SHORT COMMUNICATION

SIZE VARIABILITY AND SELF-THINNING IN WILD-RICE (ZIZANIA AQUATICA)[1]

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ABSTRACT

Size variability decreases during the course of density-dependent mortality (self-thinning) in dense, naturally-occurring monocultures of wild-rice in a tributary to the Chesapeake Bay. As self-thinning progresses, the size distribution changes from high inequality and positive skewness to become more uniform and equal. This is consistent with the hypothesis that self-thinning is driven by competition for light.

WHILE THERE HAS BEEN much interest in size variation within plant populations (e.g., Weiner, in press; Benjamin and Hardwick, 1986) and self-thinning (e.g., Westoby, 1984; Weller, 1987a), very little is known about the relationship between the two. Self-thinning has been studied at the population level in terms of concurrent changes in mean plant mass (or total biomass) and density, while size distributions have usually been studied in experiments in which density-dependent mortality is not extensive. Predictable changes in the distribution of plant sizes may occur during self-thinning, and there may be quantitative relationshps between biomass accumulation, density and other parameters of the size distribution (Weiner and Thomas, 1986). The changes in the distribution of plant sizes that accompany the process of self-thinning have important implications for the ecology and evolution of crowded plant populations.

Size variability is an important aspect of plant size distributions, and is best evaluated by measures of inequality (Weiner and Solbrig, 1984). As a dense stand grows, size variability increases because large plants have higher growth rates, but density-dependent mortality will reduce variability by removing the smallest individuals (Westoby and Howell, 1986; Weiner and Thomas, 1986). Westoby and Howell suggest that self-thinning stands develop a relative size distribution which persists due to a balance between these two forces. Kohyama and Fujita (1981) reported a decrease in size variability during self-thinning in Abies stands in Japan. In a recent review, Weiner and Thomas (1986) found only two data sets which had the information needed to determine size inequality and self-thinning trajectories for dense monocultures. Analyzing data on populations of Pinus ponderosa (Meyer, 1938) and Abies balsamea (Sprugel, 1984; Sprugel, unpublished) they found that size inequality decreased as self-thinning progressed. They interpreted this as support for the hypothesis that self-thinning is caused by competition for light. Since all the available data are for coniferous tree species, it would be valuable to observe this phenomenon in an herbaceous species with a very different growth form. To this end, we undertook a study on self-thinning in naturally-occurring monocultures of wild-rice in the Chesapeake Bay area of Maryland.

MATERIALS AND METHODS—Wild-rice (Zizania aquatica L. [Poaceae]) is an annual grass that grows in shallow waters along the shores of rivers and streams in the central and eastern U.S. and Canada, often forming dense continuous stands (Dore, 1969). In the Chesapeake Bay region of Maryland, wild-rice (Z. aquatica var. aquatica) grows in tidal streams of fresh to slightly brackish water (McCormick and Somes, 1982). Since seedlings germinate at very high densities and adult plants are very large, there is as much as a thirty-fold decrease in density during the growing season (Whigham and Simpson, 1977). This makes wild-rice an excellent plant for the study of self-thinning in natural populations during one growing sea-

TABLE 1. *Summary statistics for sequential harvests of self-thinning stands of* Zizania aquatica

Date	N	Biomass (g m^{-2})	Density (ind. m^{-2})	Gini	Skewness	Kurtosis
23 May	56	144.6	524	0.459	1.94	5.16
4 June	59	222.2	376	0.504	0.76	−0.47
6 June	63	259.5	644	0.503	1.19	0.85
17 June	43	319.2	316	0.449	1.35	1.74
2 July	82	269.0	164	0.398	1.92	6.25
16 July	85	521.9	170	0.393	1.19	1.28
2 Aug.	56	588.8	129	0.454	1.02	0.0
16 Aug.	25	1,074.0	47	0.308	0.29	−1.16
29 Aug.	38	839.0	38	0.244	−0.26	−1.07

son. Since wild-rice grows in nutrient-rich estuarine wetlands at Jug Bay, it is unlikely that competition for water or nutrients is important. Thus, one can assume that competition is primarily for light in these populations.

The study was conducted in the Patuxent River at the Jug Bay Wetlands Sanctuary in Lothian, Maryland (38°47′N, 76°42′W). Wild-rice is one of the dominant species at Jug Bay and grows in intertidal areas where it forms almost monotypic stands which can be as wide as 25 m. Within the largest contiguous wild-rice stand in the area, randomly-placed quadrats were marked out and harvested at two-week intervals beginning on 23 May 1985. An additional harvest on 4 June was also included in the analysis. Early in the season, when the density was very high, small (approximately 0.1 m^2) quadrats were harvested, and later in the season larger (approximately 1.0 m^2) quadrats were harvested. To insure accurate measures of density, quadrats to be harvested were marked with flags, and the exact area of the quadrat was determined immediately after the plants were harvested. Each plant was cut at ground level with a razor blade and placed in a paper bag. Plants were dried for two days at 70 C in a convection drying oven and weighed at the Smithsonian Environmental Research Center in Edgewater, Maryland. The self-thinning trajectory was determined from a log biomass-log density plot, as suggested by Westoby (1984) and Weller (1987). Size variability was evaluated by the Gini coefficient (Weiner and Solbrig, 1984).

RESULTS—Mean plant mass increased from 0.28 g on 23 May to a maximum of 22.85 g on 16 August, while density decreased from 524 individuals m^{-2} on 23 May to 38 individuals m^{-2} on August 29 (Table 1). These values are within the range reported for wild-rice in New Jersey (Whigham and Simpson, 1977). The least-squares fit for the log biomass-log density relationship was log biomass = 3.95–0.60 log density (Fig. 1). Both the intercept and

the slope were significantly different from 0 ($P < 0.001$), and the r^2 (0.82) and residuals were consistent with a linear log biomass-log density thinning trajectory. The slope was not significantly different from the commonly observed log biomass-log density thinning slope of −0.5 (White, 1980; Westoby 1984; Weller, 1987). Size variability decreased as self-thinning progressed (Fig. 2). The least-squares fit for the relationship between the Gini coefficient (G) and log mean plant mass (m) was $G = 0.45–0.11 \log m$. Both the slope and the intercept were significantly different from 0 ($P < 0.001$), and $r^2 = 0.78$. Early in the growing season, the distribution of plant sizes was highly skewed and unequal (Fig. 3; Table 1). At the end of the growing season, the distribution was uniform and not skewed. Skewness as well as inequality declined significantly ($P < 0.05$) during self-thinning (Table 1).

DISCUSSION—With few exceptions (White and Harper, 1970; Bazzaz and Harper, 1976; Mohler, Marks, and Sprugel, 1978; Westoby and Howell, 1986), self-thinning has been studied only at the population level: correlated changes in mean plant mass (or total biomass) and density. To fully understand a population-level phenomenon, it is necessary to understand how it comes about through the behavior of individuals. Numerous models to explain self-thinning trajectories have been advanced, but less attention has been given to the proximate causes of density-dependent mortality. Many models of self-thinning assume, implicitly or explicitly, that the cause of death of plants during self-thinning is insufficient light. For example, allometric models (e.g., Miyanishi, Hoy, and Cavers, 1979; White, 1981; Weller, 1987b) look at the relationship between the area covered by a plant (canopy projection area) and other dimensions such as height or biomass. While allometric models are based upon the two-dimensional and three-dimensional space occupied by plants, plant canopies do not actually fill space completely,
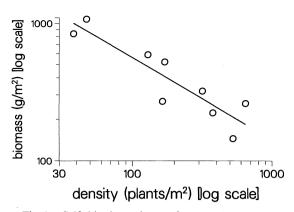
Fig. 1.   Self-thinning trajectory for natural populations of *Zizania aquatica.*

Fig. 2.   Changes in size variability with increasing mean plant mass during self-thinning in natural populations of *Zizania aquatica.*

thereby physically excluding other individuals. Rather, it is often assumed that it is not space per se that is limiting, but that space occupation reflects the ability to intercept light. The decline in size inequality with increasing mean plant mass provides support for the hypothesis that the process of self-thinning is driven by competition for light, i.e., that smaller individuals die because they are shaded. A plant that is one-half the size of another will get a progressivley smaller fraction of the available light as mean plant size increases. Because light intercepts a two-dimensional surface but shading occurs in a third dimension, greater relative variation in size can be tolerated when plants are small than when they are large (Weiner and Thomas, 1986). While mechanisms other than shading are consistent with allometric models, they are not consistent with the decrease in size variability during self-thinning. If physical space-occupation by some plants was the cause of death of others, there is no reason to expect the relative variation in size which exists at the onset of self-thinning to decrease as the process continues. In part, allometry determines the self-thinning trajectory (White, 1981; Weller, 1987b), but the decrease in size variation which accompanies the process suggests that it does so through the mechanism of light interception and extinction. Plants that remain below the compensation point will die (unless they can sustain zero or negative growth). Evidence that self-thinning is driven by competition for light is especially strong in this case because water and nutrients are not limiting.

As Weiner and Thomas (1986) found for *Abies balsamea* and *Pinus ponderosa,* the negative relationship between G and log mean plant mass of survivors during self-thinning in *Z. aquatica* was consistent with a linear model ($r^2 = 0.78$), but the slope of this relationship ($-0.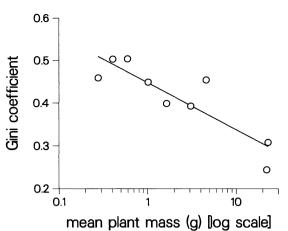1$) is signicantly different from that for the tree species (-0.2). There are two alternative general hypotheses which could account for this difference:

1) Changes in size variability during self-thinning are related to the self-thinning slope. Populations that are similar in their self-thinning trajectories will also have similar changes in size variability accompanying this process, because the thinning trajectory and changes in size variation which accompany it are determined by the same mechanisms. There should be a quantitative relationship between the thinning and variability trajectories, and we should therefore be able to predict changes in size inequality from the thinning trajectory.

2) The self-thinning trajectory reflects only population-level (i.e., mean plant) behavior. Changes in size variabilty during thinning are due to processes operating at a lower level of organization (individual interactions), although they are constrained at the population level by the thinning line. Thus, two populations with similar thinning trajectories could have very different patterns of size distribution change during the process.

The decrease in size inequality during self-thinning has important implications for the evolution of plant populations. Stands that have undergone extensive density-dependent mortality will consist of a few individuals that are relatively equal in size. If, as one might expect for polycarpic species, many of the individuals that suffer density-dependent mortality have already commenced reproduction, there will be high inequality in reproductive output. If, as in many monocarpic species like *Zizania,* only those individuals that survive self-thinning reproduce, the reproducing population will consist of very few individuals from the orig-
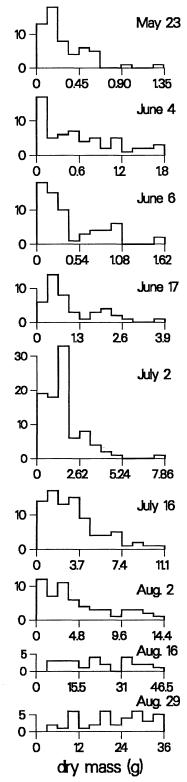
inal population, but those remaining will be of relatively equal size. Natural selection will act strongly against those that die, but there will be relatively small differences in fitness among the survivors.

LITERATURE CITED

BAZZAZ, F. A., AND J. L. HARPER. 1976. Relationship between plant weight and numbers in populations of *Sinapis alba* (L.) Rabenh. and *Lepidium sativum* L. J. Appl. Ecol. 13: 211–216.

BENJAMIN, L. R., AND R. C. HARDWICK. 1986. Sources of variation and measures of variability in even-aged stands of plants. Ann. Bot. 58: 757–778.

DORE, W. G. 1969. Wild-rice. Canad. Dep. Agric., Res. Branch Publ. No. 1393. Ottawa, Canada.

KOHYAMA, T., AND N. FUJITA. 1981. Studies on *Abies* population of Mt. Shimagare. Bot. Mag. (Tokyo) 94: 55–68.

McCORMICK, J., AND H. A. SOMES, JR. 1982. The coastal wetlands of Maryland. Maryland Department of Natural Resources. Annapolis, MD.

MEYER, W. H. 1938. Yields of even-aged stands of ponderosa pine. USDA Tech. Bull. No. 630.

MIYANISHI, K., A. R. HOY, AND P. B. CAVERS. 1979. A generalized law of self-thinning in plant populations. J. Theor. Biol. 78: 439–442.

MOHLER, C. L., P. L. MARKS, AND D. G. SPRUGEL. 1978. Stand structure and allometry of trees during self-thinning of pure stands. J. Ecol. 66: 599–614.

SPRUGEL, D. G. 1984. Density, biomass, productivity, and nutrient cycling changes during stand development in wave-regenerated balsam fir forests. Ecol. Mono. 54: 165–186.

WEINER, J. In press. Variation in the performance of individuals in plant populations. *In* A. J. Davy, M. J. Hutchings, and A. R. Watkinson [eds.], Plant population ecology. Blackwell, Oxford.

———, AND O. T. SOLBRIG. 1984. The meaning and measurement of size hierarchies in plant population. Oecologia 661: 334–336.

———, AND S. C. THOMAS. 1986. Size variability and competition in plant monocultures. Oikis 47: 211–222.

WELLER, D. E. 1987a. A reevaluation of the -3/2 power rule of plant self-thinning. Ecol. Mono. 57: 23–43.

———. 1987b. Self-thinning exponent correlated with allometric measures of plant geometry. Ecology 68: 813–821.

WESTOBY, M. 1984. The self-thinning rule. Adv. Ecol. Res. 14: 167–225.

———, AND J. HOWELL. 1986. The influence of population structure on self-thinning of plant populations. J. Ecol. 74: 343–359.

WHIGHAM, D. F., AND R. L. SIMPSON. 1977. Growth, mortality and biomass partitioning in freshwater tidal wetland populations of wild rice (*Zizania aquatic* var. *aquatica*). Bull. Torrey Bot. Club 104: 347–351.

WHITE, J. 1980. Demographic factors in populations of plants. *In* O. T. Solbrig [ed.], Demography and evolution in plant populations, 21–48. University of California Press, Berkeley.

———. 1981. The allometric interpretation of the self-thinning rule. J. Theor. Biol. 89: 475–500.

———, AND J. L. HARPER. 1970. Correlated changes in plant size and number in plant populations. J. Ecol. 58: 467–485.

Fig. 3. Distribution of plant mass for nine sequential harvests of *Zizania aquatica*. Histograms are constructed as 12 size classes from 0 to the maximum value.