The Relationship of Light and Plant Geometry to Self-Thinning of an Aquatic Annual Herb, Murdannia keisak (Commelinaceae)

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The relationship of light and plant geometry to self-thinning of an aquatic annual herb, *Murdannia keisak* (Commelinaceae)

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SUMMARY

Self-thinning was examined in shaded and unshaded populations of *Murdannia keisak* (Hask.) Hand.-Mazz. (Commelinaceae). Four mathematical descriptions of self-thinning were compared: (1) the traditional $-\frac{3}{2}$ thinning rule in which mean plant biomass is regressed on density; (2) principal components regression of mean plant biomass and density; (3) total stand biomass regressed on density, and (4) principal components regression of total stand biomass and density. Most slopes conform to the expected ones; however, confidence intervals reported here and in the literature are wide which may reduce the ecological value of the thinning line *per se*.

In addition, plants grown in full sun form significantly fewer branches than those in shade. This difference in geometry results in differences in mean plant volume, in plant packing, and thus, in different thinning trajectories.

Key words: *Murdannia keisak*, plant geometry, self-thinning, $-\frac{3}{2}$ power rule.

INTRODUCTION

Much controversy surrounds the importance of self-thinning in plant populations (White & Harper, 1970; Gorham, 1979; Hutchings & Budd, 1981*b*; Westoby, 1984; Weller, 1987) and the mathematical descriptions of this process (Mohler, Marks & Sprugel, 1978; Westoby, 1984; Weller, 1987). Traditionally, self-thinning is thought to occur once a monospecific stand is maximally stocked such that further biomass increase must be accompanied by death of individuals (density-dependent mortality). As a result, the average mass of surviving plants is related to density according to the familiar $-\frac{3}{2}$ power law (Tadaki & Shidei, 1959; Yoda *et al.*, 1963):

$$W = cN^{-\frac{3}{2}}, \tag{1}$$

where W is mean biomass of the surviving plants, N is stand density, c is a constant (intercept), and $-\frac{3}{2}$ is the slope or trajectory along which plant populations supposedly self-thin. This relationship between W and N is linearized by log-log transformation (base 10) to

$$\log W = \log c - 1{\cdot}5 \log N. \tag{2}$$

Lately, several authors have taken issue with the self-thinning law as stated in equations (1) and (2). First, it may be invalid statistically to regress $\log W$ on $\log N$ because W is derived by dividing total biomass by N (Weller, 1987). Second, average plant mass can increase simply by death of small individuals without growth of the survivors (Westoby, 1984; Weller, 1987). Total stand biomass can increase only if individuals actually grow and/or if new individuals establish. These and other criticisms have led several investigators to use

$$B = cN^{-\frac{1}{2}} \tag{3}$$

to portray the biomass–density relationship, where B is total stand biomass, N is stand density, c is a constant, and $-\frac{1}{2}$ is the slope of the thinning curve. This equation is linearized to

$$\log B = \log c - 0{\cdot}5 \log N. \tag{4}$$

Equations (1) and (3) are equivalent [as are (2) and (4)], if the relationship $B = WN$ is applied.

Questions have also arisen about the B–N relationship [equation (4)]; for example, is linear regression an appropriate method to derive its parameters? Mohler *et al.* (1978) and Weller (1987) have argued that neither B nor N is independent of the other, neither is experimentally controlled, and both are subject to variability and measurement error. Therefore, it has been proposed that such relationships be described by geometric mean regression (Ricker, 1975), the bivariate structural relationship (Jolicoeur, 1975), or some other form of principal components analysis (PCA; Sokal & Rohlf, 1981). If neither variable were subject to much error, both linear regression and PCA would bear similar results. However, if there is error or biological variability, considerably different thinning slopes may be derived by these two statistical techniques. Some criticisms of W–N can be circumvented by use of PCA rather than linear regression (e.g. Mohler *et al.*, 1978).

Deviations from the theoretical slope have been ascribed to several biotic and abiotic causes (Westoby, 1984), including shade and plant architecture. Some shaded plant populations have been shown to thin along a line of slope -1 for equation (2), or zero for equation (4) (White & Harper, 1970; Lonsdale & Watkinson, 1982). The first purpose of this paper is to examine the self-thinning slope in shaded and unshaded field populations of an emergent aquatic annual herb [*Murdannia keisak* (Hassk.) Hand.-Mazz.: Commelinaceae]. Data are described in four ways: by equations (2) and (4) using both linear regression and PCA. We assume that density-dependent mortality is occurring and that no other mortality factors cause measurable effects. The second purpose is to employ measures of plant volume and architecture to show how different light regimes and architecture might consequently affect self-thinning in these monospecific herbaceous stands.

STUDY SITES AND SPECIES

This study was conducted at four sites on the Savannah River floodplain in western South Carolina, USA. Portions of the floodplain have received cooling water, via three tributary streams, from nuclear production reactors. These thermal effluents have killed most of the natural forest vegetation at the mouths of these streams where they enter the river floodplain (Sharitz, Irwin & Christy, 1974; Dunn & Sharitz, 1987). Two study sites were located on the floodplain near the mouth of Pen Branch (PB). Here, *M. keisak* is the dominant herb, forming large monospecific stands growing in almost full sunlight (Dunn & Scott, 1987). Although both populations are exposed to elevated water temperatures (+5 °C), controlled glasshouse experiments showed that increases in water temperature (+10 °C) did not significantly affect growth or mortality of *M. keisak* whereas light levels did (Dunn & Sharitz, in preparation). Two other populations were located downstream from the PB sites, where Steel Creek (SC) enters the river floodplain. Both SC populations are shaded (5–10% of full sunlight), but are not exposed to elevated water temperatures.

Murdannia keisak is an annual plant introduced from eastern Asia (Dunn & Sharitz, 1990). Growth begins from overwintered seed in late April. Average plant biomass increases rapidly in shaded populations, but more gradually in full sun. A main stem is evident for at least half of the growing season, by which time branching may occur. Larger plants often form adventitious roots at the nodes.

METHODS

Data collection

During the 1986 growing season, above and belowground parts of *M. keisak* were harvested monthly (May–October) in two randomly located $0{\cdot}25 \times 0{\cdot}25$ m quadrats from each of the four populations. Shoot length, root length, number of leaves per plant, dry weight, and number of plants per plot were measured. Because the two populations at each site differed little (see Results), samples (4 per harvest date) were combined for analyses.

Data analysis

The $-\frac{3}{2}$ *power law.* Mean weight per plant (g dry wt) and density were calculated for each population harvest. Linear regression (procedure in SAS, 1985) was used to derive thinning lines for the log-log transformed data from both the shaded (SC) and unshaded (PB) populations.

A thinning line was also derived as the major principal component axis of the variance–covariance matrix of log-transformed data (procedure in SAS, 1985). The slope, intercept, and 95% confidence limits of the major axis were calculated using the SAS output and the formulae in Sokal & Rohlf (1981, pp. 595–597). The proportional eigenvalue (% EV) has been used to approximate the linear association between the two variables in self-thinning models (e.g. Mohler *et al.*, 1978; Hutchings & Budd, 1981*a*). Because of problems using % EV in this way (Weller, 1987; P. M. Dixon pers. comm.), we use the r^2.

B–N relationship. Total stand biomass (B, g dry wt m^{-2}) and total density (N, plants per m^{-2}) were calculated and log-log transformed. Linear regression was used to derive a thinning line, with the coefficient of determination (r^2) as the measure of linear association between the two variables (B and N). A thinning line was also derived using PCA, as described above.

Light and plant architecture. Plant architecture of the shaded and unshaded populations was compared using ratios of plant biomass to volume (B/V; Lonsdale & Watkinson, 1983). This ratio was derived from g m^{-2} divided by mean plant height in m. Volume per individual plant (v) was calculated as cm^3 plant $^{-1}$, again following Lonsdale & Watkinson (1983).

RESULTS

Population descriptions

From July onward, total biomass (B) was higher at the unshaded site than at the shaded one (Fig. 1 *a*). Mean plant weight (W) overlapped considerably throughout the year (Fig. 1 *b*), and was higher in the shade during the peak of the growing season (July and August). The decline in W in shade is probably the result of stem breakage, due to damage during harvesting and to plants rooting at the nodes. The unshaded sites supported a higher density than the shaded sites throughut the growing season (Fig. 1 *c*). Furthermore, plants in full sun were shorter but more numerous, whereas those in the shade were much longer, but less numerous. In September 1986, nodes were counted for 40 plants from each site (randomly selected from all plants harvested). A two-tailed t test suggested no significant difference in mean number of nodes per plant between the two groups ($t = 0{\cdot}105$, $P > 0{\cdot}50$, d.f. = 78, t critical = 1·991). Differences in plant height thus result from differences in internode length.

Thinning lines

Unshaded site (W–N). Linear regression using W as the dependent variable generated a slope (−1·77) that approximates the expected slope (95 % confidence interval (Table 1) includes $-\frac{3}{2}$). The r^2 (0·853) indicates a close fit to the data. The PCA slope is steeper (Table 1), but with a 95 % confidence interval that also includes the expected value of $-\frac{3}{2}$.

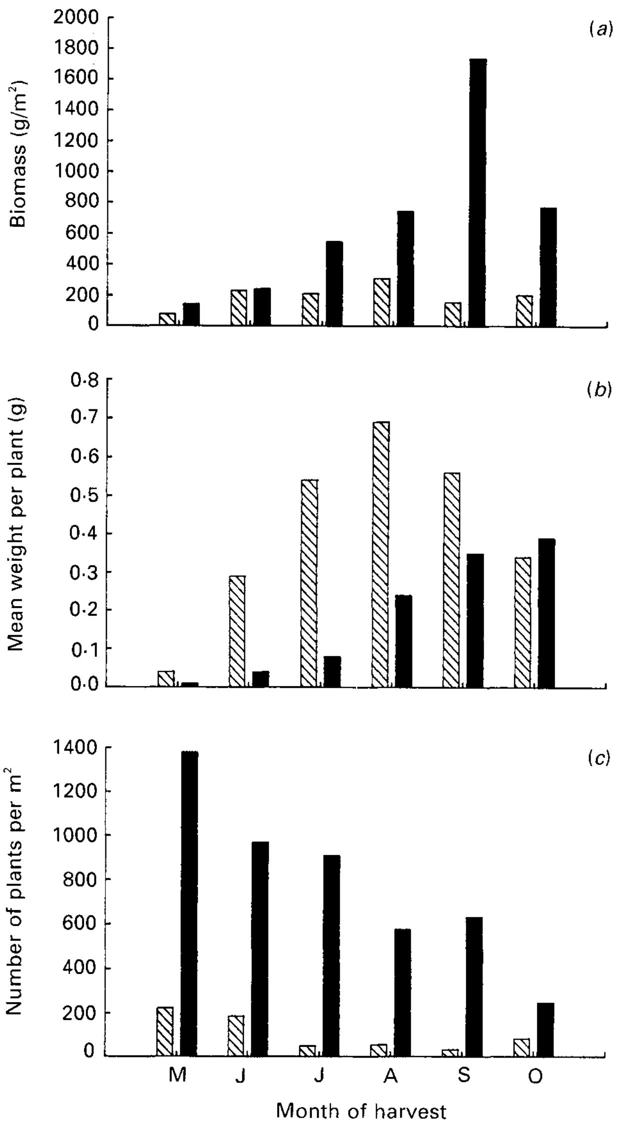

Figure 1. (*a*) Biomass, (*b*) mean plant weight, and (*c*) density during of shaded (▨) and unshaded (■) populations of an annual aquatic herb, *Murdannia keisak* during the 1986 growing season.

Table 1. *Thinning line parameters and statistics for field populations of* Murdannia keisak *growing in full sun and under canopy shade*

	Slope	95 % CI	Expected Slope	Reject H_0?	Intercept	r^2
Unshaded						
W–N	−1·77	(−2·34, −1·20)	−1·5	No	3·94	0·853
W–N (PCA)	−1·82	(−2·56, −1·31)	−1·5	No	4·05	0·853
B–N	−0·79	(−1·37, −0·22)	−0·5	No	5·60	0·520
B–N (PCA)	−1·14	(−2·15, −0·62)	−0·5	Yes	6·89	0·520
Shaded						
W–N	−1·18	(−1·65, −0·71)	−1·0	No	1·69	0·765
W–N (PCA)	−1·41	(−2·03, −0·97)	−1·0	No	2·12	0·765
B–N	−0·21	(−0·66, +0·24)	0	No	2·84	0·100
B–N (PCA)	−0·34	(−1·29, +0·27)	0	No	3·19	0·100

The null hypothesis (H_0) states tha the derived slope does not differ significantly from the expected slope. The H_0 was tested using the 95 % confidence interval.

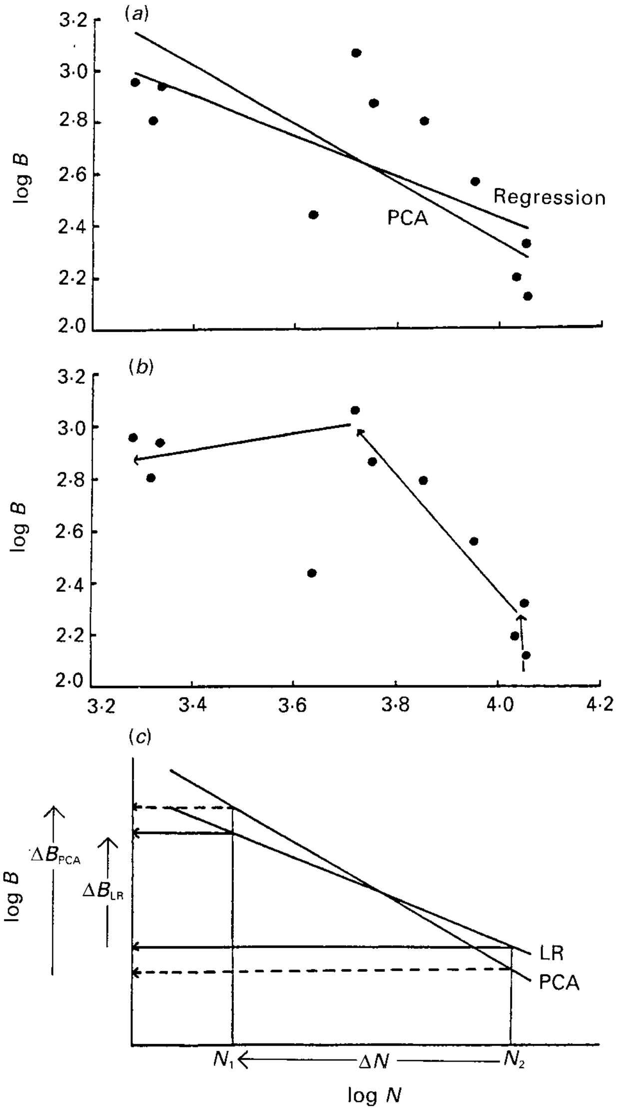

Figure 2. (*a*) Plant self-thinning curves (B–N) for unshaded populations of *Murdannia keisak* derived by regression and principal component analyses. (*b*) Possible growing season trajectory of B–N relationship for unshaded populations of *M. keisak*. Vertical line at lower right indicates increased biomass (B) by growth of established plants early in the growing season. Subsequent increase in B is at expense of stand density (N); i.e. thinning occurs. Toward the end of the growing season, further mortality (e.g. senescence) occurs and B begins to decline. The steep portion of the thinning line has a slope of $-2{\cdot}09$ (B–N using PCA). All points have a PCA slope of $-1{\cdot}14$. (*c*) Ambiguity in interpreting thinning lines derived by linear regression and PCA (see text for further discussion).

Unshaded site (B–N). The linear regression slope of B on N at the unshaded sites does not differ significantly from $-\frac{1}{2}$ (Table 1; Fig. 2*a*). However, the r^2 (0·520) suggests a poorer fit to the thinning 'law' than for the W–N relationship. By contrast, use of PCA yields a steeper slope (Table 1; Fig. 2*a*) with upper and lower 95 % confidence limits ($-2{\cdot}15$, $-0{\cdot}64$) that do not include $-\frac{1}{2}$.

Shaded site (W–N). Populations of *M. keisak* subjected to shade thin along slopes which do not differ significantly from the expected regression or PCA slopes (Table 1). Shading reduced W more than two-fold ($\log_{10}$ units; see intercept values in Table 1).

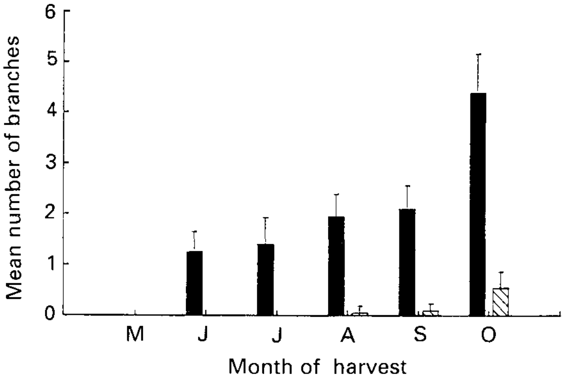

Figure 3. Branch production during the growing season in shaded (■) and unshaded (▨) populations of *Murdannia keisak*. Standard errors of the means are shown.

Shaded site (B–N). The thinning line of B–N derived by regression has a slope not significantly shallower than expected in shade (i.e. zero; Table 1). The r^2, however, is so low, and the confidence limits so wide that the regression is difficult to interpret. The slope of the first principal component (Table 1) is even further from zero. As with the W–N plot, B is reduced two-fold in the shaded populations.

Plant architecture

Shaded plants are more branched than those in full sun (Fig. 3) and are thus closer to a Type IV morphology (Miyanishi, Hoy & Cavers, 1979; Ellison, 1989), which is characterized by three-dimensional growth in height and spread. Unshaded plants, however, resemble a Type V morphology, approximating one-dimensional vertical growth. Consequently, less plant biomass can fill a particular volume of space (Lonsdale & Watkinson, 1983) in shaded populations, suggeting a greater 'canopy' spread and larger mean plant size. This observation is supported by the lower intercepts of shaded populations (Table 1).

Volume of space can also be expressed on a per plant basis (v; Lonsdale & Watkinson, 1983). Although values of v vary between consecutive harvests, they are much lower in shaded than unshaded populations throughout the growing season (Table 2), indicative of a more complex plant morphology in the shaded plants.

DISCUSSION

Biomass thinning

The self-thinning rule generally applies to the data on biomass and density of *M. keisak* presented here.

Table 2. *Changes in the biomass/volume relationship* (B/V) *and volume per plant* (v) *for shaded and unshaded populations of* Murdannia keisak *during the growing season*

	Harvest					
	1	2	3	4	5	6
Unshaded						
B/V (g m^{-3})	2042·8	1853·8	2415·3	2066·7	3052·6	1203·3
v (cm^3 plant^{-1})	4·9	21·6	31·8	116·1	114·7	324·1
Shaded						
B/V	325·0	287·5	233·0	250·0	138·1	255·0
v	123·1	1008·7	2317·6	2760·0	4055·0	1333·3

Calculations of B/V and v used the methods of Lonsdale & Watkinson (1983).

No evidence of other mortality factors (thermal influence, herbivory, disease) has been observed, giving confidence to the assumption that mortality in these populations of *M. keisak* is density-dependent. Three of the slopes from unshaded populations are close to the hypothetical values (Table 1). The fourth slope (B–N using PCA) is too low to support the self-thinning rule. Although confidence intervals are rarely reported in the self-thinning literature (but see Weller, 1987), for many species (including *M. keisak*), the confidence interval is so wide that reference should be made to a 'thinning band' rather than to a thinning line (Westoby, 1984). These wide confidence intervals are due in part to variation in B and N.

Figure 2*a* shows this variation in B and N for *M. keisak*, which is not evident when the relationship is presented simply as a linear equation. However, the individual points might reflect the true trajectory of the population during the growing season. When the data are interpreted to show this seasonal change (Fig. 2*b*), it appears that early increases in total stand biomass of *M. keisak* are accounted for by growth of established seedlings. Subsequently, crowding dependent mortality occurs while B continues to increase, but at a lower rate. Toward the end of the growing season, N declines further, but B levels off because of slower overall growth and the onset of senescence. As a result, the steepest portion of the line in Fig. 2*b* has a slope ($-2·09$ for B–N using PCA) greater than that derived when all points are included.

This interpretation is consistent with the suggestions of Lonsdale & Watkinson (1982) and Westoby (1984) that there must exist a level of biomass accumulation which a population cannot exceed even in full sunlight. Shading as low as 9 % of full sunlight has been shown to lower the thinning intercept without changing the slope (Hutchings & Budd, 1981*a*; Westoby & Howell, 1981, 1982). In all cases, shaded *M. keisak* populations had shallower thinning slopes and lower intercepts than unshaded populations; however, the confidence limits (Table 1) also include slopes typical of unshaded populations ($-\frac{3}{2}$ or $-\frac{1}{2}$).

A further problem is the interpretation of the linear regression line versus the PCA line. For example, a stand with a high density (N_2, Fig. 2*c*) would be predicted to support a higher B if linear regression were used to derive the thinning slope than if PCA were used. At low density (N_1, Fig. 2*c*), the opposite holds. Furthermore, for a given change in density (ΔN), the PCA thinning line suggests a greater increase in biomass (ΔB_{PCA}, Fig. 2*c*), and thus less vigorous thinning, than does the line derived by linear regression (ΔB_{LR}, Fig. 2*c*).

Different slopes are obtained from these analyses because the sums of squares of deviations in PCA are at right angles to the major axis; in linear regression they are parallel to the Y axis (Sokal & Rohlf, 1981). Thus, the slope of the PCA major axis will always be steeper than that of the regression line (Ricker, 1975; Sokal & Rohlf, 1981). The only instance in which the regression slope will equal the PCA slope is when all points fall precisely long a straight line. The 'expected' PCA slope for self-thinning data, given the almost certain error and natural variation in either B or N (Weller, 1987), cannot be assumed to be $-\frac{1}{2}$, but must be steeper.

Several other factors might account for a loose fit of our data (or any other field data) to the self-thinning model. First, seed output can vary greatly among plots so that poorly-seeded plots never reach high enough N for self-thinning to occur. Second, even if seeding is uniform, stands or plots may be harvested too early to show the theoretical thinning relationship. Third, crowding-independent mortality (Westoby, 1981) may lower the value of N expected for a particular B or W. Fourth, resource limitations such as shading of herbs by shrubs or trees can dampen the self-thinning line by keeping B or N low. Fifth, sample sizes may be too small to reveal a relationship. Finally, the equations commonly used might be too robust. Similar factors have been suggested by Mohler *et al.* (1978) and Zeide (1987) to account for the poor fit of data for trees.

Because of this loose fit, several authors have recommended the elimination of outliers. Such data editing, however, is subjective and does not take into account this natural variation. If the self-thinning 'law' is valid and widely applicable, it should be so in spite of natural population variation. These *M. keisak* data can, within the derived confidence limits, be taken as supporting the self-thinning hypothesis; however, supporting evidence does not necessarily verify a hypothesis. Our results (except the unshaded *B–N* using PCA) do not cause us to reject the null hypothesis that the derived slopes differ significantly from $-\frac{3}{2}$ or $-\frac{1}{2}$. However, different statistical approaches could yield different ecological interpretations because of variability in population data. Beause *W–N* data can be examined statistically using PCA (e.g. Mohler *et al.*, 1978), the *B–N* relationship is not the only useful description of thinning. Grounds for rejecting the use of *W–N* have been discussed (Weller, 1987). However, in some instances, for example in forest management, mean plant size (e.g. weight) is a feature of a stand worth considering (Ginrich, 1967; Roach, 1977; DeBell & Whitesell, 1988) and may be done so in a statistically valid manner (Prairie & Bird, 1989).

Volume thinning

Lonsdale & Watkinson (1983) have shown that, for three herbaceous species, thinning is also related to average plant canopy volume (v). As density-dependent thinning occurs, canopy volume of surviving plants can increase. For plants grown in full sunlight, Lonsdale & Watkinson (1983) derived a volume-thinning slope of approximately $-\frac{3}{2}$, the same as the usual biomass (*B* or *W*) thinning slope, and they state (p. 294) that the 'relationship between the mean volume of canopy available to each plant and the density also conforms closely to the $-\frac{3}{2}$ power law'. This proposed $-\frac{3}{2}$ slope holds only for the shaded *M. keisak* plants, whereas those grown in full sunlight thin along a considerably steeper slope and have a higher intercept (Fig. 4). Lonsdale & Watkinson (1983) also present data for *Helianthus annuus* grown in 100 and 60 % light (their Table 2; recalculated from Hiroi & Monsi, 1966). As with *M. keisak*, only the shaded *H. annuus* plants thin (with respect to v) along a slope near $-\frac{3}{2}$, whereas those *H. annuus* plants in 100 % light thin along a steeper slope (Table 2 in Lonsdale & Watkinson, 1983). Their proposed slope for plant populations in full sunlight does not appear to hold for *H. annuus* or *M. keisak*, suggesting that (*a*) these two species are anomalous, (*b*) the volume-thinning slope should be some value other than $-\frac{3}{2}$, or (*c*) the volume-thinning slope is not meaningful.

If volume-thinning does 'conform closely to the $-\frac{3}{2}$ power law', perhaps a reduced slope should occur in shaded populations. Indeed, shaded populations of *M. keisak* approximate a -1 slope, whereas unshaded ones thin more steeply (Fig. 4). Similar differences in slope have been noted for *H. annuus* populations; however, the unshaded and shaded slopes differ significantly from $-\frac{3}{2}$ and -1, respectively (see 95 % CI's in Lonsdale & Watkinson, 1983).

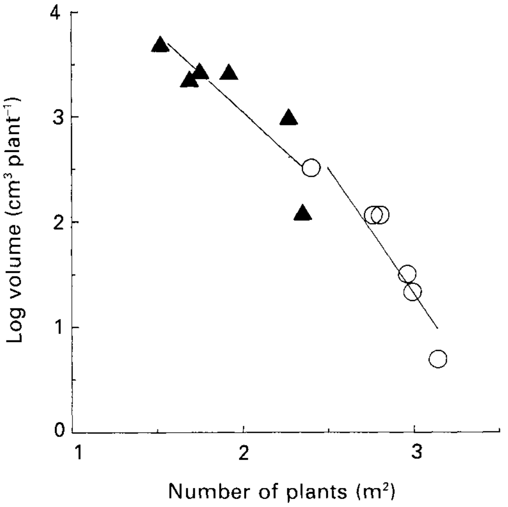

Figure 4. Relationship between volume per plant and plant density (*N*) for shaded (▲) and unshaded (○) populations of *Murdannia keisak*. The thinning line equations are $\log v = 4{\cdot}94 - 0{\cdot}92N$ (95 % CI for the slope $= -2{\cdot}01, -0{\cdot}40$) for the shaded population and $\log v = 6{\cdot}19 - 2{\cdot}64N$ (95 % CI for the slope $= -3{\cdot}16, -1{\cdot}70$) for the unshaded population. Only the shaded line follows the $-\frac{3}{2}$ thinning slope for volume proposed by Lonsdale & Watkinson (1983).

Volume-thinning relationships ultimately could be a consequence of competition for light (Ellison, 1989). At the shaded site, competition for light might promote greater 'canopy' volume in the form of more branches and leaf area (Ellison, 1989). Thus, the volume-thinning found to occur with shaded plants might be related to differences in their geometry. Because of higher light levels at the open site, a simple (Type V) morphology allows the interception of sufficient light; therefore, branching is not as necessary, plants are more upright and have lower individual biomass, and more biomass can be supported per unit volume of space (Table 2). As thinning occurs in the high light regime, the volume of space used by each plant increases more steeply than in the shaded site (Fig. 4), and by the end of the growing season, branching is eventually initiated (Fig. 3).

Consequently, the slope and intercept of volume-thinning are lower for populations of *M. keisak* in the shade than in full sunlight because volume expansion is of a lower dimension in shade (more horizontal or vertical, not always both). This conforms to field observations that shaded *M. keisak* plants tend to branch, rather than to increase in both height and spread. Therefore, the biomass per volume of space (*B*/*V*) is lower in the shaded populations because biomass increases do not appear to include as much of a vertical component.

In sum, most field data do not support the optimistic claims that the thinning rule may be of near 'universal validity' (White & Harper, 1970) or that it 'articulates population ecology with ecosystem functions' (Westoby, 1984). Plant geometry (canopy volume, branching) also increases with decreasing population density. Different volume-thinning slopes were observed in this study for shaded and unshaded populations of *M. keisak*, although strict adherence to a $-\frac{3}{2}$ volume-thinning slope (Lonsdale & Watkinson, 1983) was not observed.

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