

Light and Temperature Effects on the Growth of Wild Celery and Hydrilla

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ABSTRACT

Wild celery (*Vallisneria americana* L.) has coexisted with the dominant species hydrilla (*Hydrilla verticillata* (L.f.) Royle) since the resurgence of submersed aquatic vegetation in the tidal Potomac River in 1983. In 1989, particularly turbid, cool, and cloudy spring conditions were associated with a substantial decrease in hydrilla coverage. We measured growth and elongation potential of wild celery and hydrilla propagules under various temperature and irradiance conditions to compare these two species and in part explain the stable persistence of wild celery and the variability in hydrilla coverage. A plant growth experiment was conducted to simulate actual temperatures in the Potomac River during spring of 1986 (plant coverage increased) and 1989 (plant coverage decreased). In the 1989 temperature treatment, final heights of hydrilla and wild celery were unaffected by a 6-C decrease in temperature 2 weeks following tuber germination. Heights of wild celery, however, were more than twice that of hydrilla, and elongation rates of wild celery were greater than those of hydrilla when temperatures reached 17 to 22C. Laboratory studies conducted in complete darkness showed that wild celery tubers germinate at 13C, whereas hydrilla tubers germinate at 15C, and that wild celery elongated to heights twice those of hydrilla. Heights were positively correlated to tuber length. If irradiance is diminished at incipience, differences in tuber reserves and elongation potential may be sufficient to ensure that wild celery can survive when hydrilla is not successful.

Key words: submerged aquatic vegetation, tubers, competition, *Hydrilla verticillata*, *Vallisneria americana*.

INTRODUCTION

Since the resurgence of submerged aquatic plants in the tidal Potomac River in 1983 (Carter and Rybicki 1986, Carter et al. 1994), plant populations have fluctuated greatly in coverage and distribution. The monoecious biotype of hydrilla was the dominant species in the tidal river for many years, forming dense beds that extended as much as 500 m from shore and outcompeting other species. Populations of wild celery, Eurasian watermilfoil (*Myriophyllum spicatum* L.), spiny naid (*Najas minor* Allioni), water stargrass (*Heteranthera dubia* (Jacquin) MacMillan), and coontail (*Ceratophyllum dem-*

ersum L.), however, continued to exist mixed within and on the edges of dense hydrilla beds or in small, isolated patches.

In 1989, hydrilla coverage declined substantially in the upper tidal river coincident with an extended spring period of low temperature and below-average available sunshine combined with poor water clarity (spring Secchi depths <0.6 m, Carter et al. 1994). Mean daily water temperature rose gradually from 8C in March to a high of 18C at the end of April and then declined to 12C in mid-May. Temperatures remained below 22C until early June, increasing to above 22C in late June (James et al. 1989). Under these conditions, aquatic plant beds did not return in 1989 to areas that were densely vegetated with hydrilla the previous year.

Understanding the relative responses of hydrilla and wild celery to temperature, water clarity, and other factors is critical to understanding population dynamics. The optimum temperature for photosynthesis of dioecious hydrilla (36.5C, Van et al. 1976) is greater than that of wild celery (33.6C, Titus and Adams 1979). Published values for photosynthesis show that both species are well adapted to low irradiance, and their compensation points (I_c), the irradiance levels at which respiration equals photosynthesis, are extremely low. I_c ranged between 7 and 20 (Van et al. 1976, Bowes et al. 1979, Steward 1991) and between 10 and 36 (Harley and Findlay 1994, Madsen et al. 1991) for monoecious and dioecious hydrilla and wild celery, respectively. I_k , the photosynthetic light saturation point, clearly depends on the ambient light regime under which the plants are grown (Bowes et al. 1977); but for these species, it is generally less than one-third of full summer irradiance [$\sim 2,000 \mu\text{mol m}^{-2}\text{s}^{-1}$ of photosynthetically active radiation (PAR)]. I_k ranged from 100 to 600 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for hydrilla and wild celery tested under a variety of conditions (Van et al. 1976, Bowes et al. 1979, Titus and Adams 1979, Steward 1991, Harley and Findlay 1994). The relative photosynthetic response of monoecious hydrilla and wild celery was not measured in any of these published studies.

In addition to light and temperature, availability of nutrients and inorganic carbon affect the competitive abilities of hydrilla and wild celery. Wild celery may have an advantage over hydrilla under conditions of low sediment fertility (Smart et al. 1994). Hydrilla, however, has been shown to outcompete wild celery under more eutrophic conditions (Van et al. 1999). Hydrilla was found to be more efficient at utilizing carbon than other species (Holaday and Bowes 1980, Bowes and Beer 1987).

Both hydrilla and wild celery vegetatively produce subterranean tubers, hereafter referred to as tubers (but also called winter buds in the case of wild celery, and subterranean turions, in the case of hydrilla). In temperate regions, these overwintering storage organs sequester and transfer energy

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stored from the previous year's growth. The tubers germinate in spring when temperatures rise. Much is known about hydrilla tuber productivity and tuber characteristics (Haller et al. 1976, Bowes et al. 1977, Spencer et al. 1987, Titus and Hoover 1991, Spencer and Ksander 1996), but comparatively little is known about wild celery.

In this study, our objective is to better define some of the differences in tuber biomass, plant height, elongation, and growth characteristics of hydrilla and wild celery. Tuber biomass is an indicator of tuber energy reserves. Plant height is an importance characteristic in determining survival because PAR is attenuated exponentially with depth below the surface. We conducted a series of laboratory experiments to measure (1) tuber biomass distribution, (2) height, elongation rate, biomass, and root:shoot ratio of plants as a function of spring temperature regimes and irradiance, and (3) germination temperature, height, and elongation potential from tubers deprived of light and retained at four constant temperatures. A study of the relative tuber size, germination temperature, and elongation potential of these two species grown under various conditions will contribute to our understanding of population dynamics observed in the wild.

METHODS

Tuber experiments were conducted in 1991 and 1992. In both years, tubers of each species were collected in February from an area dominated by that species during the previous growing season, and tubers were stored in the dark in chilled (5C) river water for several days before experiments were initiated. The length of tubers from base to tip (wild celery) or longest dimension (hydrilla) was measured. Sediment (silty sand; 13.3% particle size $\leq 50 \mu\text{m}$ diameter; 1.81% organic) used in the experiments was collected from Pohick Bay, a small, unvegetated embayment of the tidal Potomac River. The experiments were conducted in aerated indoor tanks that were filled with a culture solution without added nitrogen or phosphorus (Smart and Barko 1985). In this study, analysis of variance (ANOVA) and Student's t-test were used to compare means (SAS Institute 1991).

Tuber Biomass Distribution

Thirty hydrilla tubers and 70 wild celery tubers from those collected in February 1991 were randomly selected, weighed, dried in an oven at 105C, and reweighed for comparison of fresh and dry weights. Tuber fresh weight was determined after wet tubers were placed on a cotton towel for ~30 seconds. More wild celery tubers were used because they were considerably more variable in size than hydrilla tubers.

Growth from Tubers as a Function of Spring Temperature and Irradiance

Two temperature and three irradiance treatments were established in six adjacent 170-L white polycarbonate tanks placed 1 m below two metal halide lamps (1,000 Watt). Water temperature for the 1986 and 1989 spring treatments mimicked those measured once daily on the Potomac River (James et al. 1986, 1989). The temperatures (Figure 1) were

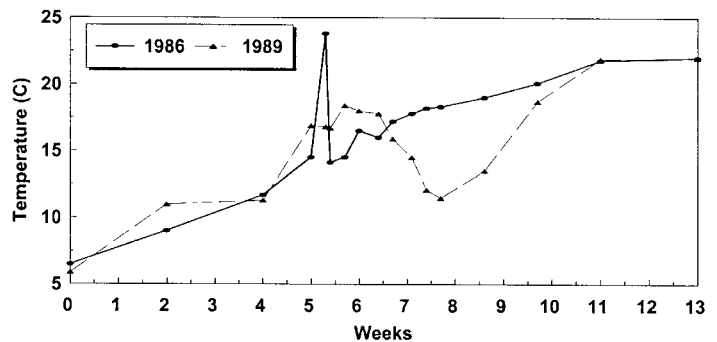


Figure 1. Water temperature during an experiment to determine elongation rates and plant biomass under 1986 and 1989 spring temperature scenarios.

regulated with chillers (Remcor Products, Glendale Heights, IL). Irradiance levels at the sediment surface (~45, ~88, and ~290 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) were controlled by covering the tanks with multiple layers of 1-mm mesh, fiberglass screens. A 14-hr photoperiod was maintained.

In February 1991, tuber length was measured, and either two wild celery or three hydrilla tubers were planted in each of 16 plastic containers (9 by 9 cm), filled with 6 cm of sediment, and covered with a 3-cm layer of pea gravel. Emergence of plants through the sediment surface was recorded at 3-day intervals. Plant height (the length of the longest leaf (wild celery) or stem (hydrilla)) in each container was measured at the end of weeks 6, 8, 10, 11, and 13 to determine elongation rate. After 9 weeks, plants became entwined, and lengths of individual plants in a container were impossible to determine.

The experiment was terminated after 13 weeks. Plant height, the number of leaves (wild celery) or branches (hydrilla), the width of three randomly chosen leaves (wild celery) at a point about two-thirds of the way from the leaf base, and the internode length at the mid-point of five hydrilla branches was measured for the primary plant that sprouted from each tuber. In addition, plants were separated into above- and below-ground biomass and oven-dried (105C). Total biomass and total root:shoot ratios were determined for all plants and young plantlets produced in each container.

Germination Temperature and Elongation Potential for Tubers Grown in the Dark

This experiment to measure the relationship between tuber reserves and plant height was conducted in the dark at four constant temperatures. To ensure that plants elongated using stored energy rather than creating new photosynthetic products, they were completely deprived of light. Initially, hydrilla and wild celery tubers from a February 1992 population were measured, randomly placed in 125-ml plastic cups with and without sediment, and capped with fine gauze. Cups with hydrilla in water (n = 12), wild celery in water (n = 12), and wild celery in sediment (n = 10) were assigned to an 80-L tank containing culture solution. Two tanks were assigned to each temperature treatment. The water temperatures were maintained with an environmental growth chamber (13C), chillers (15 and 17C), and aquarium heaters

(22C). All tanks were covered continuously with blackout curtains except while tubers were measured.

Beginning 2 weeks after planting, plant height was measured weekly for 17 weeks. The presence or absence of roots was noted. Average elongation rates were calculated for each week.

RESULTS AND DISCUSSION

Tuber Biomass Distribution

Wild celery tubers had a mean fresh weight (0.52 ± 0.03 g) three times that of hydrilla tubers (0.17 ± 0.007 g) and a mean dry weight (0.18 ± 0.01 g) 2.4 times that of hydrilla tubers (0.07 ± 0.004 g). The mean fresh weight (0.11 to 0.26 g) of hydrilla tubers was within the range of other studies (Spencer et al. 1987, Titus and Hoover 1991). Figure 2 compares the distribution of dry weights of hydrilla and wild celery tubers, giving an indication of their relative reserves of carbohydrate and other organic compounds.

Growth from Tubers as a Function of Spring Temperature and Irradiance

During the 1986 to 1989 simulation experiment, temperatures were raised slowly (Figure 1). In week 5, however, an interruption in electrical supply caused the temperature in the 1986 regime tubs to rise to room temperature (22C) for ~24 hrs before the problem was corrected (Figure 1). During weeks 0 to 6, the median temperature was 12C for the 1989 simulation and 10C for the 1986 simulation (Figure 3); by week 6, some wild celery tubers had sprouted, but plants remained <1 cm tall, and growth was negligible. After 13 weeks, percent germination of tubers in all treatment tanks (data not shown) was slightly greater for wild celery (94 to 100%) than for hydrilla (83 to 96%).

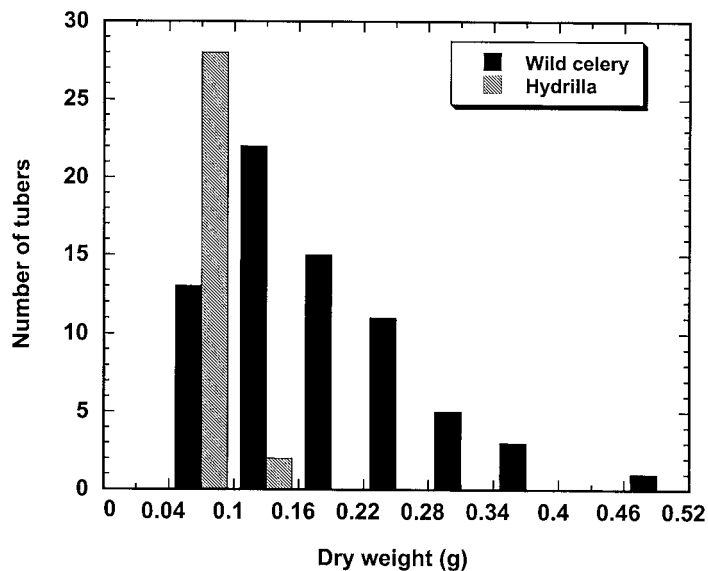


Figure 2. Weight distribution of wild celery and hydrilla tubers collected in the tidal Potomac River, February 1991.

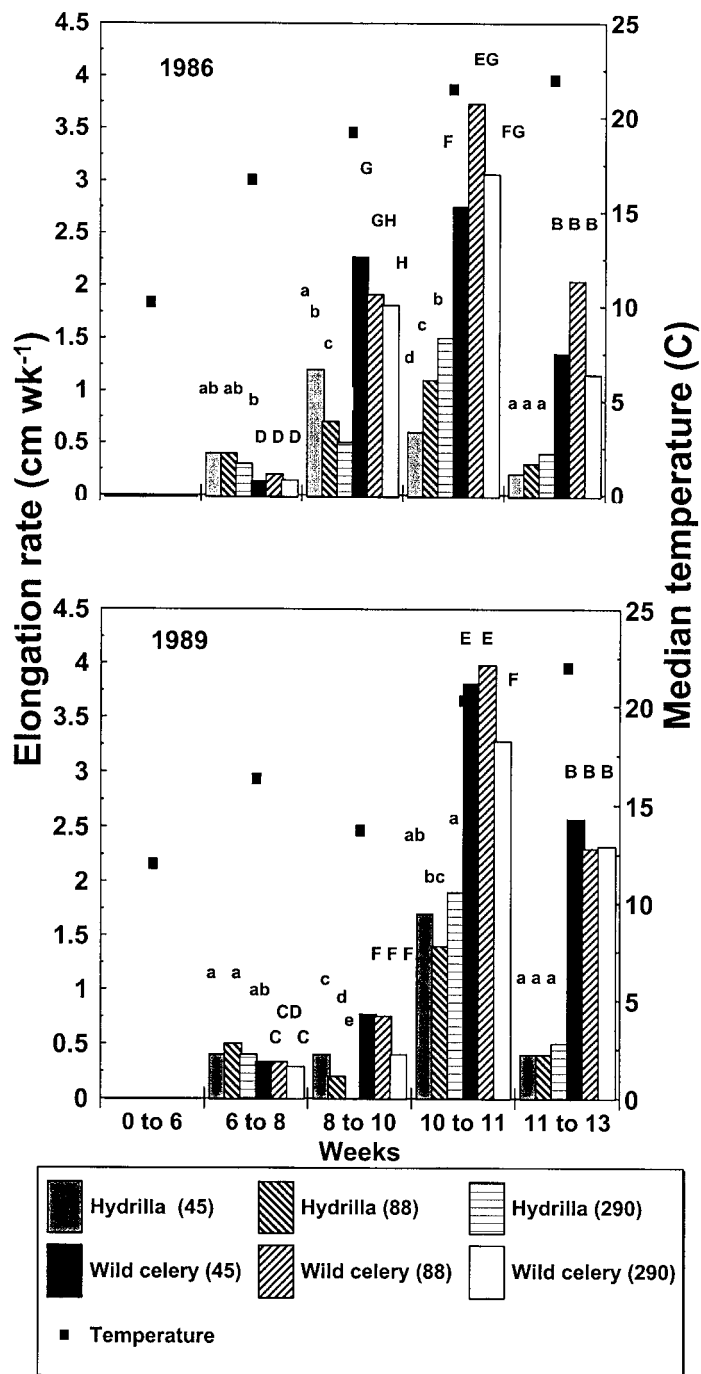


Figure 3. Average elongation rates and median temperature for wild celery and hydrilla grown at 45, 88, and 290 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and at 1986 and 1989 temperature treatments. Within a time period, values sharing the same letter do not differ at the 5% level of significance. Lower case letters show comparison results for hydrilla; upper case for wild celery.

Under both temperature regimes, wild celery elongated more rapidly than hydrilla except for the initial emergence period between weeks 6 and 8, when median temperatures were $\leq 17\text{C}$ (Figure 3). From weeks 8 to 10, the lower temperature in the 1989 simulation resulted in slower-than-1986 elongation rates for both species (Figure 3). After week 8,

wild celery plants elongated at ~2 times the rate of hydrilla in all temperature and irradiance treatments and were twice the height of hydrilla by the end of week 13 (Figure 4). Elongation rates for 1989 temperatures were greater than 1986 for hydrilla (at 45 and at 290 $\mu\text{mol m}^{-2} \text{s}^{-1}$) following the simulated 1989 decrease in temperature (Figure 3). The final heights of hydrilla (~30 cm) and wild celery (>60 cm) did not differ appreciably under the two temperature treatments (Figure 4).

No consistent relation was observed between irradiance and elongation rate or biomass for either species. Final height of wild celery, however, was greater at 88 than at 290 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for both temperature treatments (Figure 4). The temperature treatment produced greater biomass in 1986 than in 1989 only at the greatest irradiance (Figure 5). Results suggest that in areas with an irradiance of 290 $\mu\text{mol m}^{-2} \text{s}^{-1}$, a dip in temperature as occurred in 1989 would have decreased the biomass of both species.

Root:shoot ratios for both species were greatest at 45 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 5). Wild celery root:shoot ratios were greater than those for hydrilla at all irradiance levels. This finding was similar to results found by Haller and Sutton (1975). A large below-ground biomass provides an advantage for acquiring sediment nutrients in areas of low sediment fertility and for anchoring in rocky substrates, high current velocity, or in areas exposed to wind and waves.

This experiment showed that the number of hydrilla branches increases with irradiance (Table 1). The average number of branches for hydrilla increased dramatically from the 45 $\mu\text{mol m}^{-2} \text{s}^{-1}$ treatment to the 88 $\mu\text{mol m}^{-2} \text{s}^{-1}$ treatment, and there were too many entangled branches in the 290 $\mu\text{mol m}^{-2} \text{s}^{-1}$ treatment to make an accurate count. Wild celery, on the other hand, produced only slightly more leaves when irradiance was higher (Table 1) and diverted most of the energy into increasing leaf length. Interestingly, the average

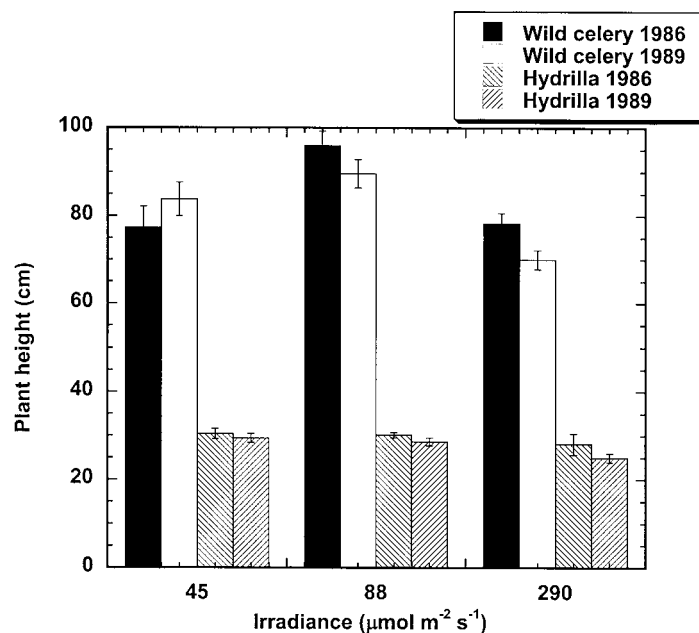


Figure 4. Average height (± 1 standard error) of wild celery and hydrilla for 1986 and 1989 temperature and three irradiance treatments.

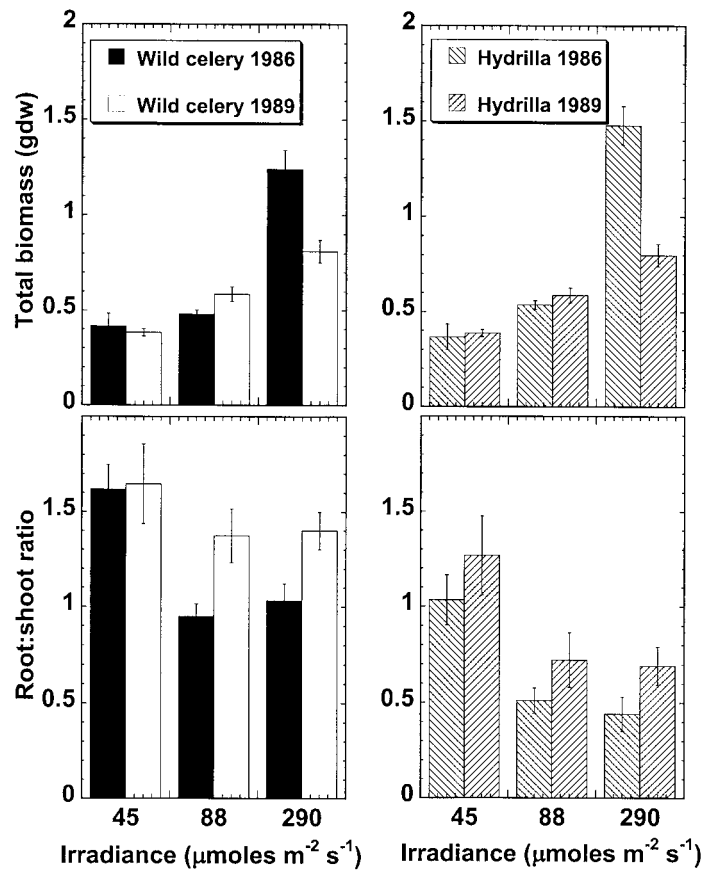


Figure 5. Average total biomass and root:shoot ratio (± 1 standard error) of wild celery and hydrilla for 1986 and 1989 temperature and three irradiance treatments.

length of the internodes in hydrilla did not increase consistently with decreasing irradiance, as might have been expected. The length of the internodes of hydrilla did not appear to be related to irradiance or temperature (Table 1). For monoecious hydrilla, allocation of energy was diverted to increasing the number of branches rather than the height. Monoecious hydrilla in contrast to dioecious hydrilla has a more prostrate growth form in the initial period of growth.

Germination Temperature and Elongation Potential for Tubers Grown in the Dark

For tubers that were held in the dark and maintained at a constant temperature, more than 50% of wild celery and none of the hydrilla tubers sprouted at 13C (Table 2). Germination of wild celery in either sediment or water was >90% at 15C, while germination of hydrilla was <50%. According to the results of this experiment, the majority of tubers of either species should germinate when temperatures reach 17C. These findings are similar to those of Haller et al. (1976) who found <10% germination of dioecious hydrilla at <14C with optimum germination achieved at temperatures between 18 and 35C. This provides wild celery an earlier start in the spring as temperatures slowly rise; and, under some circumstances, PAR immediately following germination might differ markedly from that later in the season.

TABLE 1. SUMMARY FOR MEAN NUMBER OF BRANCHES AND LEAVES, LEAF WIDTH, AND INTERNODE LENGTH (± 1 STANDARD ERROR) FOR HYDRILLA AND WILD CELERY GROWN UNDER SPRING 1986 AND 1989 TEMPERATURE TREATMENTS AND THREE IRRADIANCE CONDITIONS FOR 13 WEEKS.

Species	Temperature simulation date	Irradiance	Irradiance	Irradiance
		($\mu\text{mol m}^{-2}\text{s}^{-1}$) 45	($\mu\text{mol m}^{-2}\text{s}^{-1}$) 88	($\mu\text{mol m}^{-2}\text{s}^{-1}$) 290
Number of branches				
Hydrilla	1986	8.7 \pm 0.4	20.6 \pm 1.3	No data
Hydrilla	1989	8.9 \pm 0.4	16.2 \pm 1.3	No data
Length of internodes (cm)				
Hydrilla	1986	1.54 \pm 0.06	1.28 \pm 0.02	1.48 \pm 0.04
Hydrilla	1989	1.15 \pm 0.03	1.16 \pm 0.02	1.41 \pm 0.04
Number of leaves				
Wild celery	1986	8.7 \pm 0.6	11.2 \pm 0.5	9.1 \pm 0.3
Wild celery	1989	8.2 \pm 0.3	9.8 \pm 0.3	10.3 \pm 0.3
Leaf width (mm)				
Wild celery	1986	4.5 \pm 0.2	5.3 \pm 0.2	6.8 \pm 0.3
Wild celery	1989	4.7 \pm 0.2	5.1 \pm 0.3	6.5 \pm 0.3

Both species reached their maximum height in 6 weeks at 22C. The time to reach maximum height (an indication that tuber reserves were depleted) increased with decreasing temperature (data not shown). At lower temperatures after week 6, some plant heights continued to increase, but plants were so brittle that they began fragmenting. In some cases, wild celery lost the tip of the longest leaf, but other leaves continued to elongate. Plants were etiolated. The length at week 6 was used for the remaining comparisons, and statistical tests and means were based on observations pooled (not significantly different) by temperature treatment.

At 22C, maximum elongation rates occurred during week 4 for all three experimental groups (Figure 6); whereas, at 15 and 17C, elongation rates increased with time. At 13C (not shown), the elongation rate of wild celery in water and sediment was $<0.03 \text{ cm wk}^{-1}$, while the elongation rate in sediment was 0.04 to 0.08 cm wk^{-1} after week 2. Similar to these results, Spencer and Ksander (1996) found monoecious hydrilla tuber reserves were maximally depleted in 3 to 4 weeks at 25C.

By week 6, wild celery was $>30 \text{ cm}$ in height and was twice the height of hydrilla in the 22C treatment (Figure 7). In a medium of water, the height of wild celery was greater than hydrilla at 22C; the height of wild celery was greater in sediment than in water at temperatures $\geq 17\text{C}$. Significant linear relationships ($R^2 = 0.23$ to 0.61) were detected between tuber

size (including tubers that did not germinate) and plant height at 22C for all three experimental groups. A second analysis comprising only tubers that germinated improved the relationship (Figure 8), indicating that tuber size explained more than 47% of the variability in plant height at 22C.

We found that wild celery tubers planted in sediment elongated significantly more than those planted in water. Spencer and Ksander (1996) grew monoecious hydrilla and *Potamogeton gramineus* L. tubers in the dark, with and without sediment, and found that plants in sediment grew taller and produced more leaves. Both hydrilla and wild celery grew roots in all temperature regimes, and plants in sediment had access to nutrients and micronutrients in both the sediment and the culture solution.

Overwintering propagules of wild celery are generally more than twice the size of hydrilla propagules. The dark experiment revealed an inherent elongation potential for wild celery which was twice that of hydrilla at 17 and 22C (Figure 6). Interestingly, wild celery deprived of any light (Figure 7) was the same height ($\sim 30 \text{ cm}$) as hydrilla at 45 to 290 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (Figure 4).

In agreement with our data, Bowes et al. (1977) found that reserves in the dioecious hydrilla tubers may support elongation for an extended period of time (2 months) in the dark, and that larger tubers resulted in longer shoot lengths. They found that apical stems of hydrilla placed under very low irradiance (6 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) elongated, but decreased in total dry weight. As a result of their experiments, they concluded that shoots from hydrilla tubers must have at least 12 to 20 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (irradiance above the I_c) within 0.5 to 0.75 m above the hydrosol or they will not survive. Hydrilla and wild celery each have low I_c values; and when these two species grow together, the greater elongation rate of wild celery provides a competitive advantage for growing to a height where PAR exceeds I_c . The previous year's conditions affects the production of storage organs; therefore, not only current year, but previous growing season PAR can affect the height and survival of these tuber-forming species.

TABLE 2. GERMINATION (%) OF HYDRILLA AND WILD CELERY FOR PLANTS GROWN FROM TUBERS AND HELD IN THE DARK FOR 6 WEEKS UNDER FOUR TEMPERATURE CONDITIONS.

Species	Temperature (C)			
	22	17	15	13
Hydrilla in water (n = 24)	100	79	46	0
Wild celery in water (n = 24)	92	100	96	58
Wild celery in sediment (n = 20)	92	95	94	100

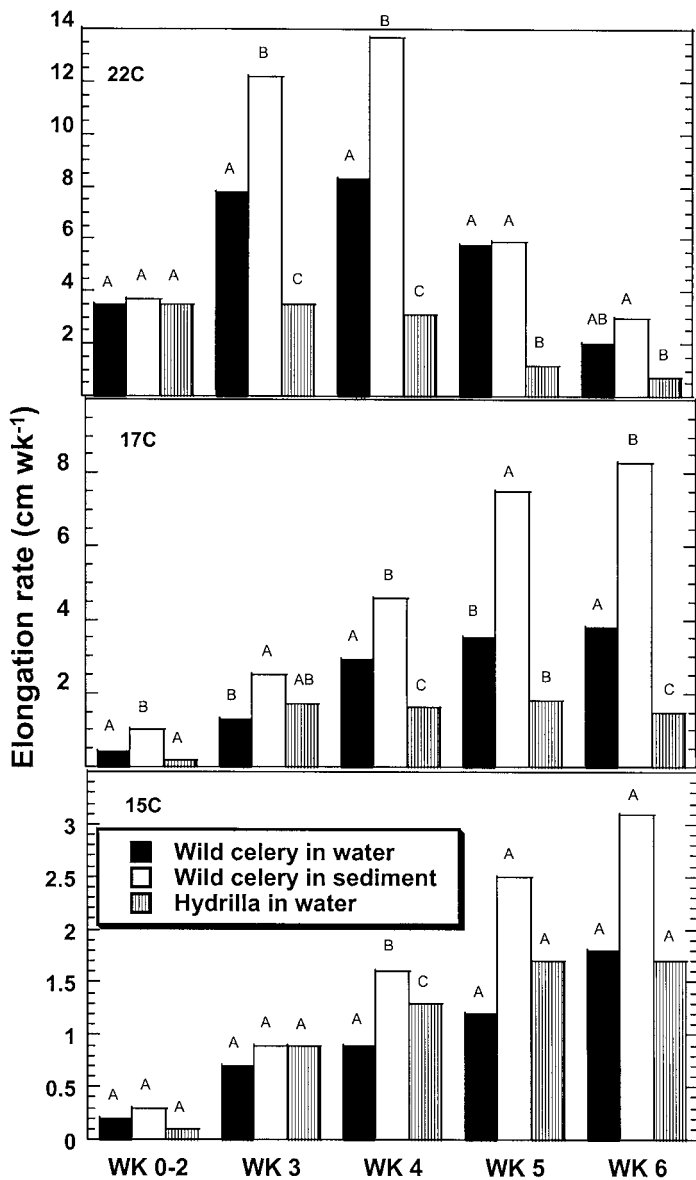


Figure 6. Average elongation rates for wild celery and hydrilla plants grown from tubers and held in the dark under three constant temperatures for 6 weeks. Values sharing the same letter do not differ at the 5% level of significance within temperature treatments by date.

In the turbid conditions found in the Potomac River (median April to October Secchi depths between 0.5 and 1.0 m (Landwehr et al. 1999)), elongation of leaves toward the surface is essential if plants are to survive, particularly as water depths approach 1 m. It is striking that both species can continue to elongate for as long as six weeks at 22C in the dark, in spite of respiratory demands. Plants grown under dark conditions became exceedingly brittle, however, and under the normal stress of wave and current in the nearshore environment would be expected to disintegrate if irradiance was below the irradiance at which respiration equals photosynthesis ($\sim 20 \mu\text{mol m}^{-2} \text{s}^{-1}$).

The cloudy and turbid conditions in 1989 provided a situation where the energy reserves in hydrilla tubers could have

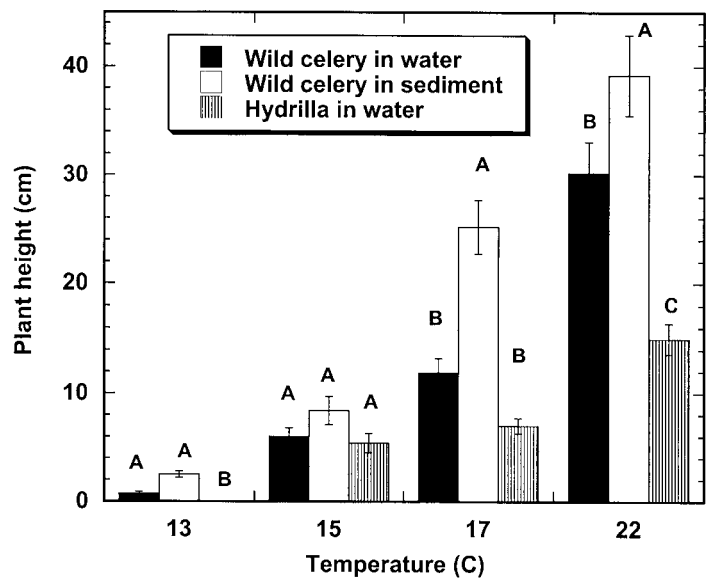


Figure 7. Average height after 6 weeks for wild celery and hydrilla plants grown from tubers and held in the dark under four constant temperatures for 6 weeks. Within a temperature treatment, values sharing the same letter do not differ at the 5% level of significance.

been depleted before plants reached a height where irradiance was above $20 \mu\text{mol m}^{-2} \text{s}^{-1}$. The percent available sunshine (actual minutes of sunlight as a percent of possible minutes of sunlight for the month) was extremely low (NODC 1989, Figure 9). On cloudy days, incoming irradiance just below the surface may diminish to approximately $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR or less.

Irradiance is attenuated with depth, and light attenuation at depth (K_z) can be calculated using Beer's law:

$$I_z = I_0 e^{-Kz},$$

where I_0 is irradiance measured just below the surface, and I_z is light measured at depth z . According to this equation, we derived a plot of K_d (light attenuation m^{-1}) and irradiance (PAR) at depths of 1 m and 1.3 m for conditions when irradiance just below the surface was 700 and $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 10). Based on the growing season mean Secchi depth (measured twice monthly) of 0.6 m (Carter et al. 1994), K_d was 2.4 for the upper tidal Potomac River in 1989 (calculated as $K_d = \text{Secchi depth}/1.45$, Batiuk et al. 1992). Results indicated that, for a K_d of 2.4, irradiance was $\sim 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 1.3 m below the surface when irradiance is $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ just below the surface. At 1 m below the surface, irradiance was ~ 40 to $60 \mu\text{mol m}^{-2} \text{s}^{-1}$. Therefore, irradiance doubles at elevations 0.3 m closer to the surface. Irradiance decreases by one-half when irradiance is $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ just below the surface in cloudy conditions. A 30-cm difference in height could make a difference between survival and death for plants that must elongate to the height where irradiance is adequate.

Our findings are consistent with the hypothesis that larger tubers, increased elongation potential, and earlier germination temperatures of wild celery compared to hydrilla may allow wild celery to persist and expand at times when hydrilla is less successful, such as in 1989. Under most conditions, hy-

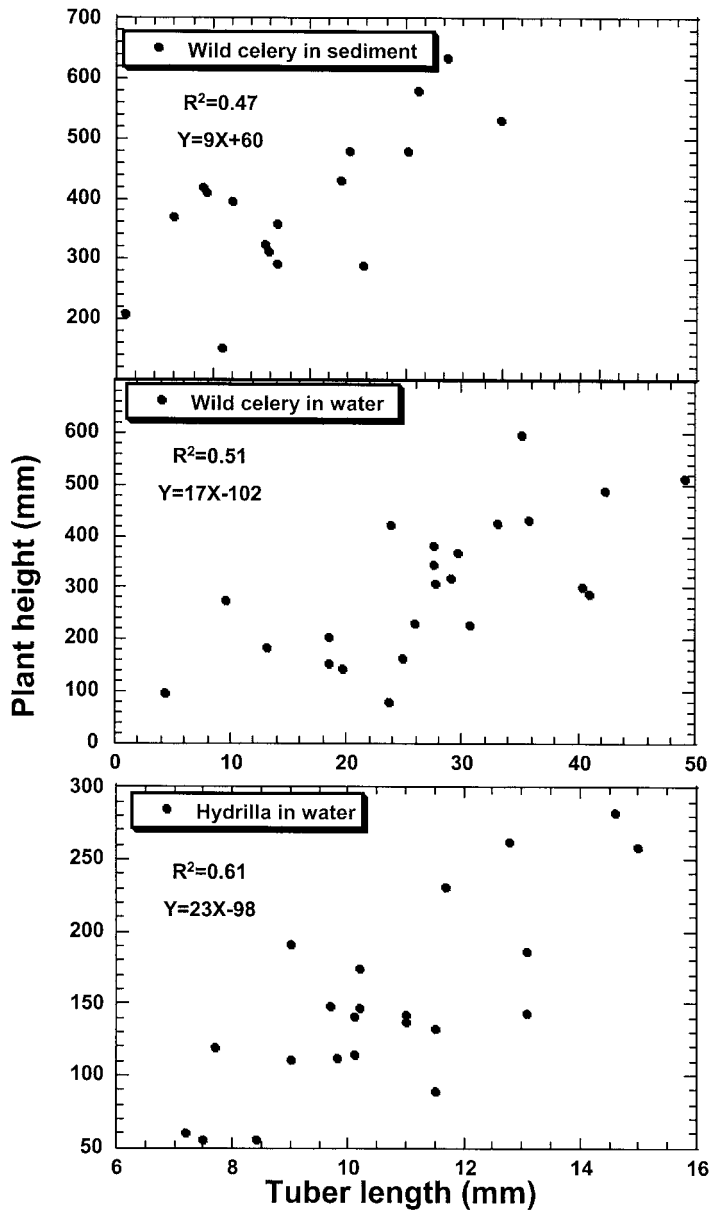


Figure 8. Relationship between plant height after 6 weeks and tuber length for wild celery and hydrilla plants grown from tubers and held in the dark at 22C.

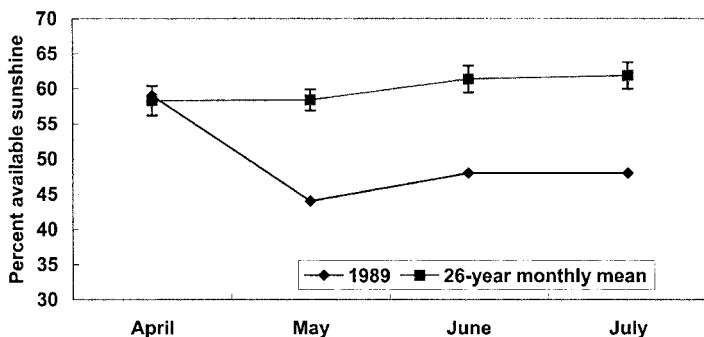


Figure 9. Mean monthly percent available sunshine for 1989 and for 1970 to 1995 in the upper tidal Potomac River. Bars represent 1 standard error for the 26-year monthly mean.

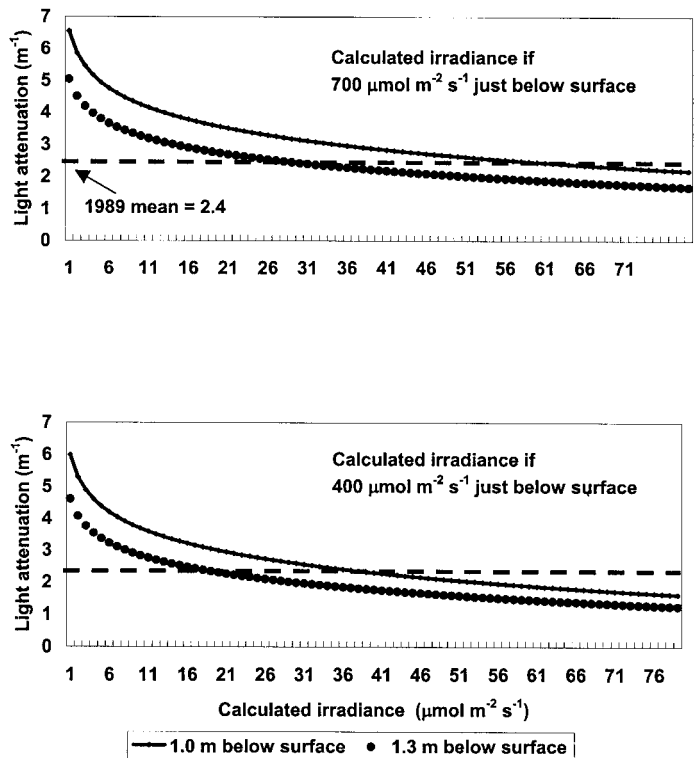


Figure 10. Light attenuation versus irradiance at 1 m and 1.3 m below the surface when irradiance is 700 and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ just below the surface. Dashed line indicates 1989 mean light attenuation (K_d) in the upper tidal Potomac River.

drilla is observed to overwhelm wild celery growth by the end of the growing season. Due to the greater elongation potential from tubers, however, wild celery may better endure cloudy and turbid spring conditions. Further field work is necessary to better understand this critical period following tuber germination.

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