

matters arising

Generalisation of self-thinning of plant populations

WESTOBY'S attempt¹ to generalise self-thinning of plant populations by relating leaf area per plant (L) to surviving plant density (p) is spurious. The result, therefore, is not of 'more general application than the original statement of the rule'².

The measured value of leaf area index (LAI) in many plant stands may vary from <1 to 20, but rarely exceeds 10 (refs 3, 4, 5). Westoby's Fig. 3 shows not merely an error in graphical labelling (the ordinate values are 10 times too large), but reveals a more fundamental misconception about the dynamics of thinning. The relationships between leaf area (L) and dry weight (W) shown in Fig. 2 are not applicable to the experimental circumstances depicted in Fig. 1 on at least two grounds. Firstly, Blackman & Wilson⁶ derived their leaf area ratios (LAR = L/W) from spaced plants (~ 20 plants m^{-2}). LAR varies significantly with density^{3,7,8} and with light intensity⁶ (as Fig. 2 shows) and may vary with age⁹. Secondly, the range of W in Fig. 2 seldom exceeds 1.0 g, whereas its range in Fig. 1 is generally an order of magnitude greater: the extrapolation of equations derived from Fig. 2 over this range is unjustified. The neglect of density effects on LAR, coupled with graphical extrapolation cause the error in Fig. 3.

The behaviour of LAI in plant stands (both of herbs and trees) is simply stated: it rises rapidly, as a function of density and light intensity *inter alia*, to a plateau value, which is commonly <10 . Thinning may occur while LAI is increasing and/or for a prolonged period while LAI remains constant, or even declines. The most general statement of the dynamics is $L = K^{-1.0}$, where K varies significantly with light intensity. This is shown very clearly for *Helianthus annuus* in the original source from which Fig 1 was derived: 'the convergent leaf area index at 100%, 60% and 23% daylight was respectively 8, 6.5 and 1.5' (ref. 3), an empirical result which belies Fig. 3, where stands with least light have highest LAI for a given chronological age!

It should also be noted that the author's use of K in both equations

relating W and L to p is misleading, as it implies similar constants: they are quite different.

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¹ Westoby, M. *Nature* 265, 330-331 (1977).

² Moore, P. D. *Nature* 265, 295 (1977).

³ Hiroi, T. & Monsi, M. *J. Fac. Sci. Univ. Tokyo III* 9, 241-285 (1966).

⁴ Monteith, J. L. in *Physiological Aspects of Crop Yield* (eds Eastin, J. D. et al.) 89-111 (American Society of Agronomy, Madison, 1969).

⁵ Art, H. W. & Marks, P. L. *XVth I.U.F.R.O. Congress, Sect. 25 (Growth & Yield)* 3-32 (1971).

⁶ Blackman, G. E. & Wilson, G. L. *Ann. Bot. N.S.* 15, 63-94 (1951).

⁷ Lommis, R. S. et al. *Crop Sci.* 8, 352-356 (1968).

⁸ Hodanova, D. *Biol. Plant (Praha)* 9, 424-438 (1967).

⁹ Evans, G. C. *The Quantitative Analysis of Plant Growth* (Blackwell, Oxford, 1972).

WESTOBY REPLIES—I thank Dr White for his helpful remarks. Firstly, he is quite correct that the scaling of the y axis in my Fig. 3 was $\times 10$ too high; I apologise for confusing readers. Figure 3 was not intended as a simulacrum of a real experiment, but as a demonstration that the response of LAR to shading is the right kind to return the slope of a low-light thinning line to $-3/2$. That remains my basic point. Certainly LAR responds to planting density, among other factors. But does high planting density obliterate the response of LAR to shading?

I should like to suggest that perhaps the underlying determinant of relative mortality rate is how fast the light climate is deteriorating for the smallest plants in the population. Which descriptor of the population would correlate best with this process would depend on circumstances. During early growth biomass would be adequate unless LAR was varied by light treatments, in which case leaf area would be better. As the death rate of leaves rises LAI asymptotes, but the location of the canopy continues to rise, which has the effect of putting the smallest plants lower in the light profile. Here cumulative production of leaf area or biomass (as measured by Hiroi and Monsi) would be the most relevant descriptor. Where stem production is cumulative and comes to dominate the biomass (for example, in tree stands), stem weight or volume will be the best

available indicator of cumulative leaf area production.

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Atlantic palaeotemperatures during the Cainozoic

IT is comparatively easy to make generalisations in palaeo-oceanography, and Cifelli¹ has made several postulates regarding the Cainozoic palaeotemperatures of the North Atlantic; but the test of speculation in palaeo-oceanography is detailed biostratigraphy. For example, Cifelli¹ postulated that during the Miocene, the North Atlantic Gyre "extended perhaps 10° further north than they do now". The limited evidence, by Berggren², DSDP Leg 12, Sites 116 and 117 hardly support this: Berggren's² zonation of the Miocene planktonic foraminifera is reminiscent of that established in the cooler higher latitudes of New Zealand^{3,4} than of the tropical belt zonations by Bolli⁵ and Blow⁶. Work recently completed⁷ on a cored Lower Miocene Burdigalian borehole sequence 110 km south-west of the Isles of Scilly has yielded an excellent planktonic foraminiferal fauna which lacks the following warm-water taxa recorded in Trinidad⁸: *Globigerina venezuelana* Hedberg, *Catapsydrax unicavus* Bolli, *C. dissimilis* (Cushman and Bermudez), *C. stainforthi* Bolli, *Globorotaloides suteri* Bolli, and *Globigerinatella insueta* Cushman and Stainforth. Conversely, the fauna contains cooler water modern species such as *Globigerina bulloides* d'Orbigny and *Turborotalita quinqueloba* (Natland) as well as cooler water extinct fossils such as *Globigerina woodi* Jenkins and *Globorotalia zealandica* (Hornibrook).

Thus from the limited, but accumulating evidence available, the planktonic foraminifera in Miocene of the North Atlantic indicate that near-surface palaeotemperatures of the ocean were not as warm as postulated by Cifelli¹.

There is well documented evidence⁸ which clearly indicates that a number