Abstract  Experimental and observational studies of the submersed, freshwater macrophyte *Vallisneria americana* Michx. revealed that depth, wind and wave exposure, and current velocity may all influence fruit set. In this dioecious species, long-pedunculate female flowers are pollinated by free-floating male flowers at the water surface. Average fruit set in the natural populations studied varied from zero to 97% of the flowers observed. With increasing water depth in New York and Pennsylvania lakes, female plants continued to flower, though these flowers were unable to reach the surface, and consequently, did not set fruit. Fruit set was also lower in relatively open sites exposed to wind and waves, presumably because male flowers do not remain in the vicinity of female flowers long enough for effective pollination. This was particularly striking at a site with low male flower densities, but fruit set was increased to 100% at that site by confining the floating male flowers within a field enclosure. In a river, fruit set was negatively correlated with surface current velocity, and was reduced to zero in current velocities greater than 0.30 m·s⁻¹. Fruit set in *V. americana* appears to be restricted or precluded by physical environmental conditions in a variety of sites.

Key words  Pollen limitation · Fruit set · Dioecious · Macrophyte · Hydrophilous pollination

Introduction

Many plant populations can be characterized as producing more flowers than fruits, a potentially wasteful and/or detrimental investment of resources. Consequently, a rich literature has developed on what limits fruit or seed set in angiosperms (Lee and Bazazz 1982; Snow 1982; Sutherland 1987; de Jong and Klinkhamer 1989; Zimmerman and Aide 1989; Calvo and Horvitz 1990; Vaughton 1991; Karoly 1992; Whisler and Snow 1992; Campbell and Halama 1993; Lawrence 1993; Washitani et al. 1994; Ehrlen and Eriksson 1995). Several factors can interact to influence female reproductive success, such as the availability of resources (including pollen), pollinators, and weather conditions (e.g., McCall and Primack 1985; Campbell and Halama 1993). However, Zimmerman (1988) has argued that more conclusive studies are needed. Although limited pollen availability or reception may limit fruit set in many populations (Berry and Calvo 1989; Johnston 1991; Byers 1995), the extent to which this occurs is relatively unknown.

Evidence of pollen limitation is crucial if we are to evaluate or understand resource limitation of female reproduction, reproductive allocation patterns, or the evolution of pollination systems. It has long been suggested that female reproductive success should be limited by resources other than pollen (Darwin 1876; Bateman 1948; Janzen et al. 1980; reviewed in Bawa and Webb 1984; Sutherland 1986). This assumption may lead to erroneous interpretations of reproductive allocation patterns if fruit set is pollen-limited (Bierzychudek 1981). Second, several non-mutually exclusive hypotheses consistent with resource limitation have been advanced to account for non-fruiting flowers. The male function hypothesis states that non-fruiting flowers increase fitness through pollen donation. The selective abortion hypothesis argues that some fruits are aborted to favor the development of higher quality fruits. Finally, the bet-hedging hypothesis suggests that extra flowers can develop as a hedge against variation in resource availability (Janzen et al. 1980; Bawa and Webb 1984; Sutherland and Delph 1984; Sutherland 1986). These hypotheses all assume that pollen levels are adequate, and thus they may not apply to pollen-limited populations (Whelan and Goldingay...
productive ecology of a population or species. Third, theory suggests that pollen-limited populations are not evolutionarily stable (Haig and Westoby 1988; Calvo and Horvitz 1990; Cohen and Dukas 1990; Campbell et al. 1991; Olivieri et al. 1994). Within populations consistently growing under pollen-limited conditions, there should be strong selection pressure favoring individuals that increase pollen attraction or reception, until a fine balance between pollen- and resource-limitation is achieved (Galen 1985; Haig and Westoby 1988). Therefore, it remains critical to determine the conditions under which reproduction is limited by pollen supply if we are to correctly interpret the reproductive ecology of a population or species.

Previous investigations of pollen limitation have primarily focused on hermaphroditic species with populations characterized by low fruit-to-flower ratios. However, all obligate outcrossers are potentially pollen-limited, especially the dioecious species which are often thought to have high fruit-to-flower ratios (Sutherland and Delph 1984). Prior investigations have also focused chiefly on taxa with animal pollinated systems. Here we extend the examination of pollination ecology to the dioecious aquatic macrophyte *Vallisneria americana* (Hydrocharitaceae). Relatively little is known about the efficiency of pollination systems among natural populations of aquatic macrophytes, although pollination limitation in *V. americana* has previously been examined in artificial systems (Lovett Doust and LaPorte 1991). Also, by examining fruit set in a dioecious species, pollen limitation of female function cannot be confounded with resource allocation to male function. Lastly, the hydrophilous *V. americana* is of interest in that pollination occurs in a two-dimensional physical environment (the water surface), and may be uniquely influenced by the characteristics of that environment.

Prior studies of pollen or pollinator limitation have examined interpopulational differences (e.g., Galen 1985; McCaill and Primack 1985; Johnston 1991), but few have considered the role of local physical conditions in causing these differences (but see Hagerup 1951; Campbell 1987; Berry and Calvo 1989). This study investigates the potential of site characteristics to limit fruit set in *V. americana*. Although fruit set in natural populations of *V. americana* is often very high (personal observation), female flowers must reach the water’s surface to be pollinated by minute free-floating male flowers (see below) subject to wind, waves, and/or water currents. We therefore hypothesized that (1) females growing at sufficient depths either do not flower, or produce flowers that may not reach the surface to be pollinated; (2) surface wind or wave exposure may limit pollen transfer to female flowers; and (3) current velocity may be great enough to limit pollen transfer to female flowers. We combined experimental and observational studies on sites at three lakes and a river to test these hypotheses where appropriate conditions could be found.

### Materials and methods

#### Study species

*Vallisneria americana* (wild celery) is a submersed dioecious clonal macrophyte widely distributed throughout eastern North America (Lowden 1982). In east-central North America, basal rosettes of long ribbon-like leaves of *V. americana* develop in spring from perennating tubers or germinating seeds. Additional rosettes develop subsequently at the nodes of stolons arising from meristems in the axils of leaves (Sculthorpe 1967). Females develop individual flowers (Fig. 1), and males develop inflorescences, on peduncles flanking axillary stolons. Buoyant female flowers are each tethered on a peduncle elongating toward the water’s surface (Wylie 1917). Anthesis of the female flower typically occurs at the surface in relatively shallow water. Male inflorescences develop on short peduncles within a few centimeters of the bottom, with each inflorescence producing up to 2000 tiny buoyant flowers approximately 0.6 mm in diameter (Wylie 1917). The male flowers abscise after the spathe ruptures, and float to the surface to be supported on the surface film. Pollination occurs when male flowers are caught in the surface tension depression surrounding the female perianth, brushing pollinia onto the stigma (Wylie 1917; Svedelius 1932; Cox 1988). Buoyant fruits develop over several weeks, often being drawn below the surface by the coiling peduncle, where they may remain attached to the parent female through the end of the growing season (personal observation). If the flower is not pollinated, the perianth begins senescence within a few days. Although the flower remains buoyant, it is no longer supported above the surface film (personal observation). As flowers or fruits develop, additional stolons grow down into the sediment from mature or terminal rosettes, each stolon giving rise to one or more perennating tubers. The entire plant, except for the tubers, then senescles at the end of the growing season.

#### Methods

Pollen limitation was evaluated by considering differences in fruit set among plots or sites within a population and relating these dif-

![Fig. 1 Vallisneria americana](image)