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WILL THE REAL SELF-THINNING RULE PLEASE STAND UP?—A REPLY TO OSAWA AND SUGITA

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In their recent comment on my reevaluation of the self-thinning rule for even-aged plant populations (Weller 1987a), Osawa and Sugita (1989) raise three questions that require further discussion. What is the self-thinning rule? What kind of data and analyses are relevant to testing the rule? Do recent analyses support or refute the thinning rule as a quantitative law? I would like to address these questions, compare our approaches to the thinning rule, and clarify some misconceptions about my monograph (1987a).

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The classic thinning rule states that measurements of crowded, even-aged plant populations form a thinning line of slope $-1/2$ when the logarithm of stand biomass (in mass per unit area) is plotted against the logarithm of plant density (in plants per unit area); or equivalently, a line of slope $-3/2$ when average plant biomass is plotted in place of total stand biomass (see review in Westoby 1984). At its zenith (see White 1981, Hutchings 1983, Westoby 1984), the rule united several size–density relationships that were all considered facets of a single quantitative law. More recently, the rule has been divided into two concepts that should be tested and explained independently: the interspecific size–density relationship and the single-species thinning line (Zeide 1985, 1987, Weller 1987a, 1989, Norberg 1988, Lonsdale 1990).

Osawa and Sugita (1989) advocate a different definition of the single-species thinning rule than the one I tested. They define the thinning line strictly as an upper boundary of possible yield–density combinations for a species, and fit the thinning line using data from the most extreme of several hundred stands. I refer to this line as the *species boundary line*. In contrast, I focused on the straight line that is approached and

followed by the time trajectory of an individual crowded stand. I call this the *dynamic thinning line* (Fig. 1).

Osawa and Sugita (1989) argue that the species boundary line is the original definition of the thinning line, and that my examination of the dynamic thinning line was based on a more liberal interpretation. An anonymous reviewer agrees that early Japanese-language papers intended the species boundary as the primary definition. In contrast, the seminal English-language article of Yoda et al. (1963) suggested to me that the species boundary and dynamic thinning limit were aspects of a single line: "... the line of $-\frac{1}{2}$ gradient on the log average mass-log density diagram represents the locus of growth of a stand under the overcrowded condition, and at the same time [my emphasis] the interrelation between the same-aged stands growing on different soil fertility levels" (p. 122); "... the $\frac{1}{2}$ th power law gives the interrelation between the stands of different ages and on different habitats" (p. 124). Later papers considered the thinning line to represent simultaneously the boundary of maximum possible biomass-density combinations and the time trajectory of high-density populations undergoing mortality (e.g., White 1981).

Further research has shown that the dynamic thinning line and species boundary line need not coincide. By definition, the boundary line is a species constant since all stands of the species must lie on or below it. However, the dynamic thinning line is variable and may fall below the species boundary line for a variety of reasons. For example, reducing the level of illumination lowers the dynamic thinning line (Hutchings and Budd 1981, Westoby and Howell 1981) and may also flatten its slope (White and Harper 1970, Kays and Harper 1974, Lonsdale and Watkinson 1982). The dynamic thinning line can also respond to changes in site fertility (Furnas 1981, White 1981, Hara 1984, Westoby 1984, Weller 1985, 1987a, Zeide 1985) and may even be affected by the density or spatial arrangement of seedlings at the time of establishment (Peet and Christensen 1980, Weller 1985, Weiner 1988).

Although the difference between the species boundary and dynamic thinning lines has not previously been made explicit, the dynamic thinning line is the concept implicitly addressed in recent English-language reports. For example, I examined 63 thinning lines that had been cited as examples of the self-thinning rule (Weller 1985, 1987a). Twelve of the examples were from two early Japanese publications (Tadaki and Shi-dei 1959, Yoda et al. 1963) and 51 were reported between 1970 and 1983 in American and European publications. Thirty of these 51 were dynamic thinning lines fit directly to successive observations of a single stand, while the remainder inferred the dynamic thinning line using some combination of time, age, or den-

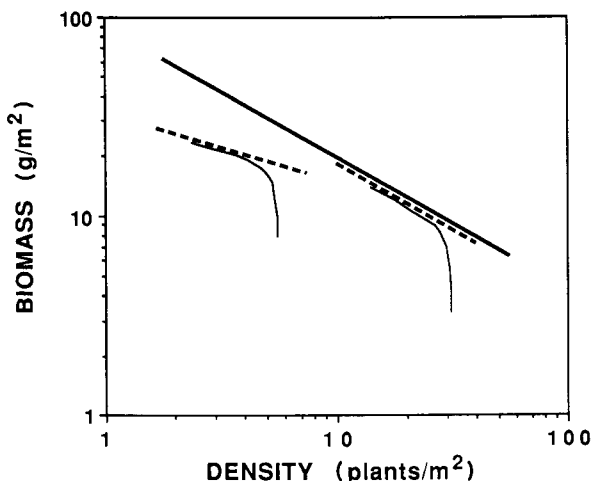


FIG. 1. Two concepts of the species self-thinning line. The species boundary line (—) is a static upper limit to the biomass and density of any even-aged stand of the species. The dynamic thinning line (---) is approached and followed as growth and mortality proceed within an individual stand (—). The dynamic thinning line may coincide with the species boundary line (right), or may fall below the species boundary (left) due to habitat limitations or to the stand's genetic composition. (Coinciding curves are offset slightly for visual clarity.)

sity series data from stands growing under equivalent conditions. None of the 51 studies fit a species boundary line using data from hundreds of stands as recommended by Osawa and Sugita (1989). If the species boundary line is the original definition of the thinning line, why does the most recent western work emphasize the dynamic thinning line? Most of the early work was published in Japanese, so perhaps western scientists did not accurately understand or propagate the original definition. More importantly, the thinning rule has been the focus of much experimentation and speculation, so prevailing concepts have changed with the accumulation of new evidence and hypotheses.

Regardless of which concept is the most original one, the three concepts of the thinning line are all interesting, but may have different explanations and interpretations. Separate explanations have been proposed for the slopes of the interspecific relationship (Norberg 1988, Weller 1989) and the dynamic thinning line (Weller 1987b, Norberg 1988, Weiner 1988). Like the interspecific relationship, the species boundary line is a static constraint applying across different stands, so the slope and position of the species boundary line may likewise be related to trends in maximal slenderness and biomass packing across stands (see Weller 1989). In contrast, the slope of the dynamic thinning line depends on the way plants within a single stand change

shape and biomass packing with growth (Weller 1987b, Norberg 1988, but see Weiner 1988).

The divided thinning rule is a less powerful statement than the combined version. The boundary line concept has been used in density control diagrams for managing even-aged forest stands (e.g., Drew and Flewelling 1979), but only provides the uppermost limit of possible biomass–density combinations. A given stand may follow a dynamic thinning line well below the species boundary line (Fig. 1) because of environmental limitations or the stand's genetic composition. In this case, the species boundary line is largely irrelevant to understanding or predicting stand dynamics in any detail. In contrast, the dynamic thinning line describes more proximal limits on stand dynamics, but those limits are population and site dependent. Therefore, the dynamic line is not a constant to be measured once and applied to all stands of a species.

Analyses of the interspecific size–density relationship (Weller 1989, Lonsdale 1990), the species boundary line (Osawa and Sugita 1989), and the dynamic thinning line (Weller 1985, 1987a, Zeide 1985, 1987) have all revealed significant departures from the ideal $-1/2$ slope. Together with the subdivision of the thinning rule, such departures mean that the thinning rule is not the unifying quantitative law envisioned at its zenith. In future reports, authors should consider the differences among the three size–density relationships and specify which relationship they are addressing.

Osawa and Sugita (1989) conclude that the data I examined (Weller 1987a) were largely irrelevant to testing the thinning rule. I agree that most of the data were irrelevant to their definition of the thinning line as a species boundary. Instead, my analysis tested the rule's relevance to the dynamic thinning line because the methods and data implicitly addressed that concept (see above).

Osawa and Sugita (1989) also imply that most of the data sets I examined included stands not on the thinning line. However, I did not include all stands undergoing density-dependent mortality, but instead tried to select stands along the linear portion of the thinning trajectory and to exclude uncrowded prethinning stands (Hutchings and Budd 1981), senescent postthinning stands, and stands affected by density-independent mortality (Mohler et al. 1978). Because of the inherent subjectivity in selecting thinning data (see below), other scientists may well disagree with some of my choices or interpretations. Final resolution of any resulting controversies will await the verification of more objective methods for selecting test data. Also, earlier studies had been too quick to reject possible evidence against the thinning law (see Weller 1985, 1987a, 1989, Zeide 1985, 1987, Lonsdale 1990), so once I examined a data set as a presumptive thinning

line, I did not discard it without an objective reason. This conservative approach, together with the subjectivity of data selection, probably did result in the inclusion of some nonthinning stands (Weller 1987a).

Osawa and Sugita (1989) use idealized yield–density diagrams to illustrate that inclusion of nonthinning stands biases the thinning slope. However, the potential for bias is well established (Mohler et al. 1978, Hutchings and Budd 1981, Weller 1985, 1987a), and further analysis of idealized curves does not address the real issue, i.e., how can appropriate points be selected from real data confounded by measurement error and biological variability? This is a very difficult and messy question. The most obvious methods are arbitrary, subjective, and even circular, but methods to avoid these problems remain undeveloped and may even be impossible.

Unfortunately, comparison to the species boundary line (Fig. 3 in Osawa and Sugita 1989) does not help identify data for testing the dynamic thinning rule. The species boundary line addresses a different concept of the rule and comparison to the boundary line does not reveal whether or not a stand has reached its dynamic thinning line (Fig. 1). Nor does adopting the boundary line perspective eliminate subjectivity. Although Osawa and Sugita (1989) examined hundreds of stands, they eventually fit the boundary line to as few as nine, so the estimated slope is sensitive to subjective decisions about including particular stands. Also, even a large sample may not indicate the true species boundary if the sample does not include those few genetically superior stands that are really growing under the best environmental conditions.

The potential problems of my analysis (Weller 1987a) are shared by the body of evidence upon which the thinning rule is based. Indeed, many of the data sets I examined had been previously analyzed and presented in the literature as examples of the thinning rule. Because claims of the rule's generality relied heavily on yield table information (e.g., White 1980), I also examined information from forestry yield tables, even though yield tables are based on subjective concepts (Osawa and Sugita 1989) and present model predictions, not data (Weller 1987a, b). I differed from many previous analyses primarily in attempting to identify and apply more rigorous quantitative methods to fit and interpret the thinning line, and in approaching the thinning law as a hypothesis to be tested rather than as a paradigm to be ratified. Had previous authors viewed their data from this perspective, many data sets cited as examples of the thinning law might originally have been seen to disagree with the law (Zeide 1987). Because my analysis shares the basic methods and much of the data base used to establish the law, rejection of most of the data I examined (Osawa and Sugita 1989)

necessarily implies that much of the original evidence for the rule was likewise irrelevant. Such a conclusion leaves little basis for further debate either for or against the thinning rule. I believe that wholesale rejection of most available data is unjustified. Many studies do present good time series data from stands grown from high initial densities under controlled experimental conditions (see Weller 1985, 1987a), and these data are the best available for testing the dynamic thinning rule.

In summary, Osawa and Sugita (1989) have in essence suggested a further subdivision of the concepts that were once united by the thinning rule, and the separate parts do not have nearly the impact of the combined version. Their preferred part, the species boundary line, is a boundary condition, not a statement about stand dynamics, and is not the interpretation implicitly followed by most ecologists. My analysis was relevant to the concept prevailing in recent western literature. Interestingly enough, our conclusions are not as different as our definitions. Where I said that a large minority of data sets alleged to support the law were irrelevant or inapplicable, Osawa and Sugita (1989) would change "minority" to "majority." We seem to agree that thinning slopes can take values other than $-1/2$ and can vary systematically with biological factors such as shade tolerance. Therefore, either perspective would still reject the thinning rule as a quantitative ecological law, so this major conclusion of my monograph seems robust to widely different approaches to defining and testing the rule.

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