COMMENT

ON THE ANALYSIS OF SELF-THINNING AMONG SEAWEEDS

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Plant self-thinning is the process that involves density-dependent mortality of plants that are actively growing in crowded conditions in a monospecific, even-aged stand (Weller 1987). This process has mainly been studied in terrestrial plants, but evidence that it occurs among seaweeds is also available (Black 1974, Dean et al. 1989, Reed 1990, Ang and De Wreede 1992, Creed 1995). A recent note (Flores-Moya et al. 1996) presented an analysis of self-thinning as it occurs for two seaweeds: the kelp *Phyllophora purpurascens* (C. Agardh) Henry et South and the red species *Asparagopsis armata* Harvey. The analytical approach that was followed in that study was unfortunately inadequate in part, but it could be improved upon. The problems, which will be outlined below, have already been discussed in the ecological literature, yet awareness among ecologists, including those acting as either authors or manuscript reviewers, does not seem to be widespread. The objective of this comment is to identify and discuss these problems and to suggest a better analysis of self-thinning among seaweeds that could help improve future efforts.

The first problem relates to the appropriate choice of variables that are used to detect and describe self-thinning through correlation and regression analyses. Originally, Yoda et al. (1963) examined the temporal variation of the relationship between the logarithm of mean plant biomass and the logarithm of plant density for crowded stands during active growth, and subsequent authors followed that choice (see a list of relevant papers in Weller 1987). However, Weller (1987) later showed that this approach presents problems for the interpretation of data, suggesting that total stand biomass (expressed per unit area) be used instead of mean plant biomass.

For example, if 1) small plants die and the growth of large plants just barely compensates for this loss of biomass (i.e. at the end of the growth season, when growth rates slow down), stand biomass will not vary while plant density decreases. If 2) later the growth of large plants stops and their biomass remains constant for a while, but some small plants are still dying, stand biomass will be negatively related to plant density. Conditions 1 and 2 do not represent active growth of plants. Active growth occurs during self-thinning and involves the highest possible growth rates of plants, which depend on plant size and can be constrained by intraspecific competition, but do not include senescence. If stand biomass and plant density are involuntarily measured during those two stages, a posteriori data editing should allow one to identify and eliminate those points from statistical analyses of correlation and regression between stand biomass and plant density (Weller 1987). However, for conditions 1 and 2, the variable “mean plant biomass” (calculated by dividing total biomass by plant density, regardless of whether one measures them for the entire stand or for a random sample with fixed size), will actually increase while plant density decreases. This will lead one to believe that surviving plants are still growing, which is obviously not the case for condition 2. Nonetheless, if one visually examines the relationship between mean plant biomass and plant density, the elimination of data points that do not correspond to the period of active growth will be more difficult than if using stand biomass. This is due to the continuous increase in mean plant biomass, which was occurring before and during self-thinning. A negative relationship between mean plant biomass and plant density may still occur if one does not eliminate those unwanted data points, but the estimation of the slope and the intercept of the self-thinning line will be biased (Weller 1987).

The study by Flores-Moya et al. (1996) plotted log mean plant biomass against log plant density to analyze self-thinning dynamics for the above-mentioned two seaweeds. The problem that was just discussed in the previous paragraph possibly occurred for *Asparagopsis armata*. The relationship between mean plant biomass and plant density changed as density decreased for this alga (Flores-Moya et al. 1996:fig. 1). The intersection of lines A1 and A2 in their Figure 1 seems to correspond to that gray area where it is difficult to detect when the growth rate of surviving plants starts to slow down, as described above. Therefore, the estimation of the self-thinning slope and intercept may have been miscalculated with respect to the real values that describe the active growth period. A reanalysis of their data set that considers stand biomass instead of mean plant biomass should give results that can be adequately compared with other seaweeds and terrestrial plants.

In a more general context, an additional problem of using mean plant biomass is that, even if only data points that correspond to the period of active growth are considered, the rate of increase of the

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variable "mean plant biomass" is greater than the real growth of surviving, large plants (Weller 1987). This occurs because initial estimates of mean plant biomass (stand biomass divided by plant density) include a greater proportion of small plants than later stages, because the smallest plants die progressively. Even if mean plant biomass is estimated from random samples with fixed size on successive sampling dates (so the denominator, number of plants, does not increase), mean plant biomass will also increase faster than the biomass of the surviving, large plants. This is because the proportion of large plants progressively increases in the successive random samples. This problem is important, because growth rates of surviving plants are sometimes compared for different stands using self-thinning lines. The growth rates of surviving plants would be better studied by directly monitoring the growth of tagged plants over time in the field.

The second aspect that could be improved in Flores-Moya et al.'s (1996) study is the estimation of the functional relationship between log stand biomass and log plant density during self-thinning. Both stand biomass and plant density are random variables, because they are not controlled by the experimenter, and they are both subject to measurement error. Plant density is a discrete random variable, and it will probably not be measured with error at low densities, but the reverse will likely be true at high plant densities (i.e. in terms of hundreds or thousands of individuals per square meter), especially in difficult field conditions. The linear relationship between the logarithmic forms of stand biomass and plant density can not be calculated using least-squares regression (Sokal and Rohlf 1981: model I regression), because this technique applies only when the X variable is fixed. Instead, principal components analysis (PCA) has been recommended by Weller (1987) as an appropriate technique. Reduced major axis regression and Bartlett's three-group method are additional alternatives, but they have been criticized by other authors (Sokal and Rohlf 1981:550–1). The use of the appropriate statistical technique is important, because the errors from doing least squares regression instead of PCA with the same data set are greater as the correlation between both variables decreases (Weller 1987). A reanalysis of Flores-Moya et al.'s (1996) data set, using PCA, should result in statistically stronger conclusions, therefore increasing the reliability of comparisons with studies published for other species.

A third important consideration for future studies is that there is no fixed value for the slope of the relationship between log stand biomass and log plant density during self-thinning. It was previously thought that the self-thinning slope was −½ when using log mean plant biomass and log plant density (Yoda et al. 1963); the mathematically equivalent slope is −½ if stand biomass replaces mean plant biomass (Weller 1987). However, an extensive and improved reanalysis of biomass–density data available for several plant populations (Weller 1987) demonstrated that −½ is only one of several possible values for the self-thinning slope, suggesting that the self-thinning rule be discarded as a quantitative law. Rather than comparing observed slopes with a single ideal value and testing for the generality of a hypothetical "power law of self-thinning," importance should be given to ecologically interpreted differences among slopes obtained for different species or the same species growing under different conditions (Zeide 1985, Weller 1987, 1990).

A final consideration relates to the objectives of the study by Flores-Moya et al. (1996). One of the objectives was to investigate the possible effects of reproduction and associated biomass loss of Asparagopsis armata on deviations of biomass–density combinations from the "ideal" self-thinning slope. For this alga, thalli become reproductive only at thallus densities lower than 500 thalli·m⁻², which occurs simultaneously with a halt of thallus growth and loss of reproductive biomass (Flores-Moya et al. 1996). Therefore, if thalli are not growing any more, it is inadequate to compare biomass–density combinations during those stages with an equation that has been proposed to describe the period of active growth. Combinations between biomass and density that correspond to such periods, including senescence, should be ignored from studies that specifically analyze active growth (Weller 1987). Factors that do affect the self-thinning slope and intercept are, for example, plant geometry, irradiance, shade tolerance, soil fertility, and water availability (see Weller 1987, Flores-Moya et al. 1996, for lists of relevant papers), because they influence plant growth rates during the period of active growth. As a suggestion, with Flores-Moya and colleagues' (1996) data set, it would probably be of interest to compare self-thinning equations for the four different cohorts of A. armata there referred to and to speculate about possible spatial or seasonal effects on them.

I wish to acknowledge Antonio Flores-Moya, for kindly clarifying for me the methodology followed in Flores-Moya et al. (1996), and two anonymous reviewers, for their useful comments.


