Aliso: A Journal of Systematic and Evolutionary Botany

Volume 22 | Issue 1 Article 20

2006

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Recommended Citation

Wyllie-Echeverria, Sandy; Wyllie-Echeverria, Victoria R.; Churchill, Algernon C.; and Cox, Paul A. (2006) "Further Evidence for Seed Size Variation in the Genus Zostera: Exploratory Studies with Z. japonica and Z. asiatica," *Aliso: A Journal of Systematic and Evolutionary Botany*: Vol. 22: Iss. 1, Article 20.
Available at: http://scholarship.claremont.edu/aliso/vol22/iss1/20

Aliso 22, pp. 243–247

FURTHER EVIDENCE FOR SEED SIZE VARIATION IN THE GENUS *ZOSTERA*: EXPLORATORY STUDIES WITH *Z. JAPONICA* AND *Z. ASIATICA*

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ABSTRACT

Recent studies found seed size variation within the seagrass *Zostera marina,* one of nine species in the genus *Zostera.* The objectives of this study were to determine if variation also exists in the seeds of two other species *Zostera japonica* and *Zostera asiatica* within this genus. Results indicate that: (1) length and weight varied between two populations (one indigenous population from Akkeshi-Ko, Japan, and one exotic population from Willapa Bay, Washington, USA) of the small-bodied intertidal seagrass species *Z. japonica,* and (2) seed-size classes were discernable. Preliminary investigations were also initiated with a Japanese population of *Z. asiatica,* a large-bodied subtidal seagrass species.

Z. japonica seeds from the exotic population were significantly ($P < 0.001$) longer and heavier when compared to those from the indigenous population, a finding which may help explain both the process of the earlier introduction and the recent expansion of this exotic in the northeastern Pacific. Also, preliminary results indicate that *Z. asiatica* seeds are heavier than both those of *Z. marina* and *Z. japonica,* which suggests that larger seeds may be associated with large-bodied plants in this genus, an observation that should direct future seed ecology studies within the genus. These findings demonstrate that, similar to the study of terrestrial angiosperms, investigations designed to describe the comparative ecology of marine seed-bearing plants should include an evaluation of seed size.

Key words: seed size variation, *Zostera asiatica, Zostera japonica.*

INTRODUCTION

Mean seed weight remains relatively constant within species (Harper et al. 1970), however, the weight of individual seeds can vary, often leading to size-class differentiation within the same species (e.g., Lortie 2000; Mandák and Pysek 2001). Studies of seed weight in both terrestrial and aquatic species indicate that this variation can influence seedling growth and establishment, thus contributing to the effectiveness of dispersal mechanisms and predation avoidance (Michaels et al. 1988; Philbrick and Novelo 1997; Gernitz 1998; Paz and Martinez-Ramos 2003). Few studies have been made, though, of variation in seed sizes in marine angiosperms or seagrasses. These studies are needed to investigate causal relationships that may exist between seed size variation and ability to escape from predation, seedling survival, or competition between species in mixed stands.

Seagrasses, divided into five families containing 12 genera and approximately 60 species, are distributed in tropical, temperate, and sub-arctic environments (Short et al. 2001; Les et al. 2002; Green and Short 2003). All are monocots (Tomlinson 1982; Ackerman 1995), nine are dioecious, one is a hermaphrodite, and two are monoecious (Cox 1988). One of the least understood aspects of seagrass ecology is the role of sexual reproduction, including seed anatomy, dispersal, and survival (Kenworthy et al. 2006).

The genus *Zostera* L., with nine species (all are monoecious; Cox 1988), is one of the larger, most widely distributed seagrass genera (Green and Short 2003), ranging from the Arctic Circle to the Tropic of Cancer in the Northern Hemisphere and from the southern coast of Australia to the Equator in the Southern Hemisphere. The most cosmopolitan member of the genus, *Zostera marina* L., grows along most coasts in the Northern Hemisphere from 30°N to the Arctic Circle (Green and Short 2003). A recent study involving seeds from this species at geographically distinct sites in North America (Long Island, New York; Puget Sound, Washington; and Izembek Lagoon, Alaska) revealed that while seed length varied within each population, mean seed length of a population corresponded to habitat differences: shorter seeds were associated with shallow-water varieties (*Z. marina* var. *typica* Setchell, Long Island; *Z. marina* var. *izembekensis* Backman, Izembek Lagoon), and longer seeds were associated with the deeper-water variety (*Z. marina* var. *latifolia* Morong) in Puget Sound (Wyllie-Echeverria et al. 2003).

The purpose of this paper is to discuss seed size variation in two other species within the genus *Zostera*: *Z. asiatica* Miki and *Z. japonica* Asch. & Graebn. *Zostera asiatica* grows on the coasts of the Russian Federation, Democratic People's Republic of Korea, Republic of Korea, Japan, and central California, USA (Aioi and Nakaoka 2003; Lee and

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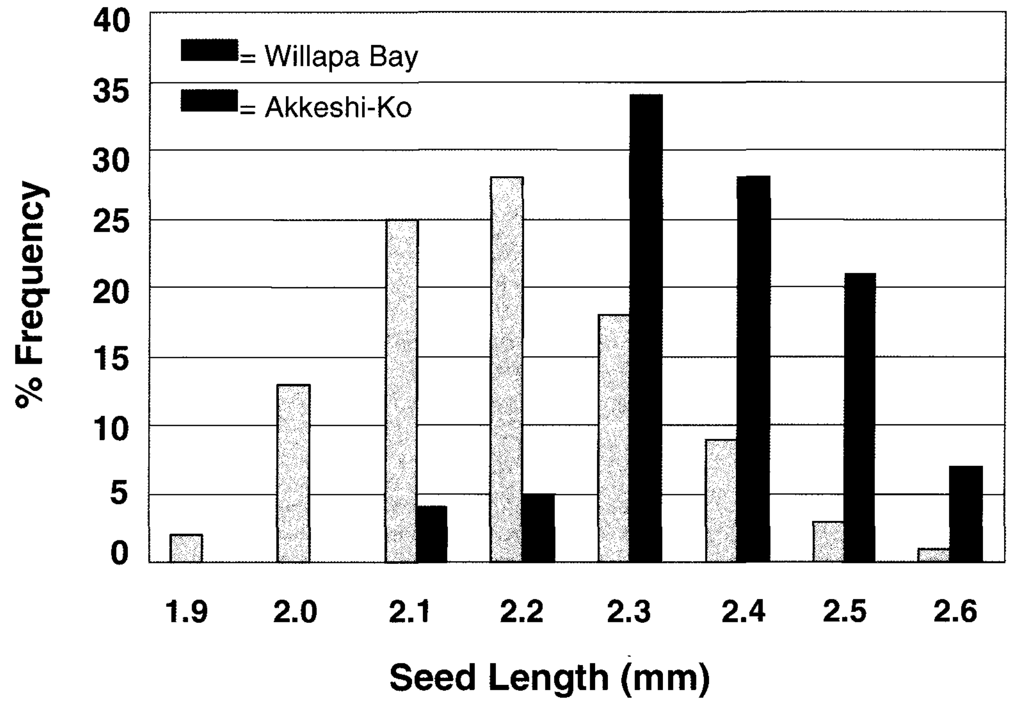

Fig. 1.—Length frequency distribution for *Zostera japonica* seeds from Akkeshi-Ko, Japan, (N = 159) and Willapa Bay, Washington, USA (N = 164).

Lee 2003; Wyllie-Echeverria and Ackerman 2003), while *Z. japonica* is found from northern Japan to Vietnam in the western Pacific and from British Columbia, Canada, to Humboldt Bay, California, in the northeastern Pacific (Aioi and Nakaoka 2003; Hahn 2003; Lee and Lee 2003; Wyllie-Echeverria and Ackerman 2003). *Zostera japonica* is believed to have been introduced to the northeastern Pacific in the early twentieth century as a result of oyster trade with Japan (Harrison and Bigley 1982). *Zostera asiatica* is a large, deep-water species with leaves up to 1.5 m long and 7–15 mm wide; *Z. japonica* is a smaller, shallow-water species with leaves up to 0.5 m long and 0.75–1.5 mm wide (Kuo and den Hartog 2001). Results from this study and previous work that describes seed size variation within *Z. marina* add to the growing body of literature that discusses both the observed variation in seed sizes within the same species and the potential ecological implication of this variation (Schaal 1980; Manasse 1990; Leishman 2001).

MATERIALS AND METHODS

Zostera japonica seeds were collected from sediment following seed release in 1997. Dr. Hitoshi Iizumi, Hokkaido National Fisheries Research Institute, provided seeds from Akkeshi-Ko, Hokkaido, Japan, and Dr. Brett Dumbauld, Washington State Department of Fish and Wildlife, provided material from Willapa Bay, Washington, USA. The seeds were inspected upon arrival and measured following established protocol (Wyllie-Echeverria et al. 2003). The length (latitudinally from the chalazal to micropylar) and width (at the widest point) of the seeds from each site (Akkeshi-Ko, N = 159; Willapa Bay, N = 164) were measured to the nearest 0.01 cm with an ocular micrometer in a dissecting microscope. Geometric shape was also noted (Stern 1983) and the frequency of seed lengths at each site was computed. The cross-sectional area was determined and the weight was estimated (N = 322) using a linear regression (Wyllie-Echeverria et al. 2003). Seed weights were then viewed in a scatter plot (Microsoft Excel) and slope changes were noted to determine seed size classes (Wyllie-Echeverria et al. 2003).

Zostera asiatica seed metrics were obtained by Ms. Masako Watanabe (Hokkaido National Fisheries Research Institute) following seed release in 2003. Weights were calculated (N = 17), but due to the small number of seeds measured, size classes were not differentiated.

RESULTS

The pooled sample of *Z. japonica* seeds ranged in length from 1.9 mm to 2.6 mm; however, mean length varied between the two sites. Seeds from Willapa Bay (N = 164) were longer (mean = 2.38 mm; SD = 0.119) than seeds from Akkeshi-Ko (N = 159; mean = 2.2 mm; SD = 0.138) and this difference was significant (t = 12.58; df = 320; $P < 0.0001$). Longer seeds were also more frequently associated with Willapa Bay (Fig. 1); also they were heavier (mean = 1.10 mg; SD = 0.44) than the Akkeshi-Ko seeds (mean = 0.75 mg; SD = 0.4). This difference also was significant (t = 7.19; df = 320; $P < 0.0001$).

When aggregate *Z. japonica* seed weights were viewed in a scatter plot, seed-size classes could be determined by comparing the slope of the line at break points (Fig. 2); small seeds ranged from 0.1 to 0.5 mg, medium ones from 0.6 to 1.6 mg, and large ones from 1.7 to 2.4 mg. While all size classes were found at each site, more medium and large seeds came from Willapa Bay (small N = 21 [13%], medium N = 127 [78%], large N = 15 [9%]) vs. Akkeshi-Ko (small N = 51 [32%], medium N = 102 [65%], large N = 5 [3%]).

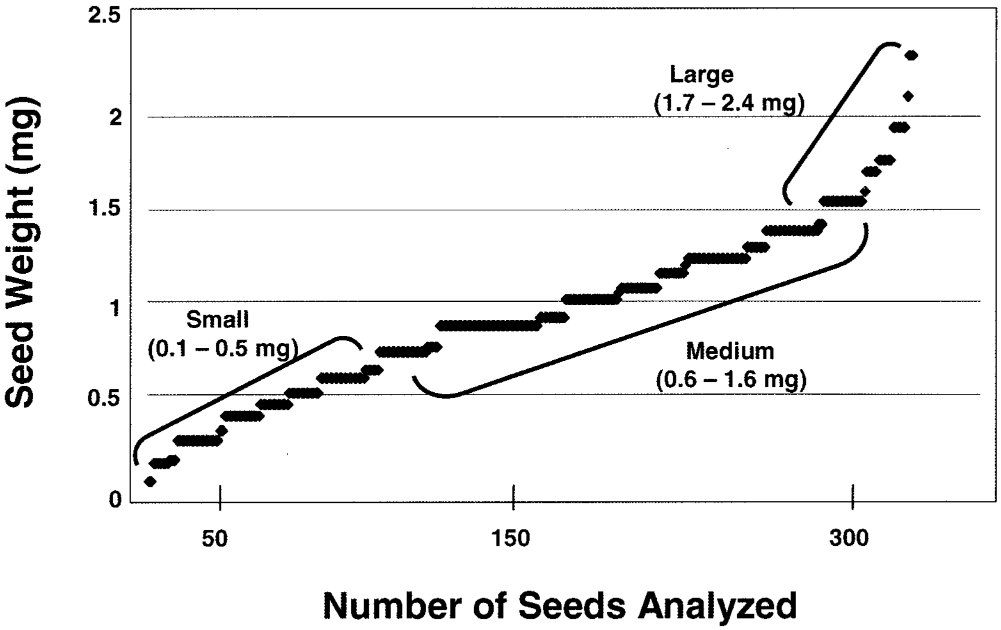

Fig. 2.—Scatter plot indicating seed size classes in *Zostera japonica* populations from Akkeshi-Ko, Japan, and Willapa Bay, Washington, USA. Small (0.1 to 0.5 mg), medium (0.6 to 1.6 mg), and large (1.7 to 2.4 mg) seed size are identified by the brackets along the scatter plot.

Zostera asiatica seeds (*N* = 17) were also variable in length, with the longest being 6.3 mm and the shortest 5.7 mm; mean seed length was 5.9 mm (SD = 0.16). Seed weight varied from 16 mg to 22 mg (mean = 19 mg; SD = 1.49).

DISCUSSION

Zostera japonica seeds from Willapa Bay were larger than seeds from Akkeshi-Ko. As mentioned, *Z. japonica* are believed to have been introduced to the northeastern Pacific early in the twentieth century through oyster trade with Japan. Akkeshi-Ko was a point of origin for oyster shipments from Japan and Willapa Bay was a destination point in the United States (Harrison and Bigley 1982). The first sighting of *Z. japonica* on the northeastern Pacific Coast occurred at Willapa Bay in 1957 (Hahn 2003). It is quite likely that larger seeds could be somewhat responsible for this introductory event. Harrison and Bigley (1982) theorize that "shoots (vegetative or seed-bearing) may have been introduced when the crates of oysters were unpacked." The notion of vegetative fragments successfully re-rooting by other species in the genus *Zostera* (*Z. marina*: Ewanchuk and Williams 1996) has been questioned at one location (Mission Bay, California), based on early observations by Tutin (1938), however, the idea that vegetative fragments are dispersal propagules cannot be dismissed. Also viable seeds of *Z. marina* can be carried over long distances (34 km) in the tidal current (Harwell and Orth 2002). Although the seeds of *Z. marina* can germinate any time after maturity (Taylor 1955), the peak season of germination occurs within four months after seeds are released (Churchill 1983). Whereas, studies describing the seed ecology of *Z. japonica* are lacking, based on experimental research with *Z. marina,* it can be theorized that if seeds remained dormant within the generative shoot, the use of these shoots as packing material could have resulted in their introduction. If, however, seeds germinated before release into a new habitat, it would be necessary for the reserves present in larger seeds to sustain the seedling until such time as it was deposited on the seafloor; therefore, suggesting that a combination of seeds and vegetative fragments (seedlings) may have contributed to the introduction of *Z. japonica* in the northeastern Pacific.

Evidence suggests that in situ populations of *Z. japonica* are expanding and new sites are being occupied in the northeastern Pacific (Hahn 2003). Conversely, populations are threatened at sites within the northwestern Pacific—the native range of this species (Lee 1997). We agree with Hierro et al. (2005) that "an understanding of the processes that enable exotics to dominate recipient communities could be greatly accelerated by an increased emphasis on the comparative ecology of plants where they are native and introduced" and contend that larger seeds could be a factor in the expansion of *Z. japonica* in the northeastern Pacific. For example, Dumbauld and Wyllie-Echeverria (2003) found that ghost shrimp (*Neotrypaea californiensis*) influenced the distribution and density of *Z. japonica,* with fewer seedlings surviving during the season with high shrimp activity (April and May). Seed germination and growth are more successful earlier in the season (February and March). A partial explanation for this occurrence is the speculation that seedlings are either displaced from the sediment or buried during high burrowing activity; whereas, earlier germination and seedling growth are less effected by more moderate burrowing activity (Dumbauld and Wyllie-Echeverria 2003). Larger seeds may contribute to the growth rate of early germination by providing the emerging seedling resources during the late winter and early spring when the water column light environment is more restricted at higher latitudes. We recommend that descriptive seed studies of *Z. japonica* be initiated at other sites to verify or reject this observation.

Variation in seed weight between species, although not surprising, is interesting and may have untested ecological relevance. The whole plant structure of *Z. asiatica* is larger than *Z. marina,* which is larger than *Z. japonica* (Kuo and den Hartog 2001), and a comparison of seed weight among these three species shows that heavier seeds are associated with larger plants. This knowledge may influence the development of conceptual models designed to elucidate competitive relationships where the distribution of these species overlaps in the northwestern Pacific. Studies with terrestrial species have shown that seed size can affect competitive interactions among species occurring in the same location, as well as the ability of species to successfully compete at new habitable sites (Paz and Martínez-Ramos 2003; Turnbull et al. 2004).

Preliminary laboratory studies with *Z. marina* indicate that while seed size does not appear to affect germination, it may influence the size of seedlings (Wyllie-Echeverria and Churchill unpubl. data). Because Churchill (1992) discovered that the emergence of the cotyledon from the sediment into the water column was a necessary first step to seedling growth, it seems advisable to determine if cotyledons are longer in larger seeds. This anatomical feature could allow these seeds to be buried more deeply. This characteristic could enhance seedling survival in years when sediment accumulation, associated with heavy rainfall, is accelerated in nearshore regions (e.g., Ibarra-Obando and Escofet 1987).

While it is known that *Z. japonica* seeds are eaten by waterfowl (Baldwin and Lovvorn 1994) and displaced by burrowing shrimp (Dumbauld and Wyllie-Echeverria 2003), the lack of investigation relative to seed loss by predation or bioturbation limits an understanding of the relationship between the size of seeds and fitness.

In summary, this study and previous work with *Z. marina* (Wyllie-Echeverria et al. 2003) suggest that further study is needed to delineate potential seed-size classes in the genus *Zostera.* Knowledge of this variation in terrestrial seed-bearing plants influenced the development of conceptual models, which, when tested, enhanced awareness that seed size variation was linked to seedling survival. We have shown that seed size variation can exist within the genus *Zostera*; however, links between this variation and seedling survival remain to be tested.

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