

Floral development, fruit set, and dispersal of the Gulf of St. Lawrence Aster (*Symphyotrichum laurentianum*) (Fernald) Nesom

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Abstract: The Gulf of St. Lawrence aster, *Symphyotrichum laurentianum* (Fernald) Nesom is listed as “threatened” according to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). This rare halophyte is found in only a few locations in New Brunswick, Prince Edward Island, and the Magdalen Islands in Quebec. Developmental evidence confirms that there are two types of florets within each flower head and that each floral type has a biseriate pappus. The centrally located “disk” florets are distinctly larger than the more numerous peripheral “pistillate” florets throughout their development. The disk florets are bisexual and consist of an ovule, a style with a bifid stigma, and four to five stamens. The peripheral florets are pistillate and consist of an ovule and a style with a bifid stigma but no stamens. The main goals of this study were to assess fruit set in both types of florets, and the wind dispersal potential of their fruit (achenes). Pistillate flowers had a lower percentage of embryo-containing (filled) achenes (15.1%) than hermaphroditic florets (27.8%) in plants grown ex situ. The majority (68.3%) of filled achenes were produced by pistillate florets. Heads grown in situ had 64.9% filled achenes. Although the achenes of this plant have structures to aid dispersal by wind, in situ observations and experimental data show that this method of dispersal may be affected by the influence of the surrounding vegetation and flooding events. The impact of other factors that may affect the reproductive biology of this rare plant are discussed.

Key words: *Aster laurentianus*, pistillate floret, disk floret, floral morphology, fruit set, threatened species, Asteraceae.

Résumé : L’aster du golfe du St-Laurent, *Symphyotrichum laurentianum*, (Fernald) Nesom est une espèce ‘menacée’, selon le Comité sur le statut des espèces sauvages menacées du Canada (COSEWIC). On ne retrouve cette espèce halophyte rare que dans quelques localités du Nouveau-Brunswick, de l’Île-du-Prince-Édouard, et des Îles de la Madeleine, au Québec. Des preuves développementales confirment qu’il y a deux types de fleurons dans chaque capitule, et que chaque type floral possède une aigrette bisériée. Les fleurons du ‘disque’, situés au centre, sont nettement plus grands que les fleurons pistillés périphériques plus nombreux, tout au long de leur développement. Les fleurons du disque sont bisexués et comportent un ovule, un style avec stigmate bifide, et quatre ou cinq étamines. Les fleurons périphériques sont pistillés et comportent un ovule et un style avec stigmate bifide, mais pas d’étamines. Les auteurs ont cherché principalement à évaluer la mise à fruit chez les deux types de fleurons, et le potentiel de dispersion de leurs fruits (akènes) par le vent. Les fleurs pistillées montrent une plus faible proportion (15,1 %) d’akènes contenant des embryons (pleins) que les fleurons hermaphrodites (27,8 %), chez les plantes cultivées ex situ. La majorité des akènes pleins (68,3 %) proviennent des fleurs pistillées. Les capitules obtenus in situ avaient 64,9 % d’akènes pleins. Bien que les akènes de cette plante aient des structures qui favorisent la dispersion par le vent, les observations in situ et les données expérimentales montrent que cette méthode de dispersion peut être affectée par la végétation voisine et les événements de submersion. On discute des autres facteurs qui pourraient affecter la biologie de la reproduction de cette plante rare.

Mots-clés : *Aster laurentianus*, fleurons pistillés, fleurons du disque, morphologie florale, mise à fruit, espèce menacée, Asteraceae.

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Introduction

The Gulf of St. Lawrence aster, *Symphyotrichum laurentianum* (Fernald) Nesom is listed as “threatened” according to the Committee on the Status of Endangered Wildlife in Canada 2004a (COSEWIC). This annual plant is a rare hal-

ophyte found in a few areas of New Brunswick (NB), Prince Edward Island (PEI), and the Magdalen Islands in Quebec, and grows in salt marshes that are flooded during spring and high tides (Houle and Haber 1990). This aster relies exclusively on its seeds to survive until the next germination season. This feature, combined with a low number of seeds in the soil’s transient and persistent seed banks, the low viability of seeds, and an often unpredictable intertidal environment, makes this endangered plant extremely vulnerable (Kemp 2004). The St. Lawrence aster can grow up to 30 cm in height. This plant has smooth, hairless, and fleshy linear-lanceolate to spatulate, generally sessile leaves (Stewart and Lacroix 2001).

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Symphotrichum laurentianum is part of the North American clade of Asteraceae and belongs to the section *Conyzopsis* (Nesom 1994; Flora of North America Editorial Committee 2006). *Conyzopsis* can be described as having a broad outer zone of pistillate flowers that are more numerous than the central disk flowers (Houle 1988; Nesom 1994). The general floral morphology of *S. laurentianum* (originally classified as *Aster laurentianus*) was first described by Fernald (1914) as “the outer corollas numerous, filiform, without rays, shorter than the style; central corollas few, filiform, with a four to five toothed campanulate limb, yellowish, about equalling the purplish stigmas”. These two types of florets in *S. laurentianum* have never been examined from a developmental perspective to compare their respective developmental pathways.

General observations of developing inflorescences in situ in a recent seed bank study of the Gulf of St. Lawrence aster led to questions relating to differences in morphology of florets within each flower head (Kemp 2003). Preliminary developmental observations suggested that even during early stages of development the central and peripheral floral primordia appear to be visibly different in size and morphology. Could these morphological differences have an impact on a floret's ability to set fruit, given that the Gulf of St. Lawrence aster is believed to be self-fertilized (Houle and Haber 1990) and the central florets release their pollen mostly inside the floret (Kemp 2003)?

In addition to the link between floral development and fruit set, dispersal may also be viewed as a potential barrier to the long-term sustainability of populations of plants. The dispersal biology of plants affects both their regional and local distribution (Clark et al. 1999). Stergios (1976) concluded that the regional distribution of orange hawkweed, *Hieracium aurantiacum* L., was affected by the small percentage of seeds that disperse over long distances, and that the majority of seeds that disperse over short distances defined its local distribution. The spatial distribution of seeds around their source is called a seed shadow (Fenner 1985). Understanding a species' seed shadow may be crucial to studying the vulnerability of these plants to extirpation and habitat loss (Okubo and Levin 1989; Andersen 1991; Gravuer et al. 2003). Dispersal is believed to be very important for pioneer species that inhabit disturbed microsites, as these sites are often relatively far apart and susceptible to disturbances and succession (Gadgil 1971; Bazzaz 1986; Murren and Ellison 1998). For example, Pitelka et al. (1983) noted that the wood aster *Aster acuminatus* Michx. is rarely established, unless there is a disturbance and leaf litter has been removed from the forest floor. The wood aster also has a specialized parachute-like structure, called a pappus, to aid in wind dispersal and produces achenes of varying weight, a potential mechanism to produce lighter achenes that travel further as well as larger achenes that travel smaller distances but have a greater chance of germinating (Pitelka et al. 1983). Gibson (2001) stated that most Asteraceae species produce achenes with a single seed, and that these seeds often possess a pappus to slow the descent of the achene and (or) align the achene for optimum contact and penetration into the soil. The pappus may also function to trap air bubbles to provide buoyancy for dispersal by water currents. Huiskes et al. (1995) determined that the achenes of *Aster tripolium* L., a saltmarsh aster, had a buoyancy period of

7 d. The achene of *S. laurentianum* consists of an embryo surrounded by a brown, hair-covered fruit wall. An accrescent pappus is also evident at maturity (Nesom 1994) and may aid in wind dispersal by slowing the descent of the fruit in the air and by providing buoyancy to the achene in water (R. Steeves, personal observation, 2004). A better understanding of fruit set and dispersal mechanisms of this saltmarsh plant may add valuable information to conservation strategies for *S. laurentianum*, as populations have declined in recent years and no new aster sites have been discovered (Committee on the Status of Endangered Wildlife in Canada 2004b).

This study focusses on two interrelated aspects of the reproductive biology of *S. laurentianum*: the contribution of different floral types to fruit set and the ability of those fruit to be dispersed. Consequently, the specific goals of this study are (i) to compare the developmental morphology of the two types of florets and their potential to set fruit, and (ii) to characterize and assess the dispersal potential for the achenes through in situ as well as ex situ observations and experiments. The ultimate goal of this study is to add valuable information to the growing body of knowledge on the reproductive biology of *S. laurentianum* to aid in developing conservation strategies for this rare endemic plant.

Materials and methods

Scanning electron microscopy

Specimens of *S. laurentianum* were collected from the Dune Slack site (46°24' 51.49"N; 62°59' 41.98"W) and the East Marsh B site (46°24' 55.27"N; 62°59' 06.11"W) on PEI in August 2002. Because of limitations imposed by the PEI National Park authority regarding the collection of this endangered plant, only a small number of inflorescences were collected.

Twenty *S. laurentianum* flower heads at different developmental stages were fixed in formalin – acetic acid – alcohol (FAA), dissected, and dehydrated in a graded ethanol series. These flower heads were then dried in a Ladd model 28000 critical-point dryer using CO₂ as a transitional medium. The dried specimens were mounted on stubs, grounded with silver paint, and coated with 300 Å (1 Å = 0.1 nm) of gold–palladium using a Denton Vacuum Desk II sputter coater. All *S. laurentianum* heads were then viewed with a Cambridge Instruments Stereoscan 604 scanning electron microscope. Digital images of various stages of development were taken using SEMICAPS® software, and thermal prints were made using a Mitsubishi P67U video copy processor.

Sectioning

A head at the floral organ stage of development was dissected to obtain individual florets, which were then dehydrated in a graded ethanol series. These florets were embedded in Spurr resin (medium mixture) in preparation for sectioning (Spurr 1969) to document the presence or absence of floral structures that were not visible using SEM. Individual florets were then placed in embedding moulds filled with Spurr resin and transferred to an oven set at 70 °C for approximately 16 h to allow the resin to polymerize. Resin blocks were sectioned using a Sorvall Porter-

Blum MT2-B ultra-microtome to obtain longitudinal sections of both types of *S. laurentianum* florets. Sections, approximately 2 μm thick, were stained with a 1% toluidine blue O solution in sodium tetraborate and photographed using a Nikon Coolpix 950 digital camera attached to an Olympus BH-2 microscope.

Fruit set

Fruit set was investigated by dissecting mature seed heads ($n = 20$) from plants grown in the laboratory. The seed heads were viewed with a dissecting microscope and dissected with forceps. Achenes were classified based on their floral origin (hermaphroditic or pistillate) and the presence of an embryo (filled) or not (unfilled) and then counted ($n = 2251$). No inferences can be made about the viability of these filled achenes, as they were not tested for their viability. The floral origin was determined visually by noting the remaining structures on the florets. The florets with relatively larger stigmas and four- to five-lobed corollas were classified as hermaphroditic in origin (i.e., disk florets), and florets with smaller stigmas and tubular corollas were classified as pistillate in origin. Achenes were classified as filled or unfilled based on visual inspection. Achenes with an embryo, or filled achenes, typically had a reddish to dark brown fruit wall, were approximately 2.5–3.5 mm in length, and were noticeably wider than the unfilled achenes, which were light-brown to tan coloured, and noticeably shorter in length. Percentages of achenes in each of the four categories were calculated. Mature seed heads ($n = 47$) from plants grown in situ were also dissected in the laboratory for potential seed predation analysis, and achenes were counted ($n = 2247$).

Achene wind dispersal experiments

Ex situ

The descent velocity of *S. laurentianum* achenes was determined in the laboratory by dropping 30 achenes from a height of 2.5 m. The achene was allowed to fall for 0.5 m to attain its maximum velocity. A stopwatch was then used to time the remaining 2 m of vertical descent. This test was performed in a small room with the door sealed with tape to minimize updrafts and turbulence. The descent times (Td, in seconds) and height of descent (Hd, in metres) was used to calculate the mean descent velocity (Vd) of the achenes using the following formula:

$$Vd = Hd/Td$$

A crude wind tunnel was constructed with plastic sheeting, a large 50 cm diameter three-speed fan, and a wire frame. A sheet of paper (0.4 m \times 2.6 m) was coated in glue, then positioned on the bottom of the tunnel to capture the achenes as they fell. This sheet of paper was marked every 5 cm to record the distance travelled. The achenes were released 0.5 m from the fan in an effort to reduce turbulence from a height of 0.1 m at a wind velocity of 2.5 m/s (the velocity at which achene abscission occurred). Wind velocity was measured using a Turbo-meter digital anemometer (Ben Meadows Co., Toronto, Ont.). Achenes were assigned to a distance

category measured in increments of 5 cm, rather than exact horizontal distance travelled, as the sample size was rather large ($n = 178$).

In situ

Wind velocities were recorded in the field using the digital anemometer on windy days during early fall. Velocity was measured at heights of 14, 40, and 60 cm above ground level in patches of *S. laurentianum*. The 14 cm height corresponded to the wind velocities at the average height of the seed head for *S. laurentianum*, the 40 cm height was the wind velocity immediately above the canopy of *Carex* spp., which surrounded *S. laurentianum*, and the 60 cm height corresponded to the wind velocity experienced by the nearby seaside goldenrod *Solidago sempervirens* L., a successful halophyte in the Asteraceae. The three heights were measured consecutively, but as quickly as possible, allowing only a second or two at each level for the anemometer to adjust its speed. Trials in which the wind gusted noticeably between first and third readings were discarded.

Achenes of *S. laurentianum* from mature seed heads were also artificially released in situ by lightly tapping on the stalk of the plant with a pencil. Since many achenes were released in a densely vegetated area, only the maximum and minimum distances travelled were measured along with the wind velocity at the height of the seed head at the time of release.

Qualitative observations of *S. laurentianum* achene dispersal, including distribution of seedlings, surrounding vegetation, and the effect of flooding on the mature seed heads were recorded using a Nikon Coolpix 950 digital camera.

Results

Floral initiation

Floral primordia are initiated centripetally on the broad receptacle of the flower head meristem, which is surrounded by the involucre (Fig. 1A). Initially, all floret primordia appear as hemispherical protuberances of similar size. During later stages of development, prior to the initiation of floral organs, the floret primordia become tubular shaped and two floral morphological types become evident (Fig. 1B). Florets located in the centre of the head are larger and fewer in number ($\bar{x} = 11.6 \pm 2.8$, $n = 12$) than florets located at the periphery ($\bar{x} = 45.5 \pm 7.8$, $n = 4$). The central florets will eventually develop into bisexual disk florets, and the more numerous and smaller peripheral florets will become pistillate florets (Figs. 2F and 2G).

Disk florets

The first structure to be initiated is the corolla tube. At initiation the corolla forms a continuous ring at the periphery of the floret meristem (Fig. 1B). Soon after, four to five corolla lobes become visible (Figs. 1C–1E). Stamens are initiated more or less simultaneously in a position alternate to the lobes of the corolla (Fig. 1D, arrows). As the stamens grow in size and take up most of the space within the floret, the corolla tube begins to cover the inner floral organs (Figs. 1C, 1E, and 1F) and eventually encloses them completely (Figs. 1G, 2B–2D, 2F, and 2G). There is no visible evidence of a style or stigmas prior to

Fig. 1. Developmental flower head morphology of *Symphotrichum laurentianum*. (A) Side view of flower head showing the initiation of floral primordia (arrow on inflorescence shows one floral primordium). Note the presence of phyllaries (P) on the periphery of the inflorescence. Scale bar = 75 μm . (B) Large bisexual florets (*) are distinguishable from smaller female florets (♀) during early stages of development of floral primordia. Scale bar = 75 μm . (C) Initiation of stamen primordia (arrow indicates one stamen) alternate to lobes of the corolla (C). Scale bar = 75 μm . (D) Higher magnification of a bisexual floret at a slightly earlier stage of development than Fig. 1C showing all stamen primordia (arrows). Note the first visible sign of initiation of stamens (*) in adjacent floret labelled A. Scale bar = 30 μm . (E) Corolla lobes (C) begin to cover developing stamen primordia (arrows) shortly after they are initiated. Scale bar = 30 μm . (F) Extent of corolla tube (C) development on female floret in comparison with bisexual floret shown directly above (♀♂). Scale bar = 30 μm . (G) Relative sizes of female (♀) and bisexual (♀♂) florets at a slightly later stage of development than Fig. 1F. O, ovary; Pa, pappus; C, corolla. Scale bar = 30 μm .

bud closure (Fig. 1F). By the time the floral bud is completely closed, the pappus forms at the base of the corolla (Fig. 1G), and the inferior ovary continues to develop (Figs. 1G and 3B). Throughout development, the disk florets are comparatively much larger than the pistillate florets (Figs. 1B and 1G, Figs. 2B, 2D, and 2G). From an anatomical and morphological point of view, the disk florets appear to be functionally hermaphroditic.

Pistillate florets

Similarly to their hermaphroditic counterparts, the corolla tube of the pistillate florets is initiated as a continuous ring at the periphery of the floral bud (Figs. 1F and 1G). The tubular shape of the floret is also evident as the inferior ovary develops (Figs. 1G and 3A). Lobes are visible shortly after the initiation of the corolla tube, but in contrast with hermaphroditic florets, stamens are not initiated (Figs. 2A and 2B). This is also confirmed in longitudinal sections of older florets (Fig. 3A). The corolla of the pistillate florets does not develop to the same extent as that of the hermaphroditic florets and, as a consequence, never completely encloses the floral bud. Two prominent stigmas protrude from the corolla tube shortly after the lobes have formed (Figs. 2C and 2D). In addition, a ring of developing pappus surrounds the base of the corolla at that stage of development. A second ring of pappus forms at a later stage of development, and the lobes of the corolla tube are no longer visible (Fig. 2E). A biseriate pappus is also visible on centrally located bisexual flowers (Fig. 2D). The pappus becomes a prominent and noticeable characteristic on nearly mature flower heads (Figs. 2F and 2G).

Fruit set

Dissection of seed heads grown in the laboratory revealed that 17.6% of achenes had an embryo. Most of the achenes from both disk and pistillate florets were unfilled, but pistillate florets had a higher proportion of unfilled achenes than hermaphroditic ones (Table 1). Although pistillate florets had a lower percentage of filled achenes (15.1%) than disk florets (27.8%), the majority (68.3%) of filled achenes were produced by pistillate florets, since pistillate florets were more abundant than disk florets. Heads grown in situ had 64.9% filled achenes. Distinction between types of florets was not considered accurate enough in this situation to separate them in two categories. There appears to be no morphological differences in mature flower heads between pistillate or disk floret-derived achenes; they are indistinguishable in all visual aspects at maturity.

Achene dispersal experiments

Ex situ

The mean descent velocity of *S. laurentianum* achenes in the lab trials was 0.26 m/s and ranged from 0.2 to 0.36 m/s ($n = 30$). In the wind tunnel experiment, achenes broke free from the inflorescence at a velocity of 2.5 m/s. The dispersal of the achenes released at a height of 0.1 m produced a triangular-shaped seed shadow that started at the 0–5 cm mark, was densest (achenes per distance category) at 15–20 cm, and generally decreased in density until no achenes were found beyond 90–95 cm (Fig. 4). Additional experiments were conducted at various wind velocities. However, low wind velocities (<2.5 m/s) failed to detach achenes, and higher wind velocities created too much turbulence for analysis.

In situ

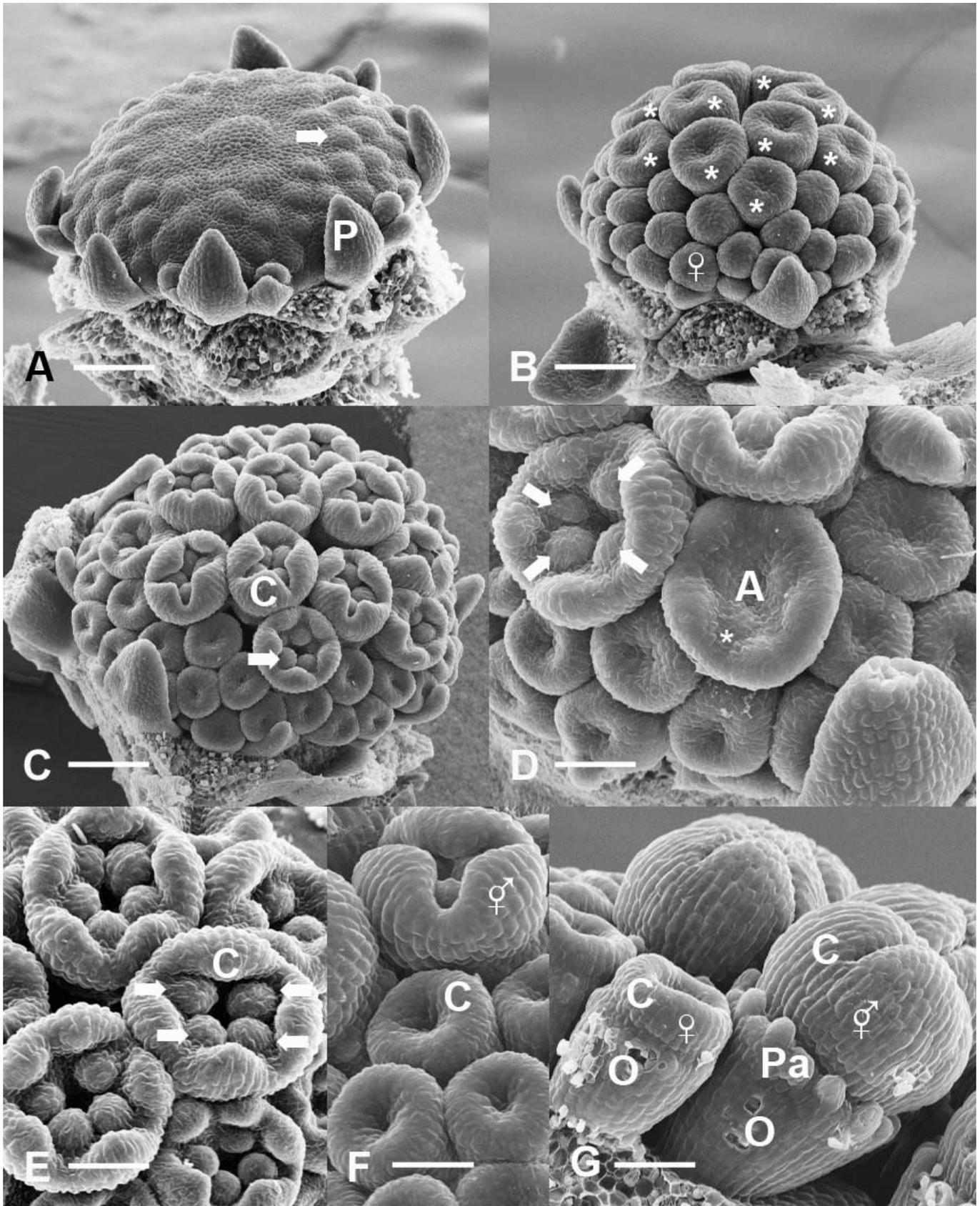
Wind velocities increased with height above the ground at the National Park site (Fig. 5). The achenes that were artificially released travelled horizontally a minimum of 0.5 cm and a maximum of 23 cm from their point of release in horizontal wind velocities of 1–2.1 m/s. It was noted that achene travel was impeded when they hit the surrounding vegetation of *Carex* spp., and no updrafts could be detected with the anemometer.

Symphotrichum laurentianum seedlings were generally found in the immediate area surrounding the previous year's plants. These areas were precisely identified by the presence of remnants of stem and inflorescence heads from the previous growing season. Another common observation was "clustering" of many seedlings (approximately 20–30) in a small area, suggesting that seed heads failed to lose most of their achenes before they fell onto the soil. A high, storm-generated tide in mid-October flooded all three sites in the Park. This caused the seed heads to close up. When the bracts dried, they encapsulated the achenes. This made the pappus structure of the achenes less available to the wind, and therefore harder to detach. These closed seed heads were experimentally subjected to wind velocities up to 6.9 m/s, and no achenes were dislodged.

Discussion

Floret dimorphism

Our developmental evidence confirms that there are two distinct floral types, disk florets and pistillate florets, from the onset of floral organ initiation. This condition, referred to as gynomonoeicy (Weberling 1989), is common within the Asteraceae family. *Symphotrichum laurentianum* has more numerous peripheral pistillate florets than disk florets,



a morphological difference in comparison with other members of the genus. Since pistillate florets do not produce pollen, a costly expenditure in terms of resource allocation, this

condition may be perceived as a strategy, at the level of the plant, for increased seed production and (or) seed quality. More specifically, a reallocation of resources in pistillate

Fig. 2. Developmental flower head morphology of *S. laurentianum*. (A) Absence of stamens (arrow) within the corolla tube (C) in female florets. Scale bar = 30 μm . (B) Side view of inflorescence showing the relative sizes and stage of development of the corolla of female ($\text{\textcircled{f}}$) and bisexual ($\text{\textcircled{m}}$) florets. Scale bar = 75 μm . (C) Top view of inflorescence showing the number and relative distribution of the two floral types. Scale bar = 150 μm . (D) Appearance of stigmas (arrows) on female florets coincide with the development of the pappus (Pa) on those florets. Scale bar = 75 μm . (E) Higher magnification of female floret at a later stage of development than Fig. 2D showing pappus (Pa), corolla tube (C), and protruding stigmas (St). Scale bar = 30 μm . (F) The difference in size between the two floral types is consistent throughout development. Arrow, protrusion of stigmas on female florets. Scale bar = 150 μm . (G) Side view of nearly mature inflorescence showing large, closed, centrally located hermaphrodite florets ($\text{\textcircled{m}}$) surrounded by smaller female florets ($\text{\textcircled{f}}$) embedded in a well-developed mass of pappus. Scale bar = 300 μm .

flowers may offer this plant a greater success in seed production (Charlesworth and Charlesworth 1978; Williams et al. 2000).

An interesting aspect of the developmental morphology of the two floral types is the fact that they remain strongly dimorphic throughout their development. They are similar in appearance (not size) only during the initiation of the corolla tube, the earliest stage of floral organ development. Further stages of development are strikingly different. In contrast with dimorphic floral systems in other taxa (e.g., Cheng et al. 1983; Gallant et al. 1998; and Caporali et al. 2003), the pistillate florets of *S. laurentianum* did not show any evidence of vestigial or aborted stamens. Thus, the strong dimorphism between floral types is further accentuated by the lack of development of male organs in pistillate florets.

Another noteworthy aspect of the developmental morphology of the two floral types in *S. laurentianum* that may contribute to its taxonomy is the presence of a biseriate pappus. Although this feature is difficult to assess on mature florets, it was clearly visible on floral primordia of *S. laurentianum* during early stages of development (Figs. 2E and 2F). Even if it is not always obvious, the presence of a biseriate or triseriate pappus is believed to be consistent in all sections of the genus and its close relatives (J.C. Semple, personal communication, 2004).

Pistillate florets

From an evolutionary perspective, the peripherally located pistillate florets are believed to be modified rays (Luc Brouillet, personal communication, 2004; Flora of North America Editorial Committee 2006). In some members of this tribe, the corolla of the peripheral florets can be reduced to the tubular portion of the corolla or to a short ring (Heywood et al. 1977). Strother (1997) suggests the term "disciform heads" to characterize composite inflorescences that do not have the standard "radiate head". Developmentally, the pistillate florets of *S. laurentianum* show evidence of lobing on the corolla tube only during early stages of development. However, there is no sign of a strap that would characterize the pistillate floret of *S. laurentianum* as a ray floret by the time the second row of pappus forms and the stigmas begin to protrude from the corolla tube during later stages of development (Fig. 2E). A developmental study of an ancestral sister species, such as *Symphotrichum frondosum*, with florets that have short ray straps could provide a good comparative basis to confirm the idea that these pistillate florets are modified rays.

Heterogamous capitula (those with more than one sexual form found on the flower head) and radiate capitula (with ray florets) do not always display the typical acropetal pat-

tern characteristic of primary capitula. Numerous members of the Asteraceae with these types of primary capitula display a lag in the initiation of ray or peripheral florets and therefore have a centripetal sequence of floral initiation (Classen-Bockhoff 1996; Harris 1999). This appears to be the case for *S. laurentianum*, where the initiation of the corolla tube in pistillate florets only begins after organogenesis has taken place in the central bisexual florets.

Fruit set

The percentage of filled achenes from laboratory-grown plants (17.6%) was over three times lower than plants from in situ locations (64.9%). This low rate of fruit set may be due to a lack of wind (to move pollen within inflorescences) and (or) insect pollinators in the laboratory setting. It is important to note, however, that *S. laurentianum* is believed to be self-fertilized (Houle and Haber 1990). Another important aspect of the reproductive biology of *S. laurentianum*, in addition to fruit set, is the ability of this fruit to be dispersed.

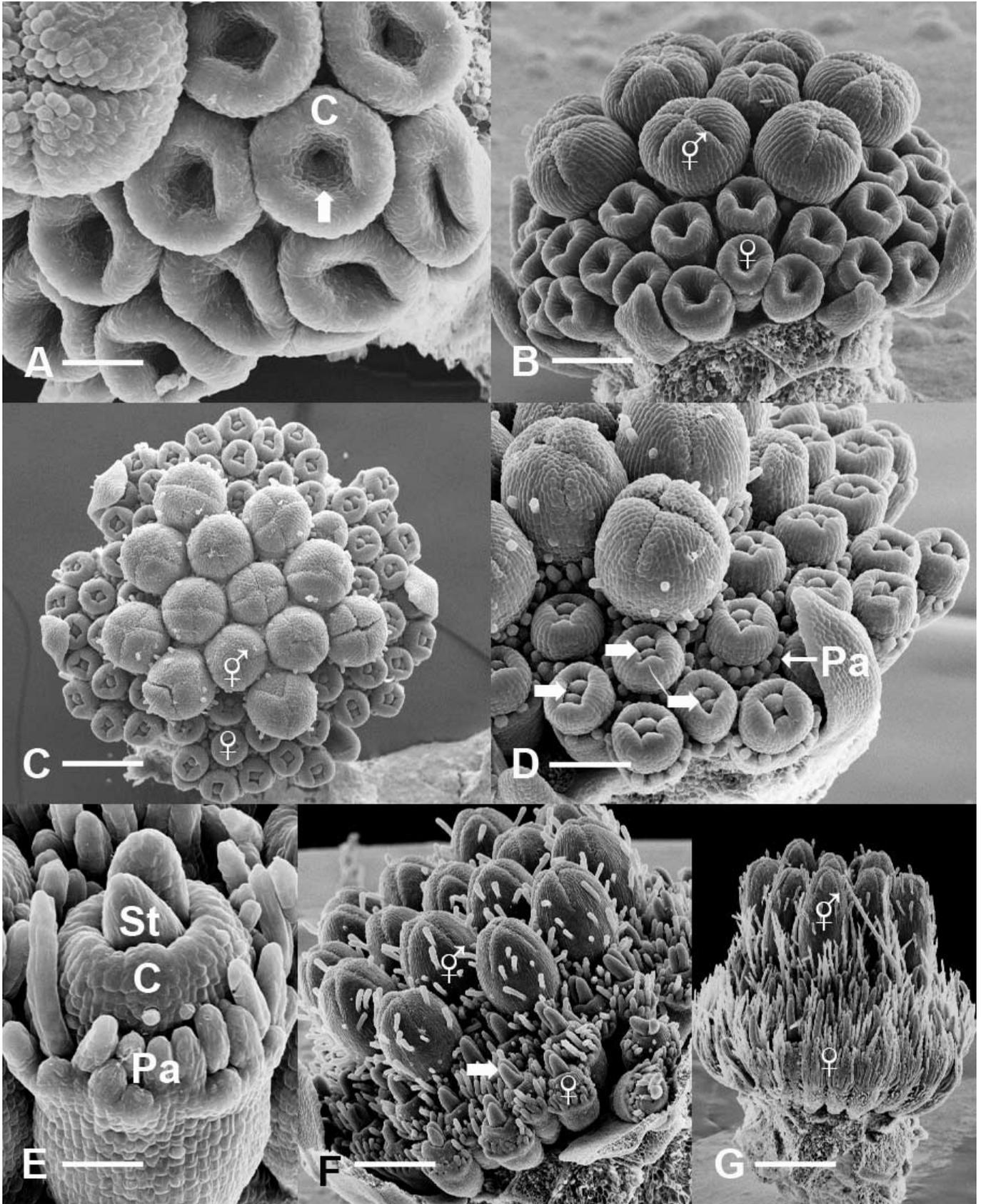
Wind dispersal potential

Ex situ

The descent velocity calculated for the achenes of *S. laurentianum* was much slower than those of three common and widespread members of the Asteraceae family (ACCDC 2004) determined by Matlack (1987) (Table 2). A slower descent velocity is more favourable to dispersal, because the slower the achene descends, the further it will travel laterally in a horizontal wind before it rests on the ground (Sheldon and Burrows 1973). The descent velocity of seeds is regarded by some as the single most important factor in determining a species' dispersal ability (Andersen 1991; Tackenberg et al. 2003), but in many circumstances, environmental and physical conditions must also be considered (Sheldon and Burrows 1973). These environmental and physical conditions may include humidity, wind velocity, a threshold wind needed for seed abscission, height of release from plant, and the effect of any surrounding vegetation (Sheldon and Burrows 1973). Matlack (1987) proposed that the average dispersal distance (D) in horizontal laminar flow could be calculated with the horizontal wind velocity (V_h), height of release (H_t), and descent velocity (V_d) of a given plant using the formula:

$$D = V_h(H_t/V_d)$$

In the wind tunnel, a velocity of 2.5 m/s was required to detach the achenes from their seed head. With this velocity,



a height of release of 0.1 m, and a descent velocity of 0.26 m/s, the achenes of *S. laurentianum* traveled a median distance of 0.45–0.5 m in the wind tunnel. In these same

conditions, the formula used by Matlack (1987) would predict an average dispersal distance of 0.96 m, more than three times the observed mean. Therefore, this formula for aver-

Fig. 3. Floral anatomy of *S. laurentianum*. Longitudinal sections of nearly mature florets. (A) Pistillate floret with corolla (C) encircling the protruding stigmas (St). Note the presence of an ovule (O) and pappus (Pa). Scale bar = 28 μm . (B) Bisexual floret with corolla (C) enclosing anthers (A) and style (S). Note presence of an ovule (O) and pappus (Pa). Scale bar = 49 μm .

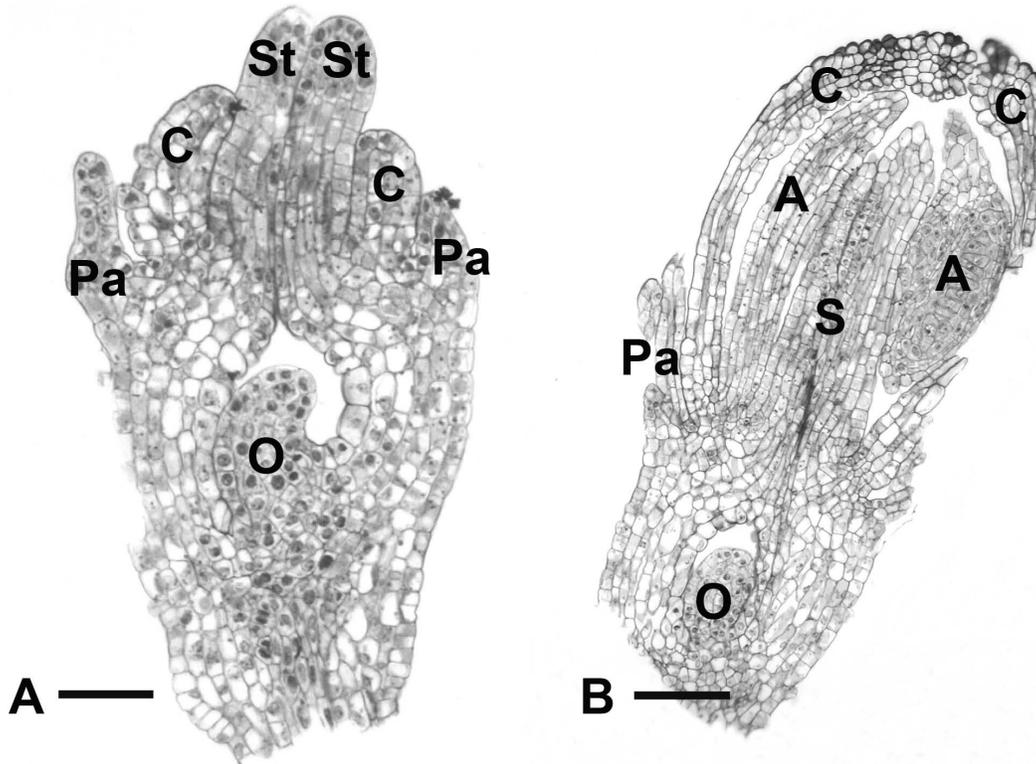


Table 1. Percentages of filled and unfilled achenes counted ($n = 2251$) for fruit-set experiment of *S. laurentianum* plants grown ex situ.

Floret type	% of total achenes			% for each floret type		
	Filled	Unfilled	Total	Total	Filled	Unfilled
Hermaphroditic (disk)	5.3	13.6	18.9	18.9	27.8	72.2
Pistillate	12.3	68.9	81.2	81.1	15.1	84.9
Total	17.6	82.5				

age dispersal distance did not correspond well with the results of the wind tunnel experiment. However, absolute laminar flow was not achieved in the wind tunnel, and there was turbulence, a factor the formula doesn't take into consideration. The wind velocity used in the tunnel was also greater than the maximum wind velocity that was measured at the level of the asters in the field (1.6 m/s). Sufficient wind velocities needed for achene detachment may occur during storms or in stronger wind events. In addition, the wind tunnel also did not have any structures to mimic the effect of the surrounding vegetation found in situ. Consequently, the wind tunnel experiment cannot be used as a reliable model of the actual dispersal capability of *S. laurentianum*, but at least gives an idea of possible dispersal distances. Based on the shadow of *S. laurentianum*, the highest number of achenes travelled 0.15–0.20 m, and the number of achenes per 0.05 m generally decreased thereafter. This trend for the majority of the achenes to disperse relatively short distances from the plant is consistent with the finding of many other studies of seed dispersal (Sheldon and Burrows 1973; Stergios 1976; Andersen 1991; Courtney

and Ellison 1998). For example, Stergios (1976) found that 94.9% of *H. aurantiacum*, achenes fell within 1 m of the source plants.

In situ

The wind velocity recorded at the level of the seed heads of the Gulf of St. Lawrence aster was considerably lower (<1 m/s) than the wind velocities of 3 m/s experienced above the surrounding canopy of sedges and nearly 5 m/s over the nearby seashore goldenrods. This difference was measured over a very small vertical differential of 0.46 m between the goldenrod and *S. laurentianum* and 0.26 m between the sedges and *S. laurentianum* plants. Increasing wind velocity with increasing height above ground was also found in a study by Burrows (1973). This low velocity below the canopy is most likely caused by a sheltering effect of the dense vegetation of sedges. A critical difference noted between those common members of the Asteraceae and the rare *S. laurentianum* is that all common members studied by Matlack (1987) typically grow to heights greater than surrounding vegetation, whereas *S. laurentianum* did not. Nu-

Fig. 4. Seed dispersal potential of *S. laurentianum*. Distance travelled by achenes ($n = 178$) in wind tunnel (height of release = 0.1 m, and wind velocity = 2.5 m/s).

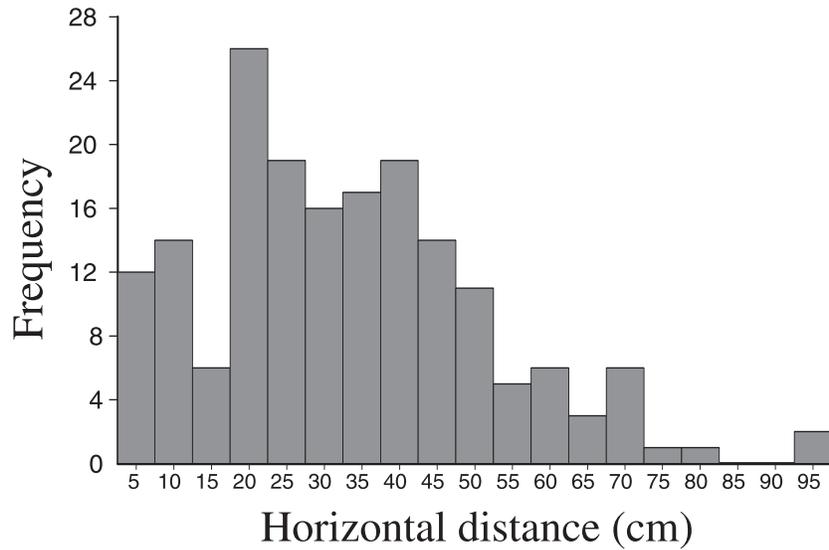
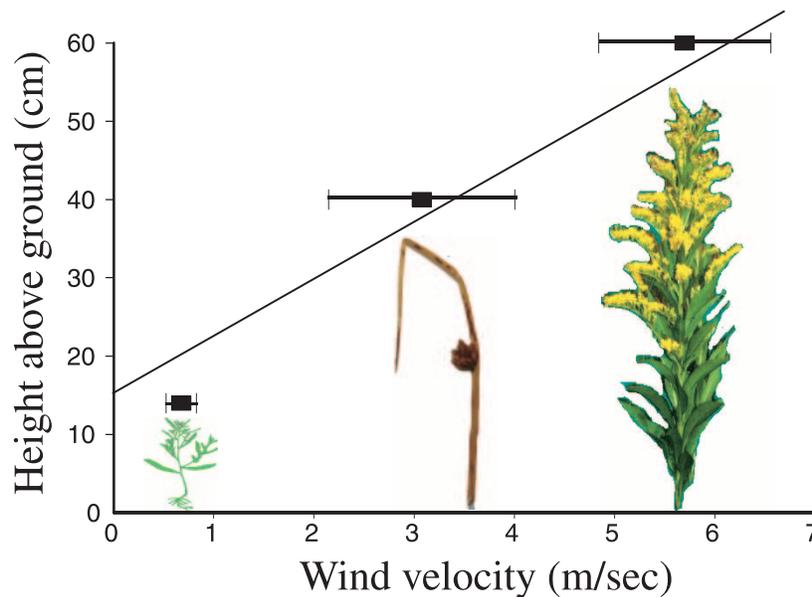


Fig. 5. Relationship between mean wind velocity measured at three heights above the ground at Blooming Point, PEI National Park. Measurements were taken at 14 cm (height of *S. laurentianum*), 40 cm (height above canopy of *Carex* spp. surrounding *S. laurentianum*), and 60 cm (height of nearby *Solidago sempervirens*). The line indicated linear regression ($r^2 = 0.88$, $y = 8.23x + 12.21$). Whiskers indicate standard deviation.



merous studies have noted that species whose flowers are sheltered by the surrounding vegetation are at a disadvantage to wind dispersal, because the surrounding vegetation decreases the wind velocity experienced by the seeds and obstructs the movement of achenes (Sheldon and Burrows 1973; van Dorp et al. 1996). It is also important to note that the maximum velocity measured at the height of *S. laurentianum* was not sufficiently fast enough, based on lab results, to detach the achenes from their inflorescences. However, wind velocities were only measured on two different days, and velocities needed for achene abscission may occur during more extreme meteorological conditions.

The achenes that were artificially released in the field in a

maximum wind velocity of 1.6 m/s and from a height of 0.14 m travelled a maximum of 0.23 m, the same pattern observed in the wind tunnel experiment. Using the same parameters, Matlack's (1987) formula (eq. 2) predicts a mean dispersal distance of 0.86 m, more than three times the observed maximum distance. Therefore, the formula does not accurately predict *S. laurentianum* achene dispersal because it does not take into account the fact that the surrounding vegetation impedes the horizontal travel of the achenes by altering the wind patterns in a similar manner to the turbulence in the wind tunnel. The difficulty with Matlack's (1987) formula is that it assumes a constant wind velocity between the point of release and the ground. The wind ve-

Table 2. Descent velocities of *S. laurentianum* compared with successful members of the Asteraceae reported by Matlack (1987).

Scientific name	Common name	Descent velocity (m/s)
<i>Taraxacum officinale</i> (L.) Weber	Dandelion	0.42
<i>Tragopogon porrifolius</i> L.	Goatsbeard	0.30
<i>Aster acuminatus</i> Michx.	Wood aster	0.41
<i>Symphotrichum laurentianum</i>	Gulf of St. Lawrence aster	0.26

locity profile for falling achenes was not investigated in this study, but results from the three heights studied suggest that wind velocity should decrease towards ground level. Turbulence, or vertical wind flow, is believed to be important to the long distance dispersal of seeds, as updrafts may carry seeds higher above the ground, effectively increasing their height of release (Sheldon and Burrows 1973; Harper 1977; Tackenberg 2003). Updrafts are not believed to be important for *S. laurentianum*, because no vertical wind velocities were measured at the level of the asters, due to the influence of the dense surrounding canopy of vegetation.

Related field observations

Field observations of the plants support the experimental results of low-dispersal capability. First, all the asters growing in PEI sites were found near the previous year's plants, sometimes forming dense aggregations immediately around the remnant plants. Second, plant density decreased with increasing distance away from remnant plants, thereby creating a seedling shadow. In other places, dense clusters of seedlings indicated that achenes failed to detach from the seed heads. These dense clusters may be related to the sheltering effect of the surrounding vegetation and (or) the occurrence of tidal flooding events causing the damp mature seed heads to close up and eventually detach as a unit.

Although the achenes of *S. laurentianum* are morphologically suited for wind dispersal, environmental conditions in the plant's natural habitat greatly limit its ability to disperse by wind. It is concluded that *S. laurentianum* probably disperses only short distances via wind currents. It is also important to remember that dispersal is highly dependent on local habitat and meteorological conditions, making predictions of a plant's dispersal ability difficult and possibly inaccurate, but in this case, the field observations were at least similar to those reproduced in the wind tunnel experiments. *Symphotrichum laurentianum* is not restricted to wind dispersal. The pappus structure and hairs on the fruit wall may provide buoyancy to the achene and increase its ability to disperse via water currents. Like many other halophytes, *S. laurentianum* may be dispersed by tides and (or) ocean currents as well (Huiskes et al. 1995).

Additional barriers to seed dispersal

Other important factors also have the potential to alter the dispersal of *S. laurentianum*. These need further investigation but are reported here as preliminary observations that

were recorded with our main data. A predispersal seed predator, identified as a member of the order Lepidoptera (butterflies and moths) consumed over 50% of the achenes ($n = 441$) in one site on PEI and attached parts of the pappus to its silken larval case.

Another potentially important threat to *S. laurentianum* is the Rayless Alkali aster, *Symphotrichum ciliatum* (Ledebour) Nesom, a first record on PEI (Sean Blaney, ACCDC, personal communication, 2005). It was found growing in similar habitats as *S. laurentianum* but fortunately not in the same locations. This exotic invasive plant may potentially invade the habitat of *S. laurentianum* or hybridize with this rare plant.

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