Factors Influencing Reproduction in American Wild Celery: A Synthesis

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ABSTRACT

Dramatic declines in American wild celery (*Vallisneria americana* Michaux), a native submersed aquatic plant, have been widely reported in the United States since the 1960s, especially from the Midwest to the Northeast. Though methods for restoration are being developed and implemented, progress has been hampered by the need for greater understanding of the species' biological traits and response to environmental change. Here, we review available literature on reproductive ecology of wild celery, focusing on environmental influences on the production and early stages of growth of different propagule types. A background profile of the species describes its ecological importance, field characteristics, taxonomy, life history, and geographical distribution. Critical gaps in present knowledge indicate much has yet to be learned to identify different ecotypes of wild celery based on phenological and genetic distinctions. Further research is also needed to assess potential establishment from seed for consideration as an alternative to (or supplement to) vegetative propagules in restoration strategies.

Key words: ecology, Hydrocharitaceae, propagules, restoration, seeds, submersed aquatic vegetation, *Vallisneria americana*, winter buds.

INTRODUCTION

Background

Management efforts to restore and maintain native submersed aquatic vegetation (SAV) have prompted much research on reproductive ecology of American wild celery (Figure 1). Established stands of this native species help to improve water quality and clarity and provide an important source of food and habitat for fish, wildfowl, and invertebrates (Haller 1974, Poe et al. 1986, Korschgen et al. 1988, Wigand et al. 2000). However, survey records since the late 1960s show declines in wild celery and other SAV, especially from backwaters of Upper Mississippi River to the Potomac River/Chesapeake Bay region (Fischer and Claflin 1995, Moore et al. 2004). These widespread losses in vegetation have raised considerable concern, and increased the need to determine causal conditions and to develop effective restoration methods. Reasons for the declines appear to vary but most are thought to be linked to severe natural and/or anthropogenic ecosys-
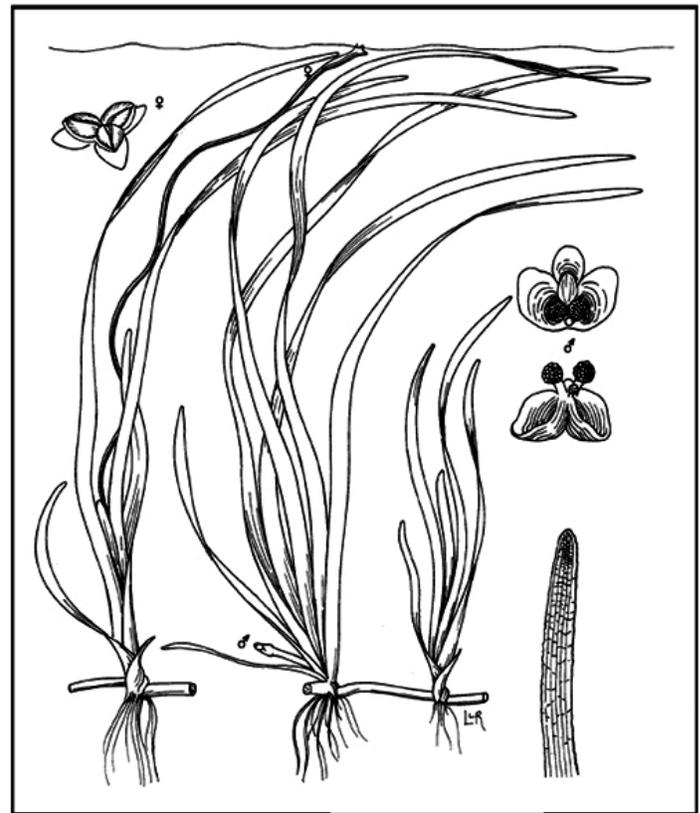
Figure 1. Morphology of wild celery (*Vallisneria americana* Michaux). Image by IFAS Center for Aquatic Plants, Univ. of Florida, Gainesville 1990.

tem disturbances, such as eutrophication, drought, flooding, herbicides, navigation, and herbivory (Cooke 1983, Kemp et al. 1983, Carter and Rybicki 1985, Twilley et al. 1985, Kimber 1994, Kimber and Barko 1994, Rogers et al. 1995, Stewart et al. 1997). Thus far, attempts to restore wild celery populations have not all been successful because requirements for propagule growth were not adequately met in the field. Developing effective restoration strategies for SAV requires thorough knowledge of species biological traits and propagule production, early stages of growth, and establishment in response to key environmental conditions (e.g., light, temperature, sediment, and water chemistry).

Approximately 20 years have passed since the report by Korschgen and Green (1988) on the ecology of wild celery for consideration in restoration programs. Although their report provides a wealth of important information, a great deal of research has been generated since their review was con-

ducted. In this paper, we present an update on the reproductive ecology of wild celery, based on a search of literature, much of which was published over the last two decades. Topics concerning propagation and transplanting techniques are not specifically addressed here because these have been described to a great extent in publications elsewhere (e.g., Smart et al. 1998, Smart and Dick 1999, Dick et al. 2005, Smart et al. 2005, Moore and Jarvis 2007).

Taxonomy and Nomenclature

Kingdom: Plantae; Subkingdom: Tracheobionta; Division: Magnoliophyta; Class: Liliopsida; Subclass: Alismatidae; Order: Hydrocharitales; Family: Hydrocharitaceae; Genus: *Vallisneria*; Species: *americana* (ITIS 2007).

Vallisneria is one of 17 genera of the frogbit (Hydrocharitaceae) family, which consists of a large, diverse group of monocotyledonous, mostly perennial, aquatic herbs. Fourteen genera including *Vallisneria* (as well as *Apalanthe, Appertiella, Blyxa, Egeria, Elodea, Hydrilla, Hydrocharis, Lagarosiphon, Limnobium, Maidenia, Nechamandra, Ottelia,* and *Stratiotes*) occur in fresh-to-brackish waters, while the remaining three genera (*Enhalus, Halophila,* and *Thalassia*) occur in marine environments (Cowardin et al. 1979, GRIN 2005, Watson and Dallwitz 2005, FNA 2007).

Identification of *Vallisneria* species has historically been problematic due to plastic responses to changes in the environment and similarities among taxa in floral morphology. The present consensus is that the genus consists of two separate species, and that each species, in turn, is differentiated into two varieties: (1) *V. spiralis* L. var. *spiralis* is found in Europe and southwest Asia, and (2) *V. spiralis* var. *denseserrulata* Makino, in Africa, Asia, Oceania and Australia; (3) *V. americana* Michaux var. *americana* is found in the Americas, East and Southeast Asia, Oceania, and Australia, and (4) *V. americana* var. *biwaensis* (Miki) Lowden, comb. nov. in Japan, Hispaniola, and Venezuela. These taxa are delineated based on floral distinctions described most recently by Lowden (1982) in his treatment of the genus.

Misidentification of field specimens of *Vallisneria* has resulted in numerous synonyms for *V. americana* in published literature. The North American plant (*V. americana* var. *americana*) originally described by Michaux (1803) has been reported by many others as a variety of the European species *V. spiralis* (Gray 1848, 1867, Chapman 1883, Britton and Brown 1913). Adding further confusion to the nomenclature, populations of large, robust plants were named *V. neotropicalis* Marie-Victorin denoting the region of natural occurrence (Marie-Victorin 1943, Long and Lakela 1971). Godfrey and Wooten (1979) expressed concern about the distinctness of this species, suggesting that large plants may result in southern climates from conditions favoring growth over a longer growing season. This is likely the case for plants growing in clearwater springs in Florida, where year round the springs remain at a nearly constant cool temperature (~21 C). Lowden (1982) has provided an extensive list of synonyms for *V. americana* (var. a*mericana*), which at the species level includes: *V. neotropicalis, V. spiralis, V. gigantea, V. asiatica, V. subulispatha, V. higoensis,* and *V. natans.* Common names include American wildcelery (with "wildcelery" spelled as one or two words), wild celery, water

celery, eel-grass, tape grass, canvasback grass, duck celery, oxtongue, plantain, and flumine-Mississippi (McAtee 1939, GRIN 2005, USDA NRCS 2007). For ease of discussion, the term wild celery will be used to indicate *Vallisneria americana* var. *americana* hereafter in this manuscript.

Distribution

Wild celery is native to eastern North America and is common from southern Canada southward to Texas and Florida. The northern part of its range extends east in Canada from Nova Scotia, west through southern Quebec and northern Ontario to southeastern Manitoba (Catling et al. 1994). Though absent from Saskatchewan and Alberta, it occurs in southern British Columbia, including two known locations on Vancouver Island (Catling et al. 1994). The species is listed in 41 states in the United States (Figure 2; USDA NRCS 2007) and is the most abundant SAV species in the Lake Huron-Lake Erie Corridor (comprised of St. Clair River, Lake St. Clair, and Detroit River; Schloesser et al. 1985, Schloesser and Manny 1986, 1990). It is found south of the United States in Mexico, Cuba, Guatemala, and Honduras, and probably because of its broad synonymy, is also reported from east and Southeast Asia, Oceania, and Australia (Lowden 1982, Korschgen and Green 1988).

Morphology and Reproduction

Wild celery is a perennial, submersed aquatic plant, with ribbon-like leaves, up to 2 m or more in length, depending on water movement and depth (Lovett-Doust and LaPorte 1991). The leaves arise in a cluster (rosette) from a short vertical stem that sends out rhizomes and stolons from which new shoots develop (Figure 1). Leaves are finely veined and show a central longitudinal stripe. Roots are unbranched and fibrous at the base of each rosette. Leaf tips are bluntly rounded; leaf margins are entire to conspicuously toothed.
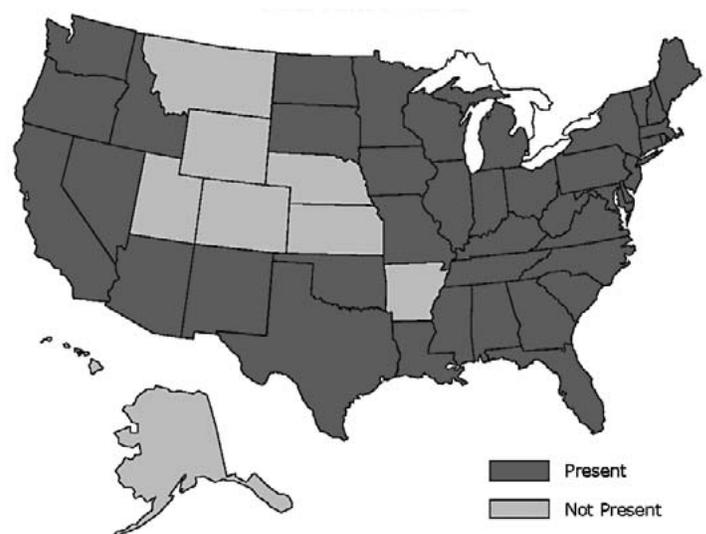
Figure 2. Distribution of wild celery in the United States, according to USDA NRCS Plants National Database 2007.

According to Lowden (1982), two variants exist in the United States:

- *Narrow-leaved variant*—with leaves <10 mm wide, from 3 to 5 longitudinal veins, and margins entire to finely toothed; blades with perceivable to invisible transverse pigmented striations; found mostly in freshwater inland waterways, lakes and lagoons.

- *Broad-leaved variant*—with leaves 10 to 25 mm wide, from 5 to 9 veins, and conspicuously toothed margins; blades with many visible transverse pigmented striations; occurs in coastal freshwater inlets or spring-fed waterways with nearly constant year-round temperatures, subject to brackish water inputs at high tide. [Catling et al. (1994) noted this variant does not occur in Canada.]

Individual plants of wild celery are either male or female (dioecious) and are capable of reproducing through asexual (vegetative) and sexual means. Pollination of pistillate (female) flowers takes place at the water surface (epihydrophily) and is adapted to avoid pollen hydration before transport onto receptive stigmata (Wylie 1917, Svedelius 1932, Kausik 1939, Hill 1965, Cox 1988). Flowering usually occurs in mid- to late summer; fruits mature by early fall (Catling et al. 1994). Pistillate flowers (Figure 3) have three sepals and three white petals and are borne singly in a tubular spathe (a large bract or modified leaf) on a peduncle (stalk) that elongates upward. As many as 2000 staminate (male) flowers, each approximately 0.6 mm in diameter, fit tightly into an ovoid spathe on a short peduncle attached near the base of the plant (Wylie 1917; Figure 3). An abscission zone develops on this short peduncle, allowing the spathe to float and release its staminate flowers on the surface. Surface-tension depressions formed by pistillate flowers force staminate flowers to slip downward and tip pollen grains onto the stigmata. During submersion by waves, pistillate flowers may also form bubbles that enclose flowers of both sexes together, enabling flower tumbling and transfer of pollen (Svedelius 1932, Cox 1988, 1993).

After pollination, the stalk of the pistillate flower begins to coil, drawing the fruit downward where it continues to develop under water. The fruits are cylindrical capsules (Figure 4), 5 to 15 cm in length, each with hundreds of tiny, dark seeds (1.8 to 2.6 mm long × 0.6 to 1.0 mm wide) embedded in a mass of clear-to-whitish gelatinous material. In field populations, each capsule may contain approximately 150 to 500 seeds with viability as high as 93 to 98% (Godfrey and Wooten 1979, Lovett-Doust and LaPorte 1991, Lokker et al. 1997).

An emphasis on clonal growth in wild celery is reflected by its ability to produce a variety of asexual propagules. Winter buds (Figure 4) are produced in the sediments in cool temperate regions as a means of reestablishing the population after over-wintering; these propagules are also referred to in the literature as tubers and turions, though discrepancies in terminology are acknowledged by some experts (M. S. Ailstock 2006, pers. comm.[2]). After lying dormant throughout the winter, the winter bud elongates in spring, sending a

Figure 3. Wild celery pistillate flowers (top: image by Maryland DNR 2005) and staminate inflorescence (bottom: image from the Dept. of Botany, Plant Teaching Collection, Univ. of Wisconsin, Madison 2006).

specialized stem (stolon) to the sediment-water interface from which a new plant emerges (Wilder 1974). In a single growing season, this new plant may generate 20 to 40 ramets (Korschgen and Green 1988, Catling et al. 1994) along prostrate stems in the form of rhizomes (belowground) and stolons (aboveground), serving to expand the population laterally over short distances. Because vegetative propagules

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[2]Ailstock, M. S. 2006. Personal communication. Director, Environmental Center, Anne Arundel Community College, Arnold, MD 21012-1895.

Figure 4. Wild celery seeds and seedpods (top: photo by ERDC 2000) and winter buds (bottom: photo by Maryland DNR 2005).

of wild celery are normally anchored or buried in sediment, they are less likely than seeds to be swept to new sites by water movements or wind. Thus, for this species, seeds provide a possible mechanism for dispersal while also serving to establish new genotypes from existing populations.

Winter buds are well documented as structures for carbohydrate storage and over-wintering of wild celery naturalized in northerly (cool) locations (Korschgen and Green 1988, and literature therein). However, basal stem sections and root stocks may play a similar role in perennation of the species growing in warmer regions, although this is less frequently reported in the literature (Haller 1974). These observed differences in plant phenology have led to recognition of northern and southern ecotypes (Smart and Dorman 1993, Smart et al. 2005), with possible genetic and other distinctions that need to be investigated. To our knowledge, no records of winter buds exist for field populations of wild celery in tropical or subtropical areas. Interestingly, Godfrey and Wooten (1979), in their taxonomy of aquatic and wetland plants, make no mention of winter buds of wild celery in southeastern states. Haller and Sutton (1975) reported none in winter harvests of the species from small (0.08-ha),

earthen ponds (1.5-m deep) in Orange County, Florida. Furthermore, in studies of the reproductive phenology of wild celery in Mobile Bay, Clark and Stout (1995) found seeds but no winter buds by coring sediments throughout the year. The lack of winter buds in the southern ecotype could be inherent—a hypothesis supported by experiments conducted at the Lewisville Aquatic Ecosystem Research Facility, in Lewisville, Texas (Dawes and Lawrence 1989, Smart and Dorman 1993). According to those studies, only the northern ecotype produced winter buds when the two ecotypes were tested under the same environmental conditions (R. M. Smart 2005, pers. comm.[3]).

REPRODUCTIVE RESPONSE TO ENVIRONMENTAL FACTORS

The abundance of SAV may vary over time for many reasons. Principal factors that interact in influencing plant morphology and biomass may also directly or indirectly impact plant reproductive capacity. Abiotic factors (e.g., light, temperature, water chemistry, and sediment nutrients and texture) have received much investigative attention to determine their role in SAV growth and propagule development. Though biotic factors (e.g., herbivory and disease) may also exert important impacts on SAV, research along this line of inquiry has been relatively limited.

In the following sections, we discuss influences of a variety of factors (both biotic and abiotic) on the production, dispersal, and establishment of different types of wild celery propagules. The first section below addresses influences on sexual reproduction, and the second section, influences on asexual reproduction. Because of increased interest in the use of seed in site restoration projects, some of the most recent quantitative work has centered on sexual reproduction. Summary tables outline reproductive responses of wild celery to different factors as addressed in selected references (Tables 1-6).

Sexual Reproduction

Literature on the reproduction of SAV indicates that these populations are maintained primarily through asexual means and that contributions from seeds are minimal (Sculthorpe 1967, Kautsky 1990). Yet, many species of SAV, despite their dominant clonal nature, have retained the ability to flower and produce large numbers of viable seeds. A major advantage of sexual reproduction is genetic variation, which increases the chance of surviving dramatic environmental change (e.g., disease, drought, flooding, drawdown, and herbicide treatment; Williams 1975, Galinato and van der Valk 1986, Watkinson and Powell 1993). Seeds may also play a key role in dispersal and colonizing new areas (Kimber et al. 1995a, McFarland and Rogers 1998) and thus may be important in shaping SAV community structure and distribution.

Though wild celery has long been known to produce viable seeds (Muenscher 1936), information is scarce concerning *in situ* establishment of its seedlings. Kimber et al.

TABLE 1. WILD CELERY FLOWERING AND POLLEN TRANSPORT IN RELATION TO ABIOTIC (A) AND BIOTIC (B) FACTORS.

Factor/type	Plant response	Ecotype and location	Reference
	Flowering (occurrence)		
Photoperiod (a)	Late Jul through Aug; long photoperiod	Northern; Lake Mendota, WI	Titus & Adams 1979
	Late Jun to early Aug; long photoperiod	Northern; a lake in WI	Witmer 1937
	Early Jul to early Sep; long (decreasing) photoperiod	Northern; Potomac River, MD	Carter & Rybicki 1985
	Jul to mid-Sep; long photoperiod	Northern; Lake Huron-Lake Erie corridor (south Ontario)	Catling et al. 1994
	Early Jun to Sep; peak Jul to Aug; long photoperiod	Northern; Pamlico River Estuary, NC	Zamuda 1976
	Mid-Jul through Aug; long photoperiod	Northern; Chenango Lake, NY	Titus & Stephens 1983
Plant biomass (b)	Plants weighing <0.75 g (dry) fail to produce flowers; >2.0 g optimal	Northern; greenhouse facility	Titus & Hoover 1991
Temperature (a)	May be affected indirectly through impacts on biomass; paucity of information on direct temperature effects	Nonspecific; based on observations of SAV in general	Grainger 1947, Sculthorpe 1967
	Pollen transport		
Water depth (a)	Though flowering occurred over a range from 0.9 to 2.5 m, sub-surface flowers at 2.1 to 2.5 m failed to be pollinated	Northern; Silver Lake, PA	Sullivan & Titus 1996
	Sub-surface flowering occurred in deepwater population at 2.25 to 5.25 m; no evidence of pollination	Northern; Seneca Lake, NY	Sullivan & Titus 1996
Water movement (a)	Increases in surface velocity can negatively affect pollination; velocities > 0.3 m s^{-1} can prevent pollination	Northern; Hudson River, NY	Sullivan & Titus 1996
	Pollination increased at sites protected from waves and wind compared with open-water, exposed locations	Northern; Cayuga Lake, NY	Sullivan & Titus 1996

(1995a) reported that following a drought in the late 1980s, sites in the Upper Mississippi River were apparently recolonized by seeds of wild celery. The seedlings produced winter buds after only one season of growth and were observed in areas where wild celery had not previously grown. Other establishments of wild celery seedlings have been observed in Ostego Lake, New York (Titus and Hoover 1991) and in populations of the southern ecotype at Toledo Bend Reservoir on the Texas-Louisiana border (Smart and Dorman 1993, Kimber et al. 1995a). These reports demonstrate that the species can become established from seed, notwithstanding a formidable array of possible limitations on the growth of young seedlings *in situ*.

Overall, seed production in SAV appears to be difficult because it is multifaceted by nature and subject to interruption at many points in the process. As identified by Titus and Hoover (1991), events that may restrict production of seed involve: (1) flowering—including floral induction, floral initiation, morphogenesis, and anthesis; (2) pollen transport and deposition onto receptive stigmas; (3) pollen tube germination and development; (4) fertilization; and (5) embryogenesis and fruit maturation. Among these, they suggest the most difficult steps to achieve are the production of flowers and transport of pollen to receptive stigmas (Titus and Hoover 1991). Though self-incompatibility and seed abortion (Stephenson 1981, Barrett 1988) are challenges that should not be overlooked (Titus and Hoover 1991), current information on these processes in SAV is insufficient for meaningful synthesis. However, it is noteworthy that self-incompatibility—a phenomenon limited to monoecious (hermaphroditic) plants (Barrett 1988)—is not likely to influence seed production in wild celery.

Flowering and Pollen Transport: Wild celery typically flowers only once a year, from late June to September (Table 1) under long (>13-hr) photoperiod and moderate-to-high (>20 C) temperature (Donnermeyer 1982, Titus and Stephens 1983, Best and Boyd 2001). Its summer flowering habit may be related to changes in plant nutrition, in that only in summer, when days are long and warm, is there sufficient plant biomass for flowers to develop (Grainger 1947, Sculthorpe 1967, Weiner 1988, Waller 1988). Because it flowers during summer, it is classified as a long-day plant (Salisbury and Ross 1985), but the critical day length to prompt flowering in this species has not been determined.

Titus and Hoover (1991) examined the role of plant biomass (on a dry weight basis) in determining the incidence of flowering in wild celery in greenhouse studies (Table 1). They reported that the percentage of plants flowering rose linearly from 7% for plants weighing <0.5 g to 100% for all plants (*n* = 148) above 2.0 g dry weight. Of 425 plants, 88% followed a 0.75-g threshold rule: plants weighing <0.75 g failed to flower, and those weighing >0.75 g produced flowers. The ratio of female flower number to plant biomass (mean = 1.47 flowers g^{-1}, *n* = 33) was significantly lower than the ratio of male inflorescence number to plant biomass (mean = 2.87 inflorescences g^{-1}, *n* = 94). Coefficients of variation for these ratios were generally quite high (50 and 54%, respectively), signaling a high level of uncertainty even in a semi-controlled (greenhouse) environment.

Water depth can pose an obstacle to wild celery pollination by limiting the ability of pistillate flowers to float on the water surface (Table 1). In field studies at Silver Lake, the percentage of female flowers reaching the surface diminished significantly along a depth gradient from 0.9 to 2.5 m:

TABLE 2. WILD CELERY SEED DORMANCY AND GERMINATION IN RELATION TO ABIOTIC (A) AND BIOTIC (B) FACTORS.

Factor/type	Seed dormancy and germination	Reference
Burial Depth (a)	Burial depths <15 mm optimal for germination	Campbell & Moore 2005
Desiccation (a)	Can kill seed embryos; no survival after 2 months of air-drying	Muencher 1936
Dissolved oxygen (a)	Germination increases under aerobic conditions (DO >4 mg l^{-1})	Campbell & Moore 2005
Light (a)	Germination can occur in both light and dark conditions, but the latter significantly increases the number of seeds that germinate	Kimber et al. 1995a
	Germination is insensitive to light gradients at low levels (i.e., from 2 to 25 percent full sun over the growing season)	Kimber et al. 1995a
Salinity (a)	Germination increases significantly at salinities <5‰	Campbell & Moore 2005
Scarification (a)	Seeds exhibit an innate physical dormancy; seed coat must be degraded (or alternatively abraded) for mature seeds to germinate	Ferasol et al. 1995
Sediment organic matter content (b)	Germination maximized in substrate with <3 percent organic matter content	Campbell & Moore 2005
	Germination may be delayed (by 2 to 5 weeks) on organic sediments	Hoover 1984
Seed age (b)	Immature (white) seeds germinate more rapidly and overall, show lower germination percentages compared to mature (brown) seeds	Ferasol et al. 1995
Temperature (a)	Cold stratification can promote germination but is not an absolute requirement for seeds to germinate	Ferasol et al. 1995
	Viability remains high in seeds after 7 months of storage in water at temperatures just above freezing (1 to 3 C)	Muencher 1936
	Over a range in temperature from 13 to 31 C, germination increases significantly at temperatures >19 C	Campbell & Moore 2005

nearly all female flowers surfaced from wild celery at 0.9 to 1.3 m, with only 6% surfacing at 1.7 m, and none at 2.1 to 2.5 m (Sullivan and Titus 1996). Wild celery surveys at Nuthatch Hollow Pond further showed that subsurface (female) flowers failed to set fruit, although among flowers reaching the surface, fruit set was 92% (Sullivan and Titus 1996). Moreover, in deep waters (from 2.25 to 5.25 m) of Seneca Lake, female plants were able to produce flowers, but because their flowers were unable to reach the surface, they consequently were not pollinated (Sullivan and Titus 1996).

Pollination of wild celery may be limited by wind, waves, and surface currents carrying male flowers away from a site before female flowers are pollinated (Table 1). Sullivan and Titus (1996) reported that fruit set in Cayuga Lake decreased to 79% at unprotected, open-water sites exposed to wind and waves; this contrasted greatly with fruit set that occurred in protected areas (97%) where leaves and female flowers along the surface hindered dispersal of male flowers. They also observed high levels of fruit set (100%) in female plants at Silver Lake where an enclosure was used to confine male flowers to increase their residence time in the vicinity of female plants. These researchers speculated that short residence time of male flowers might be offset by high densities of male flowers to increase the chance of pollination; however, the abundance of male flowers may be far less important than factors limiting their access to female flowers.

In wild celery studies in the Hudson River, fruit set correlated negatively with surface velocity and declined to zero at velocities >0.3 m s^{-1} (Sullivan and Titus 1996; Table 1). Pollen transfer was greatly hindered because male flowers were floating past the anchored female flowers, and because female flowers became oriented downstream, positioning them away from incoming male flowers. Moreover, physical damage to the female flowers and their being driven below the water surface were noted to reduce the potential for pollination in high velocity (>0.3 m s^{-1}) waters.

Dormancy and Germination: Innate dormancy has been described as an inability of the seed to germinate even in the presence of suitable external conditions (Harper 1977). Germination of innately dormant seeds often requires some special condition(s) to be satisfied, such as photoperiod, light intensity, abrasion (scarification) of the seed coat, or cold stratification (Ferasol et al. 1995). This type of dormancy is interpreted to introduce a temporal delay in germination that provides additional time for seed dispersal over greater geographical distances. It also offers a possible means of maximizing seedling survival by resisting germination until conditions for seedling growth become more conducive. In temperate climates, seeds normally germinate after adverse conditions of winter, when the seedling is more likely to experience favorable growth conditions during the spring (Salisbury and Ross 1985).

Pre-chilling wild celery seeds can potentially enhance germination but is not an absolute requirement for the seeds to germinate (Table 2). This was demonstrated in studies by Ferasol et al. (1995) in which some fruits of wild celery were stored (moist) at 4 C and others at 20 C for 75 days. Following storage, the seeds were placed in Petri dishes and allowed to germinate under a 13-hr photoperiod at approximately 12 C. This particular photoperiod-temperature regime (after storage) was selected to emulate early spring as experienced ordinarily in north-temperate regions. For the first 40 days after storage, untreated wild celery seeds (stored at 20 C) germinated more rapidly than did the cold-stratified seeds (stored at 4 C); but by the end of 100 days, compared to untreated seeds, cold-stratified seeds had a higher percentage germination.

Early work by Muenscher (1936) demonstrated that seeds of wild celery could be stored at 1 to 3 C for many months and remain capable of germinating soon after storage (Table 2). In his studies, 71% of seeds germinated within 2 months in a greenhouse at temperatures of 18 to 21 C during the day and 13 to 16 C at night. Germination percentages remained

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TABLE 3. WILD CELERY SEED DISPERSAL AND SEEDLING ESTABLISHMENT IN RELATION TO ABIOTIC (A) AND BIOTIC (B) FACTORS.

Factor/type	Seed/seedling function	Reference
	Dispersal	
Buoyancy (b)	Seeds are negatively buoyant; fruits removed from the parent plant may float up to several days; well-ripened fruits sink more readily	Wilder 1974, Kaul 1978, Clark & Stout 1995, Kimber et al. 1995a
	Seed deposition tends to be greater within or downstream of established bed	McFarland & Rogers 1998
	Establishment	
Light (a)	Seedlings survive and produce winter buds at light levels > 9 percent full sun	Kimber et al. 1995a
	The relationship between light and seedling survival is a sigmoid curve: survival increases rapidly in the range of 0 to 5 E m^{-2} d^{-1} and is excellent at levels above 10 E m^{-2} d^{-1}; levels below 3 E m^{-2} d^{-1} cause high mortality	Doyle & Smart 2001
pH (a)	Plants grown from seed at low pH (<6) produce smaller plants that are less likely to reproduce, either sexually or asexually	Titus & Hoover 1993
Turbidity (a)	Over a range in turbidity from 0.2 to 45 NTU (53 to 7 percent total incident light), seedling survival, rosette production and biomass are progressively diminished	Doyle & Smart 2001

high at 76, 87, 82% for seeds that had been cold stored just above freezing (1 to 3 C) in the dark for 2, 5, or 7 months, respectively.

Testa (seed coat) color and structure have been found to correlate significantly with the maturity and germinability of wild celery seeds (Table 2). Ferasol et al. (1995) reported that seed coats of mature seeds are rough and brown compared to the smooth, white seed coats of immature seeds. The rough surface of mature seeds is due to the many fenestrated tubercles that may help stabilize and anchor the seed once deposited onto a substrate. Compared to the immature seeds in their studies, mature seeds germinated more slowly but their germination percentage overall was significantly greater. Mechanical scarification of mature seeds increased the rate of germination; up to 90% of scarified seeds germinated within 60 days, whereas fewer than 30% of nonscarified seeds germinated over the same period. In view of their findings, Ferasol et al. (1995) proposed that the need for scarification may compensate for the lack of a strict cold pretreatment requirement. Germination may be delayed by the

seed coat until after autumn and winter when more favorable conditions for seedling growth prevail.

Seeds of wild celery can germinate in either light or dark, although the latter significantly increases percentage germination (Table 2). Kimber et al. (1995a) reported that over a range in light levels from 0% (dark) to 25% full sun (i.e., 228 μE m^{-2} s^{-1} at mid-day), 68% of the seeds germinated in the dark, while 30 to 48% germinated in the light treatments. Specific light levels did not affect percentage germination, indicating that the seeds may be insensitive to rather low light gradients. These findings are similar to those of Muencher (1936) who showed that for wild celery seeds percentage germination was unaffected by light intensity; however, he noted that germination that occurred in direct sunlight was slower and less even among seeds than in diffuse sunlight.

The contribution of seeds to recovery of declining populations of aquatic plants may be measured in part by their ability to remain viable during severe disturbances such as drought or drawdown. Relatively high germination percentages after

TABLE 4. WINTER BUD PRODUCTION IN WILD CELERY IN RELATION TO ABIOTIC (A) AND BIOTIC (B) FACTORS.

Factor/type	Winter bud formation	Ecotype and location	Reference
Photoperiod (a)	Mid-Aug through Oct; number and biomass of winter buds peak in early Oct; decreasing (mostly short) day length	Northern; Pool 9, Upper Mississippi River	Donnermeyer & Smart 1985
	Late Aug through Sep; decreasing (mostly short) day length	Northern; Chenango Lake, NY	Titus & Stephens 1983
	Late summer through autumn; decreasing (mostly short) day length	Northern; Lakes Wingra and Mendota, WI	Titus & Adams 1979
	Mid-Sep through Oct; decreasing (mostly short) day length	Northern; Lake Huron-Lake Erie corridor (south Ontario)	Catling et al. 1994
	None produced	Southern: Juniper Run, FL	Dawes & Lawrence 1989
	None produced	Southern; transplants to Lewisville from Toledo Bend, TX	Smart & Dorman 1993
Plant biomass (b)	3.25 to 3.60 winter buds produced g^{-1} plant biomass (dry), for plants initiated from winter buds; plant biomass and winter bud number closely correlated (r^2 from 0.82 to 0.92, $P < 0.01$)	Northern; greenhouse and field studies in NY	Titus & Hoover 1991
	Winter bud production is a 'high priority' in plants grown from seed (i.e., ~15 buds produced g^{-1} plant biomass, dry); plant biomass and winter bud number correlated well ($r^2 = 0.78$, $P < 0.01$)	Northern; greenhouse in NY	Titus & Hoover 1991

TABLE 5. WILD CELERY WINTER BUD SPROUTING AND EMERGENCE IN RELATION TO ABIOTIC (A) AND BIOTIC (B) FACTORS.

Factor/type	Winter bud sprouting and emergence	Reference
Burial depth (a)	Winter bud emergence decreases with increases in burial depth; burial depths ≤ 10 cm appear optimal for emergence	Carter et al. 1985, Rybicki & Carter 1986
Morphology (b)	Winter buds formed in chains often show "first-formed bud dominance," where the second bud develops into a rosette only if the first bud germinates, or is severed or clipped	Titus & Hoover 1991
Salinity (a)	Over a range in salinity from 0 to 15 ‰, germination negatively correlated with salinities ≥3‰	Carter & Rybicki 1987 (pers. comm.)[4]
	Winter buds fail to germinate at salinities >11‰	
Sediment type (a)	Percentage emergence of winter buds buried in sand is generally lower than for winter buds buried in fine-textured silty sediment	Rybicki & Carter 1986
Temperature (a)	Winter buds germinate when water temperatures reach 10 to 14 C	Zamuda 1976, Rybicki & Carter 2002
	Germination can exceed 90 percent at temperatures between 15 and 22 C	Rybicki & Carter 2002
	Initial rate of elongation is increased with elevation in temperature within a range from 13 to 22 C	Rybicki & Carter 2002
	Timing of winter bud emergence can be predicted based on accumulation of degree-days	Spencer et al. 2000

prolonged periods of drying (>3 months) have been demonstrated for seeds of Eurasian watermilfoil (*Myriophyllum spicatum* L.), water speedwell (*Veronica anagallis-aquatica* L.), and watercress (*Rorippa nasturtium-aquaticum* [L.] Hayek; Muenscher 1936, Standifer and Madsen 1997). Conversely, wild celery seeds show no great resistance to desiccation as its seeds failed to germinate after air-drying for 2 months under greenhouse conditions (Muenscher 1936; Table 2).

Current Studies on Seed Germination—Preliminary Findings: Recently, research was undertaken to address gaps the literature concerning environmental influences on germination of wild celery seeds. Campbell and Moore (2005) conducted studies to assess percentage germination over selected ranges in light availability (present or absent), temperature (13 to 31 C), sediment organic matter content (1 to 8%), burial depth (2 to 100 mm), salinity (0 to 15‰) and dissolved oxygen content (<2 or >4 mg l[1]). Their results showed that germination increased significantly at temperatures >19 C, salinities <5‰, organic matter content <3%, burial depths <15 mm, and when oxygen was present (>4 mg l[1]; Table 2). The presence or absence of light apparently had no significant effect on germination, a response differing slightly from results of Kimber et al. (1995a), probably owing to differences in experimental methods.

Dispersal: Among the primary modes of dispersal (e.g., via water, wind, and animals, including man), water is perhaps the most important in disseminating naturally buoyant fruits and seeds (Sculthorpe 1967). Though wild celery seeds are negatively buoyant, its fruits, depending on physical condition, may float for several days before falling onto the sediment (Wilder 1974, Kaul 1978, Clark and Stout 1995, D. G. McFarland, pers. observ.; Table 3). A short period of flotation could be sufficient to allow transport to sites well away from the competitive habitat of established parent vegetation (Sculthorpe 1967). In contrast, a well-ripened fruit that has become waterlogged may sink fairly quickly, distributing its contents within or in the vicinity of the parent plant bed (Kaul 1978). Seedbank studies in Lake Onalaska showed that densities of wild celery seeds were greater within or somewhat downstream of an established bed than in upstream or open areas (McFarland and Rogers 1998). Maps of water movements in the lake revealed a prevailing southward flow that coincided with the southward drift and deposition of seeds relative to mature bed location.

Frequency of transport of wild celery seed by various mechanisms is unknown, but it is highly conceivable that animals, particularly wildfowl, provide both long and short-range dissemination. For any SAV species, direct observations of this type of dispersal would be difficult, yet many researchers have provided circumstantial evidence for exo- and endozoic transport of SAV fruits, seeds, and other propagules (Sculthorpe 1967 and literature therein; Figuerola and Green 2002, Green et al. 2002, Santamaria 2002). The extent to which human activities (e.g., recreational boating, aquatic gardening, and aquarium trade), animals, water movements, and wind each accounts for the spread of wild celery warrants further investigation.

Seedling Establishment: The morphology of germination and establishment of seedlings of wild celery has been documented in detail by Haccius (1952) and Kaul (1978). Their observations provide insight into the vulnerability of tiny seedlings in the initial stages of lodging on a substrate to the emergence of roots and the first plumular leaves. Beyond studies by these two authors, little research has been conducted on the establishment of wild celery seedlings under different environmental conditions. Impacts of light have been examined in a few investigations, but information is lacking on the effects of other environmental variables (e.g., sediment instability, temperature, salinity, particle loads, and pathogens). Ranges of tolerance of young seedlings are probably much narrower than for mature plants and need to be quantified for seedlings of wild celery.

Kimber et al. (1995a) assessed light requirements for wild celery seedling growth through determinations of seedling survival and winter-bud production. Sediments from Pool 8 (Lake Onalaska) of the Upper Mississippi River were incubated in outdoor ponds shaded over the growing season with fabric that reduced light to 2, 5, 9, and 25% full sun. Though seeds germinated at all light levels, survival and bud production were significantly enhanced in treatments with at least

Factor/type	Establishment	Reference
Dissolved inorganic carbon (a)	CO_2 enrichment stimulates carbon uptake rates and may enhance growth of wild celery on different sediments and at low pH	Titus & Stone 1982, Titus et al. 1990, Titus 1992, Titus & Andorfer 1996
Herbivory (b)	Establishment may be protected through use of exclosures to protect against grazing by waterfowl, turtles, muskrats, manatees, and carp	Carter & Rybicki 1985, Hauxwell et al. 2004, Smart et al. 2005
Light (a)	Plants emerging from winter buds can potentially reach heights of ~40 cm in total darkness	Korschgen & Green 1988, Rybicki & Carter 2002
	Over a range from 2 to 25 percent full sun, plants from winter buds can produce new replacement-weight winter buds in 9 percent light or more; extending the growing period allows winter bud formation at a lower level (i.e., 5 percent full sun)	Kimber et al. 1995b
	Total biomass is significantly greater at 550 than at 125 $\mu E\ m^{-2}\ s^{-1}$; at the lower light level, biomass responsiveness to sediment fertility and CO_2 supply is diminished	Barko et al. 1991a
Salinity (a)	Tolerates between 5 and 10‰ when other conditions are suitable (e.g., light)	French & Moore 2003
	May tolerate salinity as high as 12‰ or more if increase in salinity is gradual	Twilley & Barko 1990, Doering et al. 2001
	Duration of exposure to high salinity is important in determining plant survival and ability to recover when conditions become suitable	Doering et al. 2001
Sediment (a)	Grows well on fine-textured, inorganic sediment with organic matter content < 20 percent; sands are potentially low in nutrients unless supplemented by outside inputs; high organic content diminishes sediment stability and increases organic acid concentrations to levels that may be toxic for growth	Smart & Barko 1985
Temperature (a)	Growth diminished at cold temperatures of 16 C or less; 28 to 32 C optimal for growth; high temperature, somewhere between 30 and 35 C can greatly diminish production of new winter buds	Barko et al. 1982, McFarland & Barko, unpubl. data[5]
Turbidity (a)	Winter buds showed progressively poorer survival and fewer rosettes over a range from < 1 to 45 NTU; large winter buds survived and grew better than small winter buds at all experimental turbidity levels	Doyle & Smart 2001
Water movement (a)	Waves generating a shear velocity of about 1.4 m s⁻¹ can reduce biomass, plant height and new rosette development	Doyle & Smart 2001
	Within a range of slow currents for which flow is laminar (0.02 to 0.5 cm s⁻¹), photosynthesis increases with increases in velocity	Westlake 1967
Winter bud size (b)	Mortality increases with decreases in winter bud size (e.g., weight, length)	Titus & Hoover 1991, Doyle & Smart 2001

9% of the surface light level (Table 3). This minimum requirement for growth of seedlings was the same as for plants from winter buds (Kimber 1994) and was similar to the 10% requirement for wild celery clonal reproduction, based on Potomac River studies (Carter and Rybicki 1990).

Doyle and Smart (2001) found that turbidity, due to effects on light availability, can strongly affect growth and survival of wild celery seedlings. Over a range in turbidity treatments from 0.2 to 45 NTU (53 to 7% total incident light), seedling survival, rosette production, and biomass were progressively diminished (Table 3). Calculations using their data along with that from Kimber et al. (1995a) revealed that the relationship between light and seedling survival is a sigmoid curve: survival increases rapidly at 0 to 5 E m⁻² d⁻¹ and is excellent at levels above 10 E m⁻² d⁻¹; mortality is high at levels below 3 E m⁻² d⁻¹.

Field surveys by numerous workers have revealed wild celery in aquatic systems ranging in pH from 5.4 to 10.2 (Moyle 1945, Fassett 1957, Crowder et al. 1977, Crow and Helquist 1982, Korschgen and Green 1988). However, the few reports of this species occurring at pH 6 or less indicate that it may not grow well or persist in waters with low pH. Titus and Hoover (1993) found, in greenhouse studies where effects of acidification were assessed, that at pH 5, wild celery from seed produced no flowers and too few winter buds to replace themselves. These plants were also reduced by at least 90% in dry biomass compared to those that were grown from seed at pH 7.5 (Table 3).

Asexual Reproduction

For wild celery, as for many species of SAV, asexual reproduction is the dominant means of population increase and over-wintering (Titus and Stephens 1983, Titus and Hoover 1991, Philbrick and Les 1996). During the growing season, the plant spreads laterally through rhizomes and stolons that generate new rosettes and roots at the nodes. Its winter buds serve primarily for perennation and represent a physiological commitment to carbohydrate storage, and protection of meristematic tissues during adverse conditions. These propagules become independent of parent vegetation, usually in winter when organs connecting them to the parent plant stop growing and deteriorate. Morphologies of asexual propagules of wild celery have been described by Bellrose (1941), Wilder (1974), Donnermeyer (1982), Donnermeyer and Smart (1985) and Catling et al. (1994). Discussions below focus mainly on wild celery winter buds because data specific to rhizomes and stolons are rare in ecological literature.

Propagule Induction: In north-temperate climates, winter buds form near the end of the growing season from late summer through autumn (Table 4), under decreasing tempera-

ture and shortening photoperiod (<14 hrs; and Best and Boyd 2001). These buds remain dormant in sediment throughout the winter and begin to sprout into young plants with warming temperatures of spring (Sculthorpe 1967, Hutchinson 1975, Grace 1993, van Vierssen 1993). Environmental induction of winter buds in certain SAV species, such as hydrilla (*Hydrilla verticillata*), curly pondweed (*Potamogeton crispus*), longleaf pondweed (*P. nodosus*), and sago pondweed (*P. pectinatus*), has shown sensitivity to photoperiod, temperature, nutrients, quantum flux density, and/or spectral quality (Sculthorpe 1967, Van et al. 1978, Klaine and Ward 1984, Spencer and Anderson 1987). Critical requirements of these factors, if they exist for wild celery, have not been investigated thoroughly under controlled conditions.

Titus and Hoover (1991) performed linear regressions using data from field and greenhouse studies to analyze the relationship between biomass of wild celery and the number of winter buds produced (Table 4). For plants grown from winter buds, the slopes ranged from 3.25 to 3.60 buds g^{-1} dry biomass, and for plants grown from seed, a relatively high slope (14.92 buds g^{-1} dry biomass) was obtained. For both groups, the correlation between winter bud number and plant (dry) biomass was high: r^2 ranged from 0.8 to 0.9 for plants grown from winter buds and was 0.78 for plants grown from seed. The allocation of biomass to winter buds was similar for both groups: winter bud fresh weight to plant dry weight ratios were 1.87 for plants grown from seed and 2.04 for plants grown from winter buds.

Sprouting and Emergence: Vertical profiles of the distribution of winter buds in Potomac River sediments showed that the majority were buried 5 to 15 cm deep in sand and 10 to 20 cm deep in silty clay (Carter et al. 1985, Rybicki and Carter 1986). The ability of winter buds to emerge from deeper depths in the sediment is advantageous since deeper burial offers protection from wildfowl and avoidance of desiccation. Rybicki and Carter (1986) showed that winter bud emergence was lower in sand than in silty clay and declined in both sediment types with increases in burial depth (Table 5). No winter buds emerged from depths >25 cm in either sediment, but in both sediments, 90% or more emerged from a burial depth of 10 cm.

The ability of wild celery to withstand periods of high salinity infusion may be important in determining its occurrence in tidally influenced estuaries. Studies by the U.S. Geological Survey examined germination of wild celery winter buds at salinities of 0, 3, 5, 7, 9, 11, 13, and 15‰ under laboratory conditions (Carter and Rybicki 1987, pers. comm.[4]; Table 5). The results showed that germination was little affected at 3‰ or less, but at 13‰ and greater all of these propagules failed to germinate. At 3‰, germination was 80% but declined to 7% at 11‰.

Winter buds of wild celery germinate in spring after overwintering, when water temperatures reach 10 to 14 C (Zamuda 1976, Rybicki and Carter 2002; Table 5). Rybicki and Carter (2002) reported that for winter buds held for 6 weeks (in the dark) at 13 to 22 C, germination exceeded 50% at 13 C; germination was >90% at 15 C and peaked overall at 17 C.

Rate of initial elongation was greatest at 22 C and was maximized within a 4-week period.

To enhance predictive capability, Spencer et al. (2000) developed equations that relate the timing of winter bud emergence to the accumulation of degree-days. These researchers suggest that by monitoring sediment temperature and applying the equations provided, managers would be able to estimate when the population would emerge and would be most vulnerable to practices that remove aboveground biomass. Such information could be important to restoration efforts by identifying periods when certain management practices (e.g., water-level fluctuation or drawdown), if possible, should be avoided.

Quite often, winter buds of wild celery are borne in pairs or even in triplets and show a sequential germination pattern with respect to bud position on the chain (Table 5). Titus and Hoover (1991) observed that after planting 20 double buds of this species, 19 rosettes subsequently developed but only from the first-formed bud on the chain. Their studies show that the second-formed bud can form a rosette, but only if: (1) the first bud germinates or emerges, (2) its connection to the first rosette is severed, or (3) leaves from the first germinated bud are clipped.

Vegetative Establishment: Post-germination vigor and ability to survive in suboptimal environments are plant characteristics that rely heavily on propagule size and nutritional reserves (Table 6). A large propagule with abundant carbohydrate and mineral nutrient pools appears more likely to establish a root system and emerge from deeper depths in the substrate (Spencer 1987, Titus and Hoover 1991). Titus and Hoover (1991) noted that winter buds of wild celery in Chenango Lake showed the greatest mortality (>75%) in low freshweight classes of 0.5 g or less. In contrast, survival was much greater among larger winter buds, especially in the heaviest freshweight classes from 1.1 to 1.8 g. Size may also be a good predictor of the outcome of competition because larger winter buds produce larger rosettes, more new winter buds, and greater biomass (Hoover 1984, Titus and Hoover 1991, Korschgen et al. 1997, Doyle and Smart 2001).

While a young plant from a winter bud can elongate in the dark (Korschgen and Green 1988, Rybicki and Carter 2002), subsequent growth and reproduction can be limited by low levels of light (Table 6). Juvenile plants exposed to different light levels (i.e., 125 µE m^{-2} s^{-1} versus 550 µE m^{-2} s^{-1} at mid-day) in a greenhouse facility, produced 40 to 50% more biomass under the higher light treatment (Barko et al. 1991a). Studies conducted more recently in Lake Onalaska showed that transplants from winter buds grew well and produced replacement-weight winter buds in locations where irradiance was at least 9% full sun (Kimber et al. 1995b). These findings were supported by pond investigations where, over a range in light (from 2 to 25% surface irradiance), wild celery from winter buds produced replacement-weight winter buds in 9% light or greater. Extending the growing period tended to compensate for impacts of low light: plants grown at 5% full sun also produced winter buds but only when the growth period was sufficiently lengthened (Kimber et al. 1995b).

Similar to their findings concerning growth of wild celery from seeds, Doyle and Smart (2001) reported that growth from winter buds was adversely influenced by increases in

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[4]Carter, V. and N. B. Rybicki. 1987. Personal communication. U.S. Geological Survey, 12201 Sunrise Valley Drive, Reston, VA 20192.

turbidity (Table 6). Winter buds separated into two fresh-weight groups (i.e., one averaging 0.047 g and the other 0.264 g) showed progressively poorer survival, lower biomass, and fewer rosettes in turbidities ranging from <1 to 45 NTU (about 53 to 7% incident light). Survival of small winter buds was about 50% at low turbidities (≤15 NTU), and was very poor (0 to 17%) under the most turbid conditions. Large winter buds survived well (>85%) at turbidities up to 15 NTU, but in the highest turbidity treatment, survival was lower and more variable (50 to 83%). Winter bud production was greater in plants grown from the large winter buds, and trends in winter bud number in response to turbidity mimicked those of plant biomass production.

Although wild celery has a relatively high thermal optimum, it potentially can grow over a wide range of water temperatures. According to Barko et al. (1982, 1984), plants from winter buds were greatly diminished in dry biomass, shoot density, and length at water temperatures of 16 C or less (Table 6). Growth increased with increases in temperature from 16 to 28 C, with thermal optima achieved mainly at 28 to 32 C. Patterns of response to differences in temperature were magnified at moderate to high levels of light, confirming significant interactive relationships between these two factors. Presently, information is generally lacking on growth at temperatures >32 C, but detrimental effects on winter bud formation between 30 and 35 C have been detected in wild celery (McFarland and Barko unpubl. data[5]) and other SAV species (McFarland and Barko 1999). Low numbers and biomass of these propagules resulting from high temperature exposure can lead to low population densities and smaller plants at the start of the next growing season.

Water currents and waves are key environmental factors affecting SAV establishment, distribution, and morphology, particularly in shallow waters. In some cases where movement is slow, water current serves as an important auxiliary energy source by increasing availability of nutrients and exporting waste products (Davis and Brinson 1980). Within a range of slow-moving currents for which flow is laminar (0.02 to 0.5 cm s^{-1}), Westlake (1967) demonstrated that photosynthesis of SAV in the laboratory increased with increasing current velocity; however, reductions in size or the complete absence of SAV in shallow areas may be due to negative effects of water abrasion (Hutchinson 1975, Davis and Brinson 1980). Doyle and Smart (2001) demonstrated that waves 0.15 m high generating about a 1.4 m s^{-1} shear velocity can impede the growth and reproduction of wild celery from winter buds (Table 6). In their study, wave-treated plants produced significantly less biomass, had shorter leaves and fewer new rosettes than did untreated, control plants. They concluded that wild celery subjected to wave activity might spread less rapidly and be less resilient in facing other environmental stresses (e.g., herbivory, poor water quality, water level fluctuation). Their findings concur with those of flume investigations showing that damage to aquatic plants, including wild celery, increases with wave heights above 0.1 m (Stewart et al. 1997). Kimber and Barko (1994) have reviewed the effects of water movements on aquatic plants and should be consulted for further information pertaining to this issue.

Wild celery is generally considered a freshwater plant that can grow at low salinities but is usually limited between 5 and 10‰ (Bourn 1932, 1934, Haller et al. 1974, Davis and Brinson 1976, Staver 1986, Doering et al. 2002, French and Moore 2003). This species has been noted in oligohaline regions of the Pamlico and Caloosahatchee River estuaries and is a dominant component of SAV in the transition zone of the tidal Potomac River (Davis and Brinson 1976, Carter and Rybicki 1985, Kramer et al. 1999). Early studies showed that growth from winter buds, identified as *V. spiralis*, peaked at 2.8‰ and remained high at 4.2‰, but ceased at 8.4‰ and greater (Bourn 1932, 1934). Haller et al. (1974) found that over a range from 0.17 to 16.65‰, young transplants grew best at 0.17 to 3.33‰, failed to grow at 6.66‰, and died and decayed at 13.32‰. Occasionally, the plant is found at relatively high salinities (~10 to 15‰) in the field, but often due to tidal influences, the exposure varies in strength, occurs gradually, or is short-lived (Davis and Brinson 1976, Doering et al. 2002). Laboratory studies have demonstrated wild celery may survive at salinities of 12‰ or more if the increase in salinity is gradual or of short duration (Twilley and Barko 1990, Doering et al. 2001). Close examination of the methodologies of studies under controlled conditions allude to the importance of the length and strength of the exposure, and plant age in determining salinity tolerance limit.

Wild celery is seldom found growing at a pH <6 (Crow and Hellquist 1982, Korschgen and Green 1988; Table 6) and thus appears vulnerable to effects of acidification. Grisé et al. (1986) reported that young transplants accumulated 76% less biomass and produced fewer rosettes and fewer winter buds at pH 5 than at pH 7.5. Later studies by Titus and Hoover (1993) showed that reproductive output was markedly reduced, both sexually and asexually, in plants grown from winter buds and seeds at low pH (Table 3). Their results on winter bud production generated the "closing spiral" hypothesis that continued exposure to low pH can eventually extinguish the population. Low pH can trigger a decline by reducing plant growth and reproduction through progressively smaller numbers and sizes of individual winter buds. This hypothesis was supported by field transplant investigations where wild celery growth measured as plant number and size quickly declined in two acidic lakes in the Adirondack Mountains (Titus and Hoover 1993). The results were in direct contrast to those from an alkaline lake where wild celery transplants grew vigorously and accrued far greater biomass than in the above acidic lakes (Overath et al. 1991).

Present evidence suggests that rooted species of SAV derive the bulk of their mineral nutrition from nutrient pools in sediment. Because of the greater demand and more rapid uptake of N by SAV, phosphorus (P) appears less important than nitrogen (N) in sediment in regulating SAV growth in many instances. For example, sediments from the Upper Mississippi River that were fertilized to increase available N promoted an approximate 30 to 50% increase in aboveground production of wild celery from winter buds (Rogers et al. 1995). In contrast, P additions to the same sediment had little overall positive effect on growth, consistent with findings of previous *in situ* fertilization experiments (Ander-

son and Kalff 1986, Duarte and Kalff 1988, Moeller et al. 1988). Barko et al. (1991b) proposed that SAV may be more frequently limited by N than by P due to the relatively larger amounts of the latter in most lake sediments.

Establishment of SAV can be greatly affected by sediment through textural impacts on rooting success and nutritional impacts on plant biomass (Sculthorpe 1967). Typically, wild celery grows very well on fine-textured inorganic sediments, with organic matter content <20% (Smart and Barko 1985, Barko et al. 1986, D. G. McFarland pers. observ.). Smart and Barko (1985) reported that, on fine-textured mineral sediments, SAV yields frequently exceed 1200 g (dry wt) m^{-2} sediment surface area. Sediments that are high in sand content tend to be nutritionally-poor substrates for growth and may impede rooting success due to compaction and resistance to root penetration (Barko et al. 1991b). Low levels of organic matter in sandy substrates can promote vegetative growth by enhancing ionic exchange and increasing concentrations of required nutrients (Sand-Jensen and Søndergaard 1979, Kiøboe 1980). Conversely, high organic matter content may be detrimental to growth, because of toxic concentrations of organic acids and sediment instability due to low density (Ponnamperuma 1972, Barko et al. 1991b).

Dissolved inorganic carbon (DIC) has been cited as a possible factor limiting rates of photosynthesis and growth of aquatic vegetation (Sculthorpe 1967, Barko et al. 1986, Smart et al. 1994). The photosynthetic potential of a variety of SAV species appears to far exceed photosynthesis determined by carbon available in many aquatic systems (Browse et al. 1979, Beer and Wetzel 1981). Increases in DIC have been demonstrated to stimulate carbon uptake rates (Steeman-Nielsen 1947, Titus and Stone 1982, Wetzel et al. 1985) and may help to augment the growth of wild celery on different sediments (Barko et al. 1991a, Titus 1992; Table 6) and at low pH (Titus et al. 1990). Titus and Andorfer (1996) noted dramatic increases in dry biomass of wild celery on both high and low fertility sediments, with CO_2 amended to 10x ambient (i.e., 130 µM). Moreover, with CO_2 enrichment, the increase in dry biomass on both sediments was greater at pH 5 than at a near neutral pH (7.3).

In nature, wild celery is subject to control by a variety of grazers including muskrats, red-bellied turtles, manatees, carp, and especially waterfowl. In 1980, waterfowl consumed 40% of 380,160 kg (dry weight) of wild celery winter buds on a portion of Pool 7 of the Upper Mississippi River (Korschgen et al. 1988). In a matter of days, grazing by manatees decimated newly transplanted stands of wild celery left unprotected in Kings Bay, in Citrus County, Florida (Hauxwell et al. 2004). Grass carp introduced into Lake Wingra in the late 1800s apparently caused wild celery to disappear from the lake by 1929 (Davis and Brinson 1980). One year after carp removal by rotenone in the Middle Harbor of Lake Erie, Ohio, wild celery was found where it had not been found before treatment.

A few studies of herbivory on wild celery have employed the use of full exclosures or fenced plots that offer some degree of protection (Table 6). Carter and Rybicki (1985) studied wild celery transplanted in the Potomac River and observed that plants grown in full exclosures during their first year became well-established the following year. Recent-ly, Sponberg and Lodge (2005) reported that exclosures to limit waterfowl foraging provided refuge for wild celery subject to intense seasonal grazing in Lake Mattamuskeet, North Carolina. Moreover, in a manual to guide the establishment of aquatic plants in the field, Smart et al. (2005) recommended different types of exclosures and planting strategies beneficial to establishing wild celery and other SAV. While exclosures can be advantageous to aquatic plant establishment, some may require intense upkeep and monitoring (e.g., in tidal areas) to prevent clogging that may lead to light limitation and other detrimental impacts.

FUTURE RESEARCH NEEDS

This review presents evidence of two wild celery ecotypes with life histories that differ greatly in modes of over-winter survival. While the northern ecotype produces winter buds as a means of vegetative perennation, the southern ecotype may die down in winter to a reduced evergreen condition. Data thus far suggests that the southern ecotype does not produce winter buds and that its lack of winter bud formation may be an inherent characteristic. Differences in morphology may also exist between northern and southern ecotypes—differences that may account for the two variants, narrow-leaved and broad-leaved, observed by Lowden (1982). Though Lowden did not discuss the formation of winter buds in his descriptions, it is interesting that the illustrations of narrow- and broad-leaved variants in his article were from Ohio and Texas, respectively. Further studies are needed to confirm distinctions between ecotypes of wild celery, with regard to ability to survive in different localities and risks of hybridization to population fitness.

The length of time a seed remains viable is critical to population longevity because the potential for growth exists as long as a single seed remains viable in the substrate. Gradients in the sedimentary environments where seeds become lodged, as well as the internal (genetic and physiological) properties of seeds may be important to understanding processes that may delay or speed seed germination. Further knowledge of what controls the timing and quality of germination would be useful to:

- predict depletion and replenishment rates of the seed/propagule bank

- develop protocols for planting and habitat restoration

- understand relationships between seed viability and depth of burial

- anticipate the size and viability of the seed bank from one year to the next.

Knowledge of the influence of salinity on the growth and survival of wild celery is central to understanding its distribution and abundance in tidally influenced estuaries. While much work has been conducted on growth from winter buds and transplants of this species, little is known about the effects of salinity on establishment of seedlings. Laboratory studies of wild celery seedlings are needed to assess their tolerance of salinity, with consideration of the strength and duration of exposure, and seedling age or stage of development.

Thus far, flower induction in wild celery has received little investigative attention but should be examined in relation to different factors (especially photoperiod, light, spectral quality) to determine critical levels. In addition, the positive relationship between incidence of flowering and plant biomass, as determined in the laboratory (Titus and Hoover 1991), warrants further investigation under field conditions.

Propagule dispersal is a critical feature governing plant distribution, but information is scant regarding factors controlling dissemination of wild celery propagules. For SAV in general, the principal disseminating agents are water, animals (including man), and wind, although these processes differ greatly in importance to population spread (Sculthorpe 1967). Wind-dispersal is believed to be hazardous and rare for SAV because wind-dispersed propagules could be transported to terrestrial or other areas where development would be restricted. Water-dispersal is also likely to cause high propagule mortality, although it can provide an important means of establishing in new areas. Both external and internal transport by animals, especially waterfowl, have been reported, and it is now recognized that many animals, including man, can potentially disperse SAV propagules. With regard to the spread of wild celery, it would be of interest to assess:

- transport and deposition of propagules under different flow regimes

- importance of sexual versus asexual propagules in colonization

- survival of seed after passing through digestive tracts of waterfowl and other known grazers.

Ecological studies of SAV propagules should consider handling of propagules in a manner that does not compromise collected data. It is essential that pre-study conditions be maintained as nearly as possible to conditions found in nature and do not interfere with experimental treatments being tested. Special attention should be given to:

- removal of propagules from substrate (changes in light and redox)

- method and duration of storage (changes in temperature and moisture)

- sterilization and scarification (modification of the seed surface)

- use of Petri dishes without a substrate.

Baskin and Baskin (1998) have provided guidelines to help reduce experimenter bias in seed studies, and many of their proposals could apply to the handling of vegetative propagules.

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