring is an important component of the apoplastic pathway and serves as an intermediary to distribute water and solutes to multiple leaf traces and to the entire vascular cylinder.

Eriophorum scheuchzeri

The anatomy of aerial shoots and rhizomes of E. scheuchzeri were examined to determine whether the unusual vascular structures observed in E. vaginatum are characteristic of this genus. The distinct anatomical features present in E. vaginatum, such as the vascular cylinder, vascular ring, endodermis, and vascular sclereids of E. scheuchzeri, are similar to those of E. vaginatum, but the anatomy of the xylem shows some differences.

(continued)
enchyma were not observed in *E. scheuchzeri*. The aerial part of the stem was surrounded by leaf sheaths (Fig. 5A), and the vascular bundles formed a circle in the centre of the stem (Fig. 5B).

The rhizome developed a multilayered exodermis, but an endodermis was not present (Fig. 5D). The vascular bundles were aligned with the phloem positioned outwards and xylem inwards and some of the vascular bundles

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**Fig. 2.** Development of vascular sclerenchyma in *Eriophorum vaginatum* corm. (A) Cross-section of the corm near the apex stained with berberine/aniline blue and viewed under UV light. Developing sclereids (arrow) associated with vascular bundles (vb) were positioned towards the centre of the corm, scale bar=500 μm. (B) Cross-section near the apex stained with ruthenium red. Red colouration revealed the presence of pectin in thin-walled, dividing and expanding cells of the corm. The cell walls of developing sclereids (arrow) were not stained, scale bar=100 μm. (C–F) Cross-sections of the corm stained with phloroglucinol-HCl. (C) Section taken in the middle of the corm. The cell walls of sclereids (arrows) were lignified, scale bar=500 μm. (D) Section taken at the base of corm. Lignified masses of sclereids (arrows) were associated with adventitious roots, scale bar=500 μm. (E) Higher magnification of corm-root junction. A mass of sclereids (arrow) developed in the centre of the root, scale bar=100 μm. (F) Developing sclereids with enlarged cells and thickening cell walls were lignified, beginning from the middle of the group, scale bar=50 μm. (G) Unstained section through developed sclereids associated with amphivasal vascular bundle with phloem (ph) in the centre surrounded by xylem elements (x). Massive, secondary cell walls and numerous pits were visible, scale bar=50 μm. (H) Higher magnification of developed sclereids revealed that cell lumena, with pit canals (arrow), occupied a very small portion of the cells, scale bar=10 μm.
merged together in mature regions of the rhizome (Fig. 5C), but never completed an intact circle (Fig. 5E). Vascular tissues were protected by suberized bundle sheath cells with distinctive Casparian bands in their radial walls (Fig. 5D). Lateral roots originated in the centre of the rhizome. The xylem elements of the roots must be connected at some point to the xylem of vascular bundles, but their connection to other xylem elements was not observed in this study (Fig. 5F).

Discussion

Origin of the vascular ring

The vascular ring is not a common structure in the rhizomes of the Cyperaceae. However, in an anatomical study of Scirpus cyperinus, a genus within the Cyperaceae considered to be closely related to Eriohorum spp., Plowman (1906) described `a dense plexus of transverse and oblique fibro-vascular strands in the surface of the central cylinder, just inside the endodermis', but further details of this structure are lacking in the modern literature. The plexus was considered by Plowman (1906) chiefly to provide mechanical support, but he did note that ‘fully 90% of the branching and anastomosing of bundles in the rhizome takes place in the superficial plexus’ and that all of the root-strands and many of the leaf traces are attached to it.

While the vascular ring probably does provide mechanical support to the corm, it has clearly been demonstrated that the vascular ring also functions as an intermediary structure that promotes the efficient redistribution of solutes transported in either xylem or phloem between the roots, corm and leaves (Figs 3, 4). The origin of the vascular ring in E. vaginatum was not determined in this study because it was not possible to obtain sufficient resolution with free-hand sections. The thickness of the E. vaginatum corm indicates that a primary thickening meristem, typical for larger monocotyledonous plants (Esau, 1953), may be the source of the derivative cells that form the vascular ring. It is possible that the vascular ring differentiates from isolated procambial strands originating in a peripheral primary thickening meristem as described in developing nodes of Zea mays (Pizzolato and Sundberg, 2001, 2002). Alternatively, the shortened corm axis, with nodes and internodes being very close together, raises the possibility that curving leaf traces crowded together may appear as a vascular ring (see Rudall, 1991, and references therein). If this were the case, one would expect the vascular ring to be organized similarly to the amphivasal leaf traces. However, neither cross-sections (Fig. 11) nor tangential and longitudinal sections (Fig. 1K–O) of the vascular ring revealed the presence of an amphivasal arrangement. Moreover, cell division in the vascular ring occurred in a different plane from the vascular bundles. When the corm was cut in cross-section, the axial bundles appeared as though they were cut in cross-section, as expected (Fig. 1H, I). However, the ring of vascular tissue (including the endodermis, phloem, xylem, and transfer cells) appeared as though it were cut in longitudinal section (Fig. 1H, I). When examined in a tangential section, the vascular ring contained a network of xylem elements that were horizontal and were easily distinguished from axial leaf traces (Fig. 1K). These lignified xylem elements appeared to be cross-sectioned

Fig. 3. Fluorescein transport in the Eriophorum vaginatum phloem visualized by yellow fluorescence upon irradiation with blue light. (A) Mature third leaf of one corm was inserted in a fluorescein-containing microcapillary (arrow). (B) Cross-section of a fluorescein-loaded leaf showing that fluorescein was taken up by strands of mesophyll cells, scale bar=500 μm. (C) Leaf sheath pulled back from the corm to show that vascular strands (arrows) transported fluorescein, scale bar=100 μm. (D–E) Sections of corm taken after leaf fluorescein loading and viewed under blue light. (D) An oblique section of young corm tip. Fluorescein was located in the phloem of leaf traces (arrows) and was unloaded into some of the parenchyma cells near apex, scale bar=500 μm. (E) Cross-section of the mature corm. Fluorescein was retained in the phloem of axial vascular bundles (arrows), in the sclerenchyma cells associated with vascular bundles (arrowheads), redistributed around in horizontal vascular ring and transferred into phloem of adventitious roots (r), scale bar=500 μm.

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when the longitudinal section of the corm was examined (Fig. 1L).

**Role of vascular sclerenchyma**

The vascular sclerenchyma may play multiple roles in initiating and maintaining the vascular system within the corm of *E. vaginatum*. Gunning *et al.* (1970) suggested that the role of vascular sclerenchyma in meristematic zones is to provide a pathway in which solutes from the xylem might be transferred to adjacent meristematic zones with no effective vasculature. In the early stages of development of the corm (near the apex), the vascular sclerenchyma were lignified before developing xylem elements (Fig. 2A, B). Detection of lignin implies that the vascular sclerenchyma mature earlier than the xylem because xylem cells lignify their secondary cell walls prior to disintegration of the cytoplasm and acquisition of transport function (Esau, 1953; Yaklich *et al.*, 2001). Therefore, the lack of lignification indicated that the xylem elements were not yet conductive. Because the *E. vaginatum* corm was already thickened at this point, it required a substantial amount of solutes to sustain meristematic growth and differentiation of the tissues. The position of the vascular sclerenchyma near the apical meristem, their early maturation (they are lignified before the xylem elements, Fig. 2), and their ability to aid in xylem (they conducted Safranine O, Fig. 4) and phloem (they retained fluorescein, Fig. 3) transport indicate that, indeed, the vascular sclerenchyma could fulfil the role of supplying nutrients and assimilates to the apical meristem.

Another function of the sclereids may be mechanical support because the cells were heavily lignified early in the
development of the corm. Moreover, in some parts of the senescing corm, the vascular sclerenchyma appeared to lose some of the thickness of their cell walls, and only the central region of the cap reacted positively with phloroglucinol, which indicated the presence of lignin (Fig. 2F). Although the cell wall composition is not known, observations raise the possibility that the thickened cell walls themselves may be a form of carbohydrate storage, as has been shown for the cell walls of the endosperm of seeds (Reid, 1985).

As mentioned in the Introduction, *E. vaginatum* is a perennial, tussock-forming plant. The tussock is composed of many vegetatively propagated plants that continue to grow upward while dying from the base. Thus, the living plants form a crown upon a mass of dead material that decomposes very slowly in the cold, wet environment. Within each plant, the corm grows from the apical meristem while the distal end of the corm undergoes progressive senescence. Therefore, the plant requires the ability to truncate the vascular system in a progressive way so that nutrients and photoassimilates are not lost to the dead tissues. The vascular sclerenchyma are associated with vascular bundles both within the central cylinder and within the stele of senescing roots. The authors propose...
that another role of the vascular sclerenchyma in the corm and roots is to provide a terminus to the vascular system to reduce solute leakage and/or inhibit pathogen entry as the distal end of the corm, as well as its associated leaves and roots, senesces. Rather than simply block the vascular system, these cells may aid in the recovery of nutrients and their redistribution within the plant.

The cell walls of the vascular sclerenchyma were coloured a dark red (Fig. 1D) or reddish-brown (Fig. 2G, H) in unstained sections. The nature of this colour remains to be elucidated. Seubert (1997) reported that some palm roots have thickened, red-coloured cell walls in the endodermis due to the presence of tannins. This is not the case in E. vaginatum as staining for tannins with dimethoxybenzaldehyde (Mace and Howell, 1974) was negative in the sclereids and the presence of tannins was detected only in vacuoles of some cortical cells (results not shown). Another hypothesis was also explored, whether the red colouration is due to the accumulation of iron in the cell walls. However, cross-sections of corms were examined using energy-dispersive X-ray analysis and the resulting spectra revealed no differences in the levels of iron between sclereids and parenchyma cells (results not shown).

Ecological consequences of internal recycling

E. vaginatum is competitive on cold and infertile sites with other sedges such as Carex bigelowii (Shaver and Laundre, 1997) and E. scheuchzeri (Mark and Chapin, 1989; McGraw and Chapin, 1989), in part because of its high nutrient use efficiency. It is shown that E. vaginatum’s ability to utilize nutrients more efficiently most likely results from its adaptive vascular system. The vascular ring is an unusual and important component of the vasculature as it interconnects the vascular tissues of the leaves and adventitious roots. Because the vascular ring contains both xylem and phloem, it can not only distribute newly acquired nutrients and photoassimilates, respectively, but also redistribute nutrients efficiently from senescing organs to growing organs. Secondly, the vascular ring has transfer cells that border not only vascular bundles, but also parenchyma within the vascular cylinder that can provide easily accessible storage for both mineral nutrients and photoassimilates. Longer term storage of nutrients and photoassimilates probably takes place in the cortical parenchyma because transfer must occur via the endodermis. In addition, the development of sclerified vascular sclerenchyma associated with both vascular bundles and roots allows the plant to retain some of the nutrients that may otherwise be lost during senescence of the corm and its associated adventitious roots. Although some of the nutrients may still leach from the senescing tissues into the dead tissues below the plant, studies have shown that these nutrients can be recovered from the tussock by new roots and recirculated once again to the growing tissues (Jonasson and Chapin, 1991).

The ability of E. vaginatum to retranslocate and store nutrients may also improve its ability to survive additional environmental stresses. For example, E. vaginatum rapidly regrew and expanded its population after fires on the Alaskan tundra (Racine et al., 1987). In addition, E. vaginatum was the only plant to survive and grow on areas that were experimentally surface-saturated with crude oil in a simulated winter spill (Collins et al., 1994; Racine, 1994). In both cases, the plant may have survived initially because it has a slow growth rate, a vascular structure that promotes efficient translocation of nutrients to growing regions and a large storage capacity for nutrients within the corm so that immediate nutrient uptake is not required. Afterwards, the plant could easily expand its population due to lower competition and increased availability of nutrients. Because of these attributes, Racine (1994) has recommended that E. vaginatum be planted for bioremediation of oil spills, especially in areas underlain by permafrost where physical removal of crude oil is undesirable. When used in combination with bacteria to accelerate oil breakdown in situ, planting of E. vaginatum could speed recovery by providing some vegetation cover and below-ground biomass.

One consequence of the efficient storage and recirculation of nutrients within the tissues of E. vaginatum is that minerals not required for growth may also be retained for prolonged periods and could affect the food chain (Stoltz and Greger, 2002). For example, high concentrations of 137Cs have been found to persist in E. vaginatum in ecosystems affected by contamination from the Chernobyl accident (Jones et al., 1998a, b). The mobility and retranslocation of 137Cs within the leaves and corms of E. vaginatum were shown to be similar to other mobile nutrients such as potassium and phosphate (Jones et al., 1998a). The major routes for reducing 137Cs concentrations proved to be dilution by growth and loss through senescing roots (Jones et al., 1998b).

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References

Vascular structure of Eriophorum vaginatum


