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THE SELF-THINNING RULE: DEAD OR UNSUPPORTED?— A REPLY TO LONSDALE

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Recent reevaluations have rejected the plant self-thinning rule (Zeide 1985, 1987, Weller 1987a, b, 1990), which had been widely accepted as an ecological law stating that crowded, even-aged stands form a straight line of slope $-1/2$ in a log-log plot of stand biomass vs. plant density (see review by Westoby 1984). In turn, Lonsdale (1990) found less variability from the ideal $-1/2$ value and weaker evidence of systematic variation than I did (Weller 1987a, b) and concluded that, while there is no evidence for a thinning rule, the evidence is insufficient for rejection. Here, I will discuss some problems with Lonsdale's reanalysis, clarify some points from my work, and consider whether further testing of the thinning rule is needed.

Lonsdale applied a data-screening procedure that introduced a systematic bias and prejudiced the subsequent results and conclusions. He offered three reasons for disregarding any data set with less than half an order of magnitude of density variation among the stands used to fit the thinning line: inclusion of pre-thinning data biases a thinning slope toward steepness, the steeper thinning slopes in my data base (Weller 1987a) come from data sets with small density ranges (Lonsdale 1990: Fig. 3), and the mean thinning slope becomes steadily shallower as one raises the required amount of density change (Lonsdale 1990: Fig. 4).

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Although true, these observations neither justify nor validate the screening procedure. A narrow density range does not necessarily result from including pre-thinning data, and a large density range in no way ensures the exclusion of inappropriate points (Fig. 1). Also, the thinning equation dictates that stands with steep thinning lines will be observed over narrow density ranges. Therefore, the patterns that motivated Lonsdale's data screening (Lonsdale 1990: Figs. 3 and 4) are actually natural patterns that arise independently of the issue of data selection (Fig. 2). Furthermore, a population with a steeper thinning line must accu-

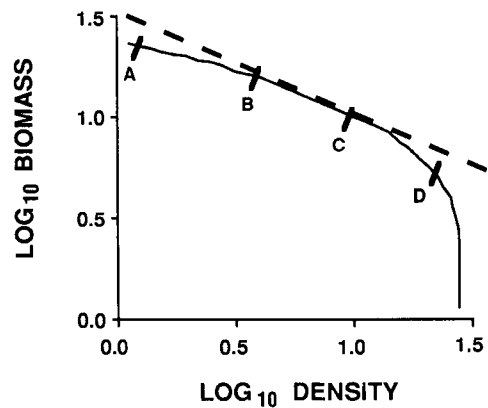


FIG. 1. Some inadequacies of the minimum density-change criterion. Biomass units are grams per square metre; density units are plants per square metre. The actual thinning trajectory (solid line) asymptotically approaches the thinning line (dashed line). Lines fit to data along AB, AC, AD, or BD include pre- or post-thinning data and do not represent the asymptote, yet these lines would pass Lonsdale's filter for inclusion in the analysis. A line fit to points along BC would accurately estimate the asymptote, but would be excluded by Lonsdale's screening. Density change is simply not a reliable indicator of how well a data set represents an asymptotic thinning line.

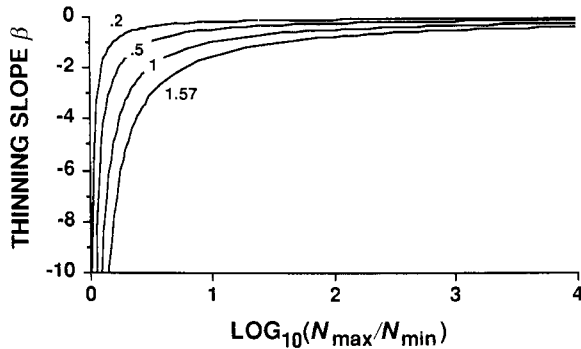


FIG. 2. The relationship of thinning slope to density change for four different levels of biomass increase [expressed as $\log(B_{\max}/B_{\min})$]. Given the thinning equation ($B = kN^c$), density decreases from N_{\max} to N_{\min} as biomass increases from B_{\min} to B_{\max} and $\beta = -\log(B_{\max}/B_{\min})/\log(N_{\max}/N_{\min})$. This shape of the curves is a mathematical consequence of the thinning equation, so the fact that data follow the same pattern (Lonsdale 1990:Fig. 3) does not indicate the inclusion of pre-thinning data or justify a data-screening procedure.

mulate relatively more biomass to accompany a given decrease in density, and will probably need more time to do so. Biomass accumulation, growing time, and observation time are limited by biological and practical constraints. Therefore, observing thinning over a fixed percentage of density decrease becomes less-and-less likely as one considers populations with increasingly steep thinning slopes. Thinning slopes above a threshold value are completely excluded from observation (steeper than -3.2 for a half order of magnitude of density change). The bias also affects thinning slopes nearer the ideal value—the probability of exclusion would be higher among thinning slopes near -0.7 than among slopes near -0.5 . Because it is biased, Lonsdale's screening criterion does not solve the troublesome problem (Weller 1990) of objectively distinguishing thinning from non-thinning data.

Lonsdale's exclusion of examples based on total plant biomass reduced sample sizes and hence the power to detect systematic variation. These data were omitted because "claims for the generality of the self-thinning rule have been restricted to shoot biomass" and because Lonsdale disliked my comparison of total-biomass and shoot-biomass thinning lines. In fact, total-biomass data were instrumental in establishing the self-thinning rule, providing 7 of 9 examples in Yoda et al. (1963), 3 of 6 examples of herbaceous species in White and Harper (1970), and at least 8 of 36 examples in White (1980). My comparison of total- and shoot-biomass thinning lines was not wrong (as Lonsdale suggests) because I used it only to see if the two groups could be pooled in further analyses, not to test the self-evident hypothesis that a population's thinning line for

total biomass is higher than its shoot-biomass thinning line.

To avoid pseudoreplication, Lonsdale averaged replicates to produce a single datum for each species, further reducing sample sizes and the chances of detecting systematic variation. Although my simple nonparametric test for differences in thinning-line parameters among plant groups (Weller 1987a:Table 2) did confound two sources of variability (differences among plant groups and differences among species within groups), I am not convinced that this is a case of pseudoreplication (sensu Hurlburt 1984). However, we need not argue. An analysis of variance with species nested within plant groups (Sokal and Rohlf 1981) can resolve the two sources of variability, test differences among plant groups using only the variability among species (as Lonsdale desires), and still use the information contained in species replicates (as I desire). Analysis of my data base reveals significant differences among plant groups and significant differences among the species within groups (Table 1). Differences among species within groups persist after Lonsdale's screening, but the among-group differences become insignificant (Table 1). Since the treatment of replicates is consistent here, the different patterns of significance in the un-screened and screened data bases are strictly due to the screening procedure. This suggests that the screening procedure itself is primarily responsible for the differences between my results and Lonsdale's.

I am unconvinced by Lonsdale's case-by-case rebuttals of individual counterexamples of the thinning rule, but further argument over individual cases would be unproductive because the inherent subjectivity and ambiguity of thinning analysis (Lonsdale 1990, Weller 1990) preclude objectively resolving many differences of opinion. I will note that Lonsdale scrutinized and dismissed all cases that disagreed with the thinning rule, but did not focus the same critical eye on data which seemed to agree with the rule. This reveals an a priori bias that cannot be defended.

I would also like to clarify some points about my earlier papers. In Table A1 of Weller (1987a), *Pinus pumila* (code 128) should have $n_s = 0$ (as noted by Lonsdale), while *Medicago sativa/Trifolium pratense* (code 57) should have $n_s = 1$. These errors arose only in preparing the table for publication and did not affect my results and conclusions. My thinning slope estimate for *Populus deltoides* (code 210) was not miscalculated (as suggested by Lonsdale), but was fit to data from the period of peak stand growth (Williamson 1913, Fowells 1965). Steeper estimates (White 1980, Lonsdale 1990) probably represent younger, pre-thinning stands (Weller 1985). I did not calculate coefficients of variation (cv) for $\log K$ incorrectly (Weller 1987a). Lonsdale's (1990:Tables 1 and 8) alternate calculation is wrong

TABLE 1. Nested analysis of variance for difference in thinning slope (single-species thinning lines only). Data were transformed to normality by the Box-Cox transformation (Sokal and Rohlf 1981) with power λ .

Effect	<i>F</i> (df)	<i>P</i> †	Variance component (%)
All data (Weller 1987a:Table 2, excluding multispecies data)			
Experimental and field data ($n = 69$, $\lambda = -0.245$)			
Plant group	4.07 (5, 19.1)	.011*	29
Species within group	1.58 (38, 25)	.12	20
Forestry yield tables ($n = 283$, $\lambda = -0.481$)			
Plant group	5.86 (2, 30)	.0071*	42
Species within group	9.48 (30, 250)	<.0001*	29
After Lonsdale's screening [$\log(N_{\max}/N_{\min}) \geq 0.5$, shoot biomass only]			
Experimental and field data ($n = 34$, $\lambda = 0.160$)			
Plant group	1.08 (4, 12.4)	.41	2
Species within group	2.49 (18, 11)	.062	53
Forestry yield tables ($n = 142$, $\lambda = 0.309$)			
Plant group	1.25 (2, 16)	.31	21
Species within group	16.1 (16, 123)	<.0001*	53

* Significant at $P \leq .05$.

† Significance of the plant group effect was tested using Satterthwaite's approximation for the experimental and field data. The forestry-yield table data did not meet all the assumptions for Satterthwaite's approximation, so the significance tests are based on a more approximate *F* test (Sokal and Rohlf 1981:300).

because it estimates the cv for untransformed values of K (see Snedecor and Cochran 1980) rather than the cv of $\log K$. Finally, I do not accept $-1/2$ as the precise slope of the interspecific biomass-density relationship. This slope is shallower than $-1/2$ (see Weller 1989), but not because stem biomass rather than total biomass is measured for trees (as suggested by Lonsdale). In fact, 72% of the tree data sets from experimental and field studies (Weller 1987a) included branch mass, and 67% even included foliage mass. Weller (1989) reviews other possible explanations.

Lonsdale and I agree that biomass packing (mass per unit of occupied volume) is important in explaining size-density relationships. Lonsdale shows that changes in biomass packing with growth can account for much of the variability in the thinning slope. Earlier explanations focusing on changes in plant shape with growth may have emphasized a less-important factor. Perhaps this is why geometric models at best account for a small, but statistically significant, portion of the variability among thinning slopes, and why some studies have found no evidence of anticipated geometric effects (see review in Weller 1987b). Although less variable and closer to $-1/2$, the volume-density thinning slope is not necessarily a better or more lawlike statement of the size-density relationship than the mass-density slope. For plants with constant shape and biomass packing, the $-1/2$ slope is a trivial geometric consequence of packing objects on a surface, while changes in shape or biomass packing with growth are predicted to cause deviations from $-1/2$ (Weller 1987b, 1989).

The volume-density thinning slope is subject only to the lesser of these two sources of variability and is therefore closer to the trivial geometric statement than the biomass-density slope.

I have presented several reasons why Lonsdale's results may underestimate the evidence against the self-thinning rule. Although I do not accept all of Lonsdale's methods or interpretations, I believe that his results still provide sufficient evidence to reject the hypothesis of a single ideal thinning slope about which all variation is random. Lonsdale himself proposed that changes in biomass per unit volume explain much of the variability among mass-density thinning slopes. This hypothesis necessarily implies that real variability can be systematically attributed to another factor. Lonsdale discounted the other evidence of systematic variability. His reanalysis obliterated the differences in thinning slope among plant groups as well as the correlation of thinning slope with shade tolerance among angiosperms. The correlation of thinning slope with shade tolerance for gymnosperms persisted, but was dismissed by discarding a data point. However, the correlations of thinning slope with allometric measures of plant geometry could not be banished. Correlation certainly does not prove causation (Weller 1987b, Lonsdale 1990), but does reveal a systematic pattern of variability even if the correlated changes in thinning slope and plant allometry are only concomitant with some unknown cause. Although numerically small (possibly because variations in biomass packing are more important), the correlations remain statistically

significant despite the biased data screening, and therefore provide very robust evidence of systematic variability.

The idea of single, ideal thinning slope seems rejected, not simply unsupported or untested. Therefore, future critical experiments (Weller 1987*b*, Lonsdale 1990) should not focus on retesting that hypothesis, but rather on relating variability in thinning slopes to other factors, such as changes in plant geometry (Weller 1987*b*) and biomass per unit volume (Lonsdale 1990). Such experiments may be difficult because explainable variations in the thinning line can arise even under controlled experimental conditions (Westoby and Howell 1986), and large data sets may be required to detect weak relationships (Weller 1987*b*). Hopefully these difficulties can be overcome, because we do need to move beyond the reanalysis of large collations of past data. This activity is clearly following a curve of diminishing marginal return.

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