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SELF-THINNING AND COMPETITION INTENSITY OVER A GRADIENT OF NUTRIENT AVAILABILITY

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SUMMARY

(1) High-density populations of *Ocimum basilicum* L. were grown in sand culture at three nutrient levels to investigate patterns of self-thinning in stands grown over a range of nutrient supply.

(2) Populations of *Ocimum* at each of three nutrient levels showed self-thinning with different biomass–density relationships (thinning lines) for each level. The lines for the stands at the two lower nutrient levels lay below that followed by the stands grown at the high level. Thus competition was more intense in the stands grown at low nutrient levels, when compared at a common plant mass. However, because thinning proceeded fastest in the stands grown at high nutrient supply, competition at a common time was most intense in these stands.

(3) It is proposed that the mechanism underlying intensified competition (irrespective of rate of development) is the extent of overlap of resource depletion zones to achieve given plant mass. If this overlap increases at lower resource levels to achieve a given plant mass, competition will intensify at the lower resource levels. However, the rate at which overlap develops at each resource level will determine the intensity of competition when stands are compared in time.

(4) Plants of *Ocimum* from stands grown at lower nutrient levels tended to have less radial extension of the canopy for a given height, and to be shorter and have less radial extension for a given shoot weight. Thus they packed their shoot weight into a smaller canopy volume plant^{-1} than plants at high nutrient levels. If canopy packing had determined the relative positions of thinning lines, populations grown at low nutrient levels would have followed higher thinning lines than those at high levels.

(5) Biomass packing, when measured at the population level, showed the reverse trend, i.e. it was lower in the stands at low nutrient levels. This occurred because of the wider spacing between plants in these stands than in the high-resource stands at a given biomass level. Canopy interactions between plants grown at low nutrient levels were less than in plants grown at high nutrient levels. Thus the major determinant of plant spacing in the stands at low nutrient levels was below rather than above ground.

(6) Plants competing for nutrients can increase uptake by increasing the absorbing power of the root, and/or by growing more root. Root and root hair measurements failed to detect any morphological evidence of increased absorbing power in the plants grown at low nutrient levels.

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(7) Plants at the two lower nutrient levels grew relatively more root (weight and length) than those at the high nutrient level. Just under half of this root growth occurred in the top 16% of the soil volume. Root densities achieved were so high that conditions for mutual overlap of depletion zones for mobile nutrients were present. This is taken as evidence that increased overlap of nutrient uptake zones occurred at lower nutrient levels in order for plants to achieve a given mass.

INTRODUCTION

The intensity of competition varies as growth conditions change. It has been suggested that competition will be more intense in resource-rich habitats, because of the greater chance of neighbour interactions (Grime 1973, 1979). The converse has been argued also: in infertile habitats, plants may have to forage further to acquire resources, and so compete with neighbours more (Newman 1973; Grubb 1985; Tilman 1987). Reviews of the available evidence have found examples of both cases (Morris & Myerscough 1984; Wilson 1988). This paper addresses this question in self-thinning monocultures grown over a range of nutrient supply.

Self-thinning in even-aged monocultures of plants (Yoda *et al.* 1963; Westoby 1984; White 1985) usually follows an initial period of growth with either no mortality, or density-independent mortality. Later, high-density populations enter a phase of self-thinning, i.e. density-dependent mortality, in which increases in biomass follow the relationship (Yoda *et al.* 1963; Weller 1987a).

$$\log B = \log K - \beta \log N \qquad (1)$$

where B = biomass per unit area, N = density, K = intercept and β = slope. Following self-thinning, some populations may achieve the carrying capacity for that environment (Donald 1961); mortality may continue but biomass remains constant (White & Harper 1970).

Self-thinning has been compared between species (White 1985; Weller 1987a; Lonsdale 1990) and between populations of the same species grown at different resource levels. Where light is the resource, populations grown in shade have consistently thinned along lower lines (i.e. lower β and/or K in eqn 1) than unshaded controls (Kays & Harper 1974; Hutchings & Budd 1981; Westoby & Howell 1981, 1982; Lonsdale & Watkinson 1982, 1983; Dunn & Sharitz 1990). When nutrient levels are varied, however, the patterns of self-thinning are less clear-cut. Populations of *Raphanus sativus* and *Brassica napus* at different fertility levels followed a common thinning line (White & Harper 1970). A similar result was found in mixed population of *Sinapsis alba* and *Lepidium sativum*, also grown at different fertility levels (Bazzaz & Harper 1974). However, populations of *Trifolium subterraneum* (Morris & Myerscough 1985) and *Fagopyrum esculentum* (Furnas 1981) grown under low-nutrient conditions thinned along lower lines than controls in more-fertile conditions. Calculations based on yield tables showed that monospecific even-aged forest stands on less fertile sites also usually thinned along lower lines than those on more-fertile sites (White 1981; Westoby 1984).

The lower thinning lines observed in shaded or in (some) stands on infertile substrata imply an intensification of competition in these stands compared to more-fertile controls. The intensity of competition in self-thinning stands can be measured by the extent of mortality, and by the ground area required to support survivors of

given mass. Comparing stands at a common time, stands that have thinned the most have undergone the most intense competition. However, comparison of the intensity of competition can be made using biomass as a frame of reference. In the shaded or nutrient-poor stands on a lower self-thinning line than those from unshaded or fertile controls, self-thinning begins at a lower mean plant mass. More individuals die in a stand to achieve a given mean mass of survivors, and the survivors require greater ground area per individual to support that mass than in control stands. Thus, using mass rather than time as a frame of reference, competition is judged to be more intense in such stands than controls. If stands of the same species grown at different resource levels follow a common self-thinning line it is probable that a competitive process common to all stands has merely been slowed down at the lower resource levels (White & Harper 1970; Bazzaz & Harper 1974).

In the light of the above problems, high-density populations of plants were established to answer the following questions: (i) do populations grown over a range of nutrient supply thin along a common line, or along different lines; and (ii) what competitive mechanisms operate to give either result?

METHODS

Seeds of *Ocimum basilicum* L. (sweet basil) (mean fresh seed weight = 1·49 mg) were sprinkled onto washed glass-blower's sand in 29-cm-diameter pots and covered with a shallow sand layer on 28–30 October 1987. The soil depth in each pot was 12 cm. Sowing densities were 1650 or 5280 seeds pot^{-1} (equivalent to 25 000 and 80 000 m^{-2}). Nutrients were applied weekly (500 ml pot^{-1}) at one of three concentrations: 100%, 60% and 30%. The full nutrient solution consisted of: $MgSO_4$ 0·37 g l^{-1}, NaH_2PO_4 0·21 g l^{-1}, $Ca(NO_3)_2$ 0·66 g l^{-1}, KNO_3 0·40 g l^{-1}, Fe EDTA to give 4·4 μg g^{-1} Fe, H_3BO_3 5·73 mg l^{-1}, $MnCl_2.4H_2O$ 3·62 mg l^{-1}, $CuSO_4.7H_2O$ 0·16 mg l^{-1}, $ZnSO_4.7H_2O$ 0·22 mg l^{-1}, and $(NH_4)6Mo_7O_{24}.4H_2O$ 0·18 mg l^{-1}. Sufficient pots for five harvests and four replicates were sown and arranged in randomized blocks in a glasshouse. As the plants grew *c.* 10 cm above the sand, a collar of 70% shadecloth was added around each pot and up to *c.* 2·5 cm below canopy height to reduce edge effects. As growth continued, successively higher collars were added. Harvests were taken 5, 10, 13, 16 and 23 weeks after sowing. Plants were sprayed with streptomycin (100 mg ml^{-1}) at 4 and 7 weeks after sowing for a bacterial soft-rot, and regularly with Rovril® (May & Baker, West Footscray) against *Fusarium* infection and Supracide® (Ciba-Geigy Australia, Pendle Hill) against insect attack.

Sampling

Before each harvest the height above which *c.* 10% of the plant tops occurred (called canopy height, *H*) was measured for each pot. Then a circular quadrat (PVC pipe, diameter either 6·2 cm or 10·3 cm) was positioned in the centre of the pot (the smaller quadrat was used for early harvests when densities were high, and the larger quadrat at later harvests as densities fell). Stems of all plants rooted in the quadrat were cut off at soil surface. A random sample of ten individuals was selected from the quadrat population and scored for height to tip of the stem (*h*), leaf number and total area of the laminae (using a Lambda Instruments Corporation Model LI 3000; Lincoln, NB, U.S.A.) and (from harvest 2 onwards) horizontal extension from the

stem of a randomly selected leaf (e) as a measure of the radial extension of the canopy.

The pipe was pushed into the soil and used to extract a soil core, which was divided into a surface (0–2 cm deep) and a subsurface (>2 cm deep) segment. Root material was washed in a 2-mm sieve. Root length was determined on a subsample by the method of Tennant (1975) using a 1·0-cm grid. The root systems of three plants were randomly selected from the washed sample of surface-layer roots; lateral roots were removed from the tap roots and arranged on two microscope slides. A random subsample of six lateral roots (three per slide) was scored under a microscope (magnification used given in parentheses) for width of lateral roots and proportion of the lateral root in the field of view bearing root hairs (scored as 0, 25, 50, 75 or 100%; ×25); number of root hairs per unit length within the zone of root hairs (×63); length (×63) and width (×400) of a randomly selected root hair. In the subsurface segment, tap roots could not be reliably distinguished; consequently, subsamples of the general root mass were arranged on two slides, and the measurements listed above repeated. Root material used for these measurements was returned to the main root mass. Shoot and root material (main root sample and root length subsample) were dried in a convective oven at 80 °C for 24 h and weighed. Because of sand contamination, root material was subsequently dry-ashed and the ash washed off; sand dry weight was subtracted from the initial weight. Total root length was calculated from the length and weight of the subsample, and the weight of the whole sample.

Data analysis

Fitting of thinning lines

Selection of points for fitting a thinning line has presented a problem to previous investigators (Mohler, Marks & Sprugel 1978; Westoby 1984; Weller 1987a). Inclusion of points below the thinning region will tend to steepen the slope; inclusion of points that have reached the carrying capacity of the environment will flatten it (Mohler, Marks & Sprugel 1978). Selection of points can only be made a posteriori (Weller 1987a). In this experiment, evidence that points had commenced self-thinning was sought by comparing density at each harvest with the sown or established density. A substantial departure (>10%) from sown or established density was taken as evidence that self-thinning had commenced. Evidence that thinning populations had reached the carrying capacity for that environment was sought from the biomass–density plot. Lack of a significant correlation between biomass and density (zero slope) for thinning populations indicates that carrying capacity has been reached (Weller 1987a). Late-harvest points were tested for the significance of the biomass–density correlation. If this was insignificant, these points were considered for exclusion. Data points that lie at the beginning or high-density end of this region of zero slope may lie at the junction of the regions of self-thinning with biomass increases, and self-thinning with static biomass; there is still an element of subjective choice in selecting these points for inclusion or exclusion. Such choices were made at the 100% and 60% nutrient levels; alternative thinning lines excluding these points were also calculated and are presented.

Thinning lines were fitted by principal components analysis (Mohler, Marks & Sprugel 1978) to selected points in each nutrient treatment on the log biomass – log density plots for each of shoot, root and total biomass (Westoby 1984; Weller

1987a). The r^2 statistic for each line was used to report the amount of variance explained (Weller 1987a). Limits to the slopes were calculated and were used for comparison of differences between slopes (Weller 1987a).

Treatment effects

Analysis of variance was used to detect the significance of treatment effects. Harvests, nutrients and densities were treated as fixed factors. Where soil depth was included as a fixed factor, two replicates were randomly assigned to each soil depth, to avoid lack of independence of data. Raw data were first analysed, and heteroscedasticity of variances was assessed by Cochran's test. If variances were not homogeneous, appropriate transformations were used until heteroscedasticity was at least significantly reduced if not entirely removed. Non-significant interactions were pooled if $P > 0{\cdot}25$; main effects were only tested if higher-order interactions were non-significant. Missing values were replaced by cell means, and the residual degrees of freedom reduced accordingly. Subsequent comparison between means was by the Student–Newman–Keuls test with $P = 0{\cdot}05$ (Sokal & Rolf 1969).

Allometric relations

Allometric relationships between components of plant growth were determined by regression equations using population means. Two of these relationships examined components of root and shoot growth i.e. shoot weight – root weight ($w_s - w_r$) and leaf area plant^{-1} – root length plant^{-1} ($a - l$). Previous authors have examined relationships between various plant dimensions and between shoot weight and canopy dimensions to explain self-thinning in terms of packing of objects onto a plane surface (see White 1981; Weller 1987b). Interrelationships between shoot growth and canopy dimensions were analysed by the following allometries: plant height – shoot weight ($h - w_s$, Firbank & Watkinson 1985; Weller 1987b); leaf extension – shoot weight ($e - w_s$, Weller 1987b); leaf extension – height ($e - h$); and shoot weight – index of canopy volume plant^{-1} ($w_s - v'$, defined below). For the $w_s - w_r$, $a - l$ and $h - w_s$ allometries, regressions for populations of a given sowing density within each nutrient level were calculated and Cochran's test used to compare heteroscedasticity of variances around the six lines (N.S. in all cases). Lines for which a significant relationship was found were compared in slopes (Snedecor & Cochran 1980). If a significant difference was detected, comparison among slopes was by the Simultaneous Test procedure (Sokal & Rolf 1969). Those lines not significantly different in slope were then tested for differences in intercepts: if these differed significantly, subsequent comparison was by the Conditional Tukey–Kramer test (Day & Quinn 1989). Some of the lines tested had slopes and intercepts that were not significantly different; such lines were pooled.

In the allometries involving leaf extension ($e - w_s$, $e - h$ and $w_s - v'$) only data from harvest 2 onwards were available for analysis. A further restriction occurred at the 100% and 60% nutrient levels because plants in these treatments developed lateral shoots towards the end of the experiment, increasing radial extension of the canopy beyond the measured e. For these three allometries at the 100% and 60% nutrient levels, only data on e from populations also used to fit thinning lines were used: plants from these stands had no lateral shoots. For the $w_s - v'$ allometry only data from points used to fit thinning lines were used at all nutrient levels. With the reduced number of data points, densities were pooled within nutrient levels at the

100% nutrient level; at the 60% level this was also done for the $e - w_s$ and $w_s - v'$ allometries. At the 30% nutrient level densities were examined separately. Regression analysis of the lines and subsequent comparison between them where warranted proceeded as described above.

Biomass packing and canopy volume

The biomass-packing value of the canopy (in g of shoot biomass (B) per m^3 of canopy volume (V)) was determined firstly by the method of Lonsdale & Watkinson (1983). The ratio of shoot biomass ($g\,m^{-2}$) to canopy height (m) measures biomass packing ($g\,m^{-3}$). To compare canopy volume–density lines with the biomass–density lines calculated earlier for thinning populations, V (canopy height (m) × area ($1\,m^2$)) was plotted against density (N, plants m^{-2}) on a log–log plot. Thinning lines for the $V - N$ plot were fitted to the points used to calculate thinning lines for biomass, using the same methods.

The volumes of space occupied by individual plants in the canopy were estimated by assuming they were cylindrical (Weller 1987b). On this basis, the mean volume occupied by the canopy of a plant in a stand (termed canopy volume index, v') was derived from the mean leaf extension (e) as a measure of its radius and the mean height (h) of plants as $\pi e^2 h$. Whilst v' is a simplification of the canopy structure of a single-stemmed plant with opposite simple leaves, it was adopted as a first approach to the problem.

Sampling for edge effect

Because concern was expressed by White (1985) about edge effects influencing measurements of biomass in pots, random sampling for mean shoot weight $plant^{-1}$ in the border area was conducted in pots where edge effects (if present) were expected to be strongest. These were the 100% nutrient pots at later harvests (harvests 3 and 5 were selected). Sampling was conducted along a contiguous grid of 5-cm × 5-cm quadrats located along a north–south axis in the border area, and running from the pot edge inwards (*c.* 10 cm of border) to the 10·3-cm central quadrat. This gave an estimate of mean shoot weight in the north and south quadrats in the outer border and inner border areas of the pot. Mean dry shoot weight in the four border positions was compared with the mean for the central harvest quadrat by asymmetrical analysis of variance. If a significant border effect was detected, the central quadrat was then compared with the inner border only to test if an edge effect on shoot weight existed between these two locations.

Analysis of seed mineral content

A comparison was made of the nutrients invested in the pots as seed capital, and applied in solution. The N content of four 1-g (dry-weight) samples of the seed of *Ocimum* was determined by the Kjeldahl method; a separate HNO_3 digestion was carried out for P and K. Inductively coupled plasma-optical emission spectrometry was used to determine P content (Zarcinas & Cartwright 1983) and atomic absorption spectrophotometry for K. A *Pinus radiata* sample of known elemental composition was analysed concurrently to check that reported P and K levels were correct. Total nutrients applied in solution were calculated from concentration and volume added.

RESULTS

Density

In the low-density treatment, over-sowing of seeds in the centre of pots resulted in established densities being *c.* 145% of nominal sown density at first harvest. Density remained at this level at second harvest in the 30% nutrient level (Fig. 1a). Substantial mortality at this sowing density was first observed at the second harvest in the full-nutrient treatment (55% established) and 60% nutrient treatment (15% established), and the third harvest in the 30% treatment (14% established) (Fig. 1a). Thus, these populations were considered to have commenced self-thinning. In the high-density treatment established densities at first harvest were *c.* 90% of sown density. Substantial mortality (47–72%) was recorded at each subsequent harvest in this treatment (Fig. 1a). At both sown densities, self-thinning, once commenced, proceeded to the greatest extent in the higher nutrient levels at each harvest (Fig. 1a).

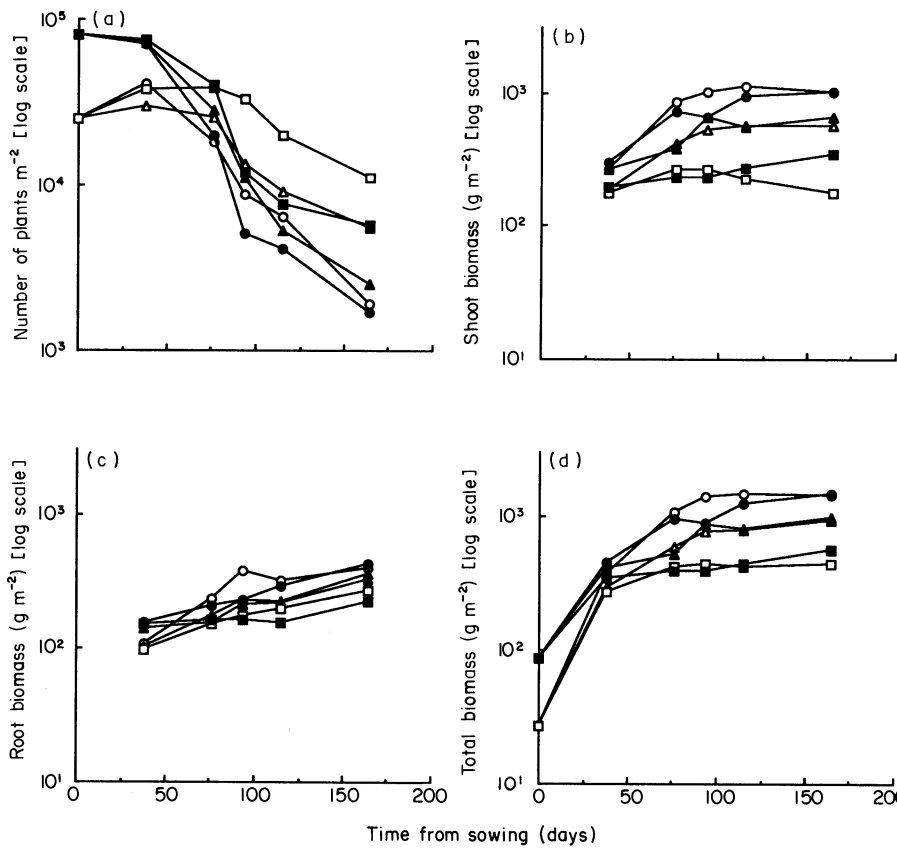

FIG. 1. Changes in (a) mean density (b) mean shoot biomass (c) mean root biomass and (d) mean total biomass of *Ocimum basilicum* sown at low density (open symbols) and high density (solid symbols) and grown at nutrient levels of 100% (○), 60% (△) and 30% (□).

Biomass

Shoot biomass varied significantly with nutrient level, depending on harvest (harvest–nutrient interaction: $F_{8,88} = 5{\cdot}20$, $P < 0{\cdot}001$; Fig. 1b). Shoot biomass changed from not being significantly different with nutrient treatment at harvest 1, to significant differences ranked 100% > 60% > 30% by harvest 3. This ranking was maintained to the end of the experiment, when there was a six-fold difference between the 100% and 30% nutrient treatments at the lower-density treatment, and a threefold difference at the higher-density treatment (Fig. 1b). Shoot biomass did not change significantly with harvest from harvest 2 at the 100% nutrient level, from harvest 3 in the 60% level, and not at all at 30%.

The effect of nutrient level on root biomass also depended on harvest (harvest–nutrient interaction: $F_{8,96} = 4{\cdot}44$, $P < 0{\cdot}001$; Fig. 1c). By harvest 3 the order of significant differences between nutrient levels was established, with 100% and 60% nutrient levels not significantly different, and the 30% level significantly less than either. An approximately twofold difference existed between the highest and lowest root yields at final harvest (Fig. 1c). Root biomass significantly increased with harvest at the two higher nutrient levels (harvests 3 and 4 excepted); at the 30% level, root biomass increased significantly only between harvests 1 and 2, and 4 and 5.

Total biomass varied significantly with nutrient level, but with differences according to harvest (harvest–nutrient interaction: $F_{8,96} = 5{\cdot}72$, $P < 0{\cdot}001$; Fig. 1d). The ranking of significant differences between nutrient levels of 100% > 60% > 30% was established by harvest 2 and maintained to the end. Total biomass did not increase significantly with harvest from harvest 3 in the 100% and 60% nutrient levels, and from harvest 2 in the 30% level.

Self-thinning

A subset of populations at each nutrient level was selected for fitting of thinning lines (see Methods). Thinning lines differed with nutrient level and with component of biomass examined. At the 100% nutrient level, populations moved along a thinning line of slope −0·56 for shoot biomass, −0·32 for root biomass and −0·50 for total biomass (Fig. 2, Table 1). The intercepts of the thinning line for shoot biomass were 5·25 at $10^0\,m^{-2}$ and 3·01 at $10^4\,m^{-2}$, a density within the range actually encompassed by the data (Table 1). (Omission of the harvest 4 low-density data point gave a steeper line (Table 1), with a slope of −0·62 for shoot yield.)

The thinning lines followed by the stands grown at the 60% nutrient level lay below those followed by stands grown at the 100% level (Fig. 2, Table 1). The slopes of the thinning lines for all biomass components at 60% were significantly flatter than those of the corresponding 100% nutrient lines (Weller 1987a). The slopes of the thinning line followed by the 60% level populations were −0·43 for shoot biomass, −0·24 for root biomass and −0·37 for total biomass. The intercepts of the thinning line for shoot biomass were 4·49 at $10^0\,m^{-2}$ and 2·77 at $10^4\,m^{-2}$.

At the 30% nutrient level, the high- and low-density populations traversed quite different biomass–density trajectories for shoot and root biomass, and so were treated separately. The high-density populations thinned along a line that lay significantly below those followed by the 100% and 60% nutrient stands for both shoot and total biomass (Fig. 2, Table 1). A thinning line for root biomass is not shown

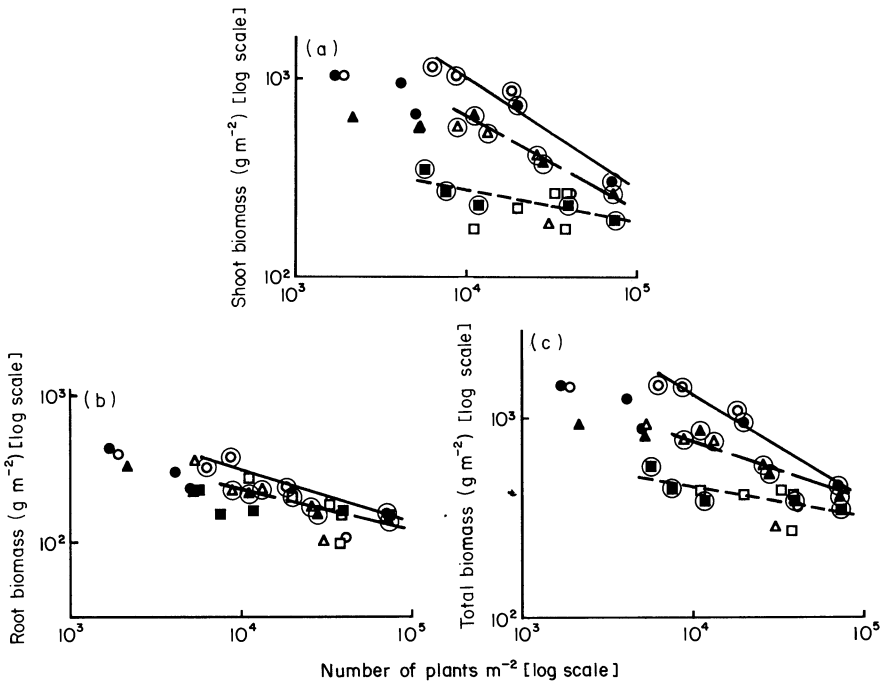

FIG. 2. Relationships between mean density and mean (a) shoot (b) root and (c) total biomass in *Ocimum basilicum* sown at low density (open symbols) and high density (solid symbols) and grown at nutrient levels of 100% (○), 60% (△) and 30% (□). Thinning lines for nutrient level of 100% (both densities) (——), 60% (both densities) (– – –) and 30% (high density) (– – –) are shown. Equations for thinning lines are given in Table 1. Points used to fit lines are circled.

for these stands in Fig. 2, because the biomass–density correlation was not significant (slope = zero). The low-density stands from the 30% nutrient level only showed self-thinning over the last three harvests, and so lines were not fitted. For shoot biomass, the populations from the lower-density treatment showed decreasing yield as they thinned along a region that lay below that followed by the high-density stands from the same nutrient level (Fig. 2a). For root biomass, however, the data points from this treatment lay above those from the high-density treatment, falling between the thinning lines for the 100% and 60% treatments (Fig. 2b). The combination of these two trends meant that for total biomass, the two sets of thinning populations followed roughly comparable paths (Fig. 2c).

Plant biomass and canopy dimension relationships

Nutrient level affected height–shoot-biomass allometry with a tendency for plants from the lower-nutrient and lower-density treatments to be shorter for given shoot biomass (Fig. 3a. Table 2). Slopes of the six possible lines were significantly different ($F_{5,18} = 2{\cdot}78$, $P < 0{\cdot}05$). The line from the low-density 30% nutrient stands had a higher slope than the other lines; however, the difference between the intercepts of the remaining lines was also significant ($F_{4,19} = 3{\cdot}487$, $P < 0{\cdot}05$); the low-density 60% nutrient treatment had a significantly lower intercept than the remaining

TABLE 1. Parameter values of the thinning lines for shoot, root and total biomass for populations of *Ocimum basilicum* sown at low and high densities and grown at 100%, 60% or 30% nutrient levels over five harvests (1–5). Data points used to calculate each line are indicated. Equation is $\log B = \log K - \beta \log N$, where B is biomass ($g\,m^{-2}$), N is density (m^{-2}), $\log K$ is the intercept (at 10^0 and 10^4 plants m^{-2}) and β is the slope. L_1, L_2 are limits of the slope, and r^2 is explained variance. Lines marked with † are shown in Fig. 2.

Nutrient level	Harvest: low density	Harvest: high density	K: 10^0	K: 10^4	β	L_1	L_2	r^2
Shoot biomass								
100%†	2,3,4	1,2	5·25	3·01	−0·56	−0·45	−0·69	0·94***
100%	2,3	1,2	5·53	3·05	−0·62	−0·49	−0·77	0·95***
60%†	2,3,4	1,2,3	4·49	2·77	−0·43	−0·35	−0·51	0·95***
60%	2,3	1,2,3	4·69	2·81	−0·47	−0·41	−0·53	0·98***
30%†	—	1–5	3·10	2·42	−0·17	−0·08	−0·26	0·74*
Root biomass								
100%†	2,3,4	1,2	3·96	2·48	−0·37	−0·26	−0·49	0·89***
60%†	2,3,4	1,2,3	3·32	2·36	−0·24	−0·17	−0·32	0·88**
30%	—	1–5	(2·61)	(2·25)	(−0·09)	(0·01)	(−0·19)	0·38
Total biomass								
100%†	2,3,4	1,2	5·13	3·13	−0·50	−0·42	−0·59	0·96***
60%†	2,3,4	1,2,3	4·40	2·92	−0·37	−0·31	−0·44	0·95***
30%†	—	1–5	3·23	2·67	−0·14	−0·06	−0·23	0·70***

* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.

TABLE 2. Allometric relationships ($\log y = b + m \log x$; b = intercept, m = slope) between shoot biomass (w_s), mean plant height (h), radial extension of the canopy (e) and index of canopy volume plant^{-1} (v') in *Ocimum basilicum* populations grown at low or high density and 100%, 60% or 30% nutrient level. Lines are shown in Fig. 3. Intercepts or slopes within each equation followed by the same superscript letter are not significantly different at $P = 0·05$.

Treatment	Intercept	Slope	r^2
$\log h = b + m \log w_s$			
100% (both densities) + 60% (high density) + 30% (high density)	0·35[a]	0·50[a]	0·99
60% (low density)	0·18[b]	0·57[a]	0·99
30% (low density)	−0·11	0·81[b]	0·96
$\log e = b + m \log w_s$			
100% (both densities)	0·06[a]	0·21[a]	0·90
60% (both densities)	0·004[b]	0·20[a]	0·96
30% (low density)	—	—	N.S.
30% (high density)	—	—	N.S.
$\log e = b + m \log h$			
100% (both densities)	−0·09	0·43	0·94
60% (low density)	−0·04	0·27	0·98
30% (low density)	—	—	N.S.
30% (high density)	−0·29	0·52	0·96
$\log w_s = b + m \log v'$			
100% (both densities)	−0·85[a]	1·02[a]	0·90
60% (both densities)	−0·86[a]	1·08[a]	0·95
30% (both densities)	−0·68[a]	1·03[a]	0·91

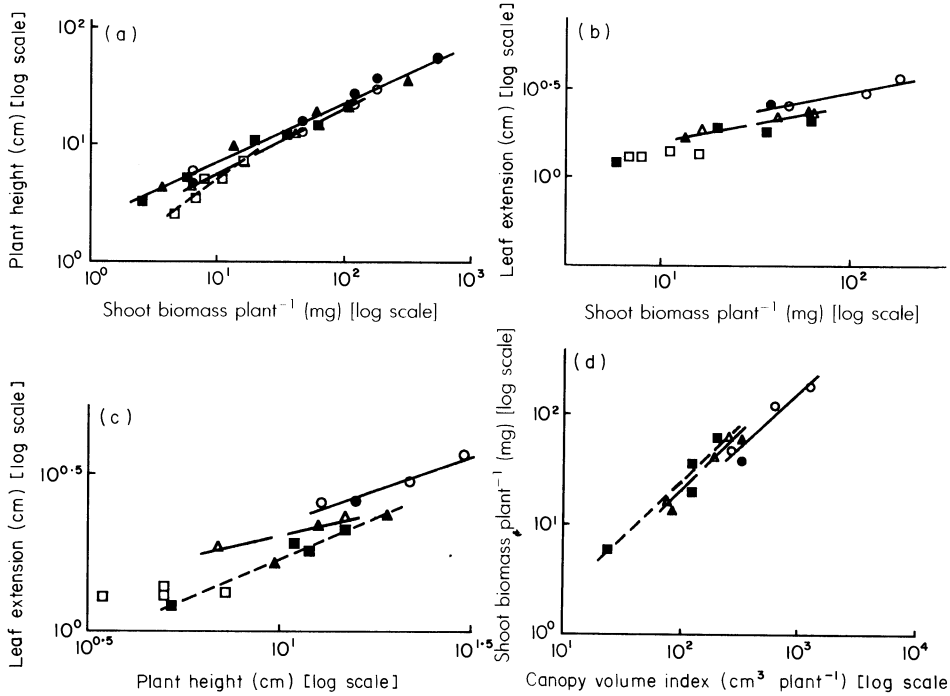

FIG. 3. Allometric relationships in *Ocimum basilicum* between (a) mean plant height and mean shoot biomass, (b) mean leaf extension and mean shoot biomass, (c) mean leaf extension and mean height and (d) mean shoot biomass and mean index of canopy volume plant^{-1}. Points and lines shown are (a) 100% nutrient level at both densities (○, ●) and high-density 60% (▲) and 30% (■) nutrient levels (——), low-density 60% (—△—) and 30% (——□——) nutrient levels; (b) 100% nutrient level at both densities (○———●), 60% nutrient level at both densities (△——▲), 30% nutrient level at low (□) and high (■) densities; (c) 100% nutrient level at both densities (○———●), 60% nutrient level at low (—△—) and high (▲) densities, 30% nutrient level at low (□) and high (——□——) densities; (d) 100% nutrient level at both densities (○———●), 60% nutrient level at both densities (△——▲), 30% nutrient level at high density (——■——). Equations for lines are given in Table 2.

lines, which were pooled. Plants in the low-density treatments at the two lower nutrient levels were shorter for a given shoot biomass than plants in the remaining treatments which were fitted by a common line (Fig. 3a).

Plants from the lower nutrient treatments also tended to have less leaf extension for given shoot biomass (Fig. 3b, Table 2). The regression was not significant in either sown density of the 30% nutrient stands, as they both showed little change in leaf extension as the plants grew. The lines for the 100% and 60% nutrient treatments differed significantly in intercept ($F_{1,5} = 22{\cdot}3$, $P < 0{\cdot}05$), with the line for the 60% level being the lower (Fig. 3b).

Canopy shape (as a function of height–leaf-extension allometry) changed with nutrient level (Fig. 3c, Table 2). At the 30% nutrient level, however, the plants in the low-density populations did not show a significant leaf-extension–height relationship (Fig. 3c, Table 2) due to little change in leaf extension. Lines for the 100% nutrient level, and low-density populations from the 60% and the 30% levels were not compared because of small sample sizes. Plants at lower nutrient

levels were more compact in shape, showing less leaf extension for a given height (Fig. 3c, Table 2).

Thus, among the populations used to construct self-thinning lines, those in the lower nutrient treatments fitted more shoot biomass into a given canopy volume of each plant (calculated as the index v') (Fig. 3d, Table 2). The small number of points and their scatter meant that there was not a significant difference between the lines for each nutrient treatment. The slopes of the three lines were all close to 1·0, indicating an approximately constant packing of biomass into canopy volume plant^{-1} (calculated on a per-plant basis). The ranking of the lines was such that at a common point of overlap ($v' = 316\,cm^3$ plant^{-1}) the shoot biomass distributed in this canopy 'volume' was 49 mg at the 100% nutrient level, 68 mg at 60% and 80 mg at the 30% level.

Biomass packing into canopy space

Biomass packing into canopy space (calculated as B/V, see Methods) ranged between 1·5 and 4 kg m^{-3}, generally decreasing with time, as canopy height continued to increase while biomass values were more static. The relationship between log V (canopy volume) and log N was plotted using the same stands as were used for biomass–density thinning lines (Fig. 4, Table 3). The $V-N$ thinning lines of the 100% and 60% nutrient treatments were slightly closer (0·14–0·19 log units) than their shoot biomass–density thinning lines (0·15–0·25 log units). The same was true of the 100% and 30%, and the 60% and 30% treatments. In this case, the B/V values for the 100% nutrient populations were generally higher than those in the 60% and 30% treatments used to calculate the thinning lines at comparable thinning densities. This indicates that there is less biomass packed into canopy space (calculated as B/V) at the lower nutrient levels.

Root density and specific root length

Root densities ranged between 40 and 100 cm cm^{-3} in the surface zone, and were generally 10–40 cm cm^{-3} in the subsurface zone. The proportion of root length located at a soil depth of 0–2 cm (*c.* 16% of soil volume) was generally 40–50%

TABLE 3. Parameter values of the volume thinning lines for populations of *Ocimum basilicum* sown at low and high densities and grown at 100%, 60% or 30% nutrient levels over five harvests (1–5). Equation is $\log V = \log K - \beta \log N$, where V is canopy volume (g m^{-3}), N is density (m^{-2}), $\log K$ is the intercept (at 10^0 and 10^4 plants m^{-2}) and β is the slope. L_1, L_2 are limits of the slope, and r^2 is explained variance. Lines are shown in Fig. 4.

Nutrient level	Harvest: low density	Harvest: high density	K: 10^0	K: 10^4	β	L_1	L_2	r^2
100%	2,3,4	1,2	1·99	−0·48	−0·62	−0·58	−0·65	0·99***
60%	2,3,4	1,2,3	1·69	−0·67	−0·59	−0·27	−1·00	0·96***
30%		1–5	1·72	−0·80	−0·63	−0·58	−0·68	0·99***

*** $P < 0·001$.

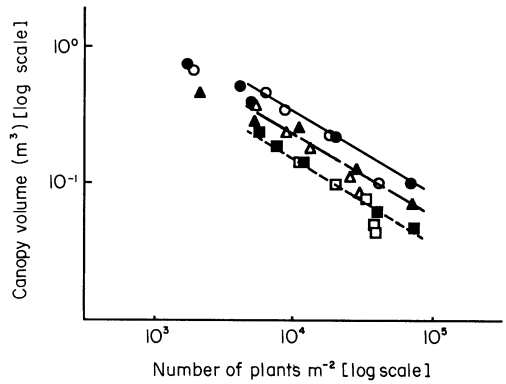

FIG. 4. The relationship between mean density and mean canopy volume in *Ocimum basilicum* sown at low density (open symbols) and high density (solid symbols) and grown at nutrient levels of 100% (○), 60% (△) and 30% (□). Thinning lines for nutrient levels 100% (both densities) (———), 60% (both densities) (— —) and 30% (high density) (— — —) are shown. Equations for thinning lines are given in Table 3.

during the experiment. There was no significant difference between nutrient treatments in the proportion of root length located in the surface zone.

Root length per unit root biomass (specific root length) did not vary significantly with nutrient level in the surface zone; in the subsurface zone, a significant nutrient–harvest effect was detected ($F_{8,100} = 2{\cdot}86$, $P < 0{\cdot}01$), with the 30% nutrient level significantly higher than higher nutrient treatments at the final harvest only.

Shoot:root ratios

The level of nutrient supply affected the allometry between root biomass and shoot biomass: at lower nutrient levels, plants had relatively more root (Fig. 5a). There was a significant effect of nutrient supply on the slopes of the allometric relation for each of the six treatments ($F_{5,18} = 4{\cdot}03$, $P < 0{\cdot}05$). This was due to the low-density 30% nutrient treatment, with its lower slope (Fig. 5a). The remaining lines differed in intercept ($F_{4,20} = 9{\cdot}8$, $P < 0{\cdot}001$). The high-density 30% nutrient treatment was significantly lower in intercept than the line for the 60% nutrient level (densities pooled), which in turn was significantly lower than that for the 100% level (densities pooled) (Fig. 5a, Table 4).

The leaf area supported by a given root length fell as nutrient level declined. There was, however, no significant rise in leaf area as root length increased in the low-density 30% nutrient treatment (Fig. 5b, Table 4). Leaf-area–root-length regressions for the remaining treatments differed significantly in intercept ($F_{4,20} = 9{\cdot}63$, $P < 0{\cdot}001$) with one line for the high-density 30% nutrient treatment, and a single line for each of the 100% and 60% nutrient levels (Fig. 5b, Table 4).

The shoot-biomass–root-length relationship was significantly affected by a nutrient-level–harvest interaction ($F_{8,84} = 3{\cdot}26$, $P < 0{\cdot}01$) and density ($F_{1,84} = 9{\cdot}87$, $P < 0{\cdot}001$) (Fig. 5c). The high-density stands supported more shoot biomass per unit root length than the low-density stands. The shoot biomass per unit root length declined with nutrient level from harvest 2 onwards; by harvest 3 the 30% nutrient treatment was

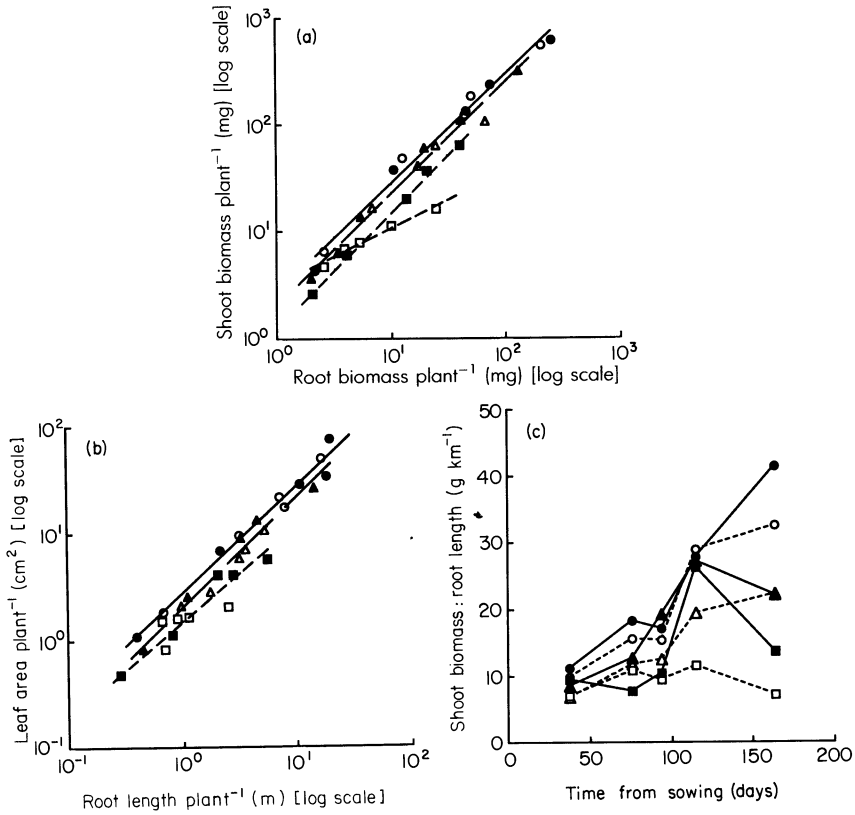

FIG. 5. Relationship between (a) mean shoot biomass and mean root biomass, (b) mean leaf area plant^{-1} and mean root length plant^{-1} and (c) mean shoot-biomass:root-length ratio and time (harvests 1–5) in *Ocimum basilicum* sown at low density (open symbols) or high density (closed symbols) and grown at nutrient levels of 100% (○), 60% (△) or 30% (□). Lines shown are (a) 100% nutrient level at both densities (○———●), 60% nutrient level at both densities (△——▲), 30% nutrient level at low (———□———) and high (———■———) densities; (b) 100% nutrient level at both densities (○———●), 60% nutrient level at both densities (△——▲), 30% nutrient level at low (□) and high (———■———) densities. Equations for lines are given in Table 4.

significantly below the higher-level treatments, and by harvest 5 the order of nutrient treatments was 100% > 60% > 30% (Fig. 5c).

Root width, root hairs

The mean diameters both of lateral roots (range 0·24–0·29 mm) and of root hairs (range 10–12·5 μm) were comparatively stable over nutrient treatments. Significant nutrient effects were detected for the proportion of root length bearing hairs ($F_{2,60} = 4{\cdot}38$, $P < 0{\cdot}05$), and root hair length ($F_{2,90} = 14{\cdot}25$, $P < 0{\cdot}001$; 100% nutrient level >60% + 30% in both cases). Root hair length averaged 0·244 mm at the 100% nutrient level, and 0·166 mm at the 60% and 30% levels. Root-hair numbers along the length of root where root hairs were found declined significantly with soil depth ($F_{1,87} = 8{\cdot}75$, $P < 0{\cdot}01$).

TABLE 4. Allometric relationships (log $y = b + m \log x$; b = intercept, m = slope) between mean shoot biomass (w_s) and mean root biomass (w_r), and mean leaf area plant^{-1} (a) and mean root length plant^{-1} (l) in *Ocimum basilicum* populations grown at low or high density and 100%, 60% or 30% nutrient levels. Lines are shown in Fig. 5. Intercepts or slopes within each equation followed by the same superscript letter are not significantly different at $P = 0{\cdot}05$; r^2 = explained variance.

Treatment		Intercept	Slope	r^2
log $w_s = b + m$ log w_r				
100%	(both densities)	$0{\cdot}43^a$	$1{\cdot}02^a$	0·99
60%	(both densities)	$0{\cdot}32^b$	$1{\cdot}03^a$	0·98
30%	(low density)	0·49	$0{\cdot}53^b$	0·97
30%	(high density)	$0{\cdot}10^c$	$1{\cdot}07^a$	0·99
log $a = b + m$ log l				
100%	(both densities)	$0{\cdot}44^a$	$0{\cdot}98^a$	0·98
60%	(both densities)	$0{\cdot}31^b$	$1{\cdot}01^a$	0·96
30%	(low density)	—	—	N.S.
30%	(high density)	$0{\cdot}17^c$	$0{\cdot}89^a$	0·96

Mineral content of seed

Levels of nitrogen, phophorus and potassium in the seeds of *O. basilicum* were significant as a source of nutrients in some populations, particularly that of nitrogen in the 30% nutrient, high-density populations (Table 5).

Edge effect

Tests for edge effects in the 100% nutrient, high-density treatments at two harvests showed that, at the third harvest, the mean shoot biomass of plants in the central quadrat and in the inner border did not differ significantly ($F_{1,83} = 1{\cdot}731$, $P > 0{\cdot}05$).

TABLE 5. N, P and K mineral contents of seeds of *Ocimum basilicum* (mg g^{-1} dry wt), applied amounts of N, P and K over whole experimental period and seed N, P and K levels as a percentage of applied nutrients.

Nutrient level	Applied nutrient (mg)	Nutrient content of seeds (mg g^{-1})	Nutrient content of seeds (% applied) low density	Nutrient content of seeds (% applied) high density
Nitrogen				
30%	379·5	38·1	22·8	72·9
60%	759·0		11·4	36·5
100%	1265·1		6·8	21·9
Phosphorus				
30%	122·0	6·1	11·0	36·0
60%	244·1		5·6	18·0
100%	406·8		3·4	10·9
Potassium				
30%	351·5	8·4	5·4	17·4
60%	703·0		2·7	8·7
100%	1171·7		1·6	5·2

Plants in the outer border had a significantly lower mean shoot biomass than those in the inner border, or central quadrat (mean ln shoot biomass: outer border, 3·38 mg; inner border, 4·20 mg; central quadrat, 4·49 mg; $F_{8,24} = 4{\cdot}11$, $P < 0{\cdot}005$). At harvest 5, there was no significant effect of position in the pot on the mean shoot biomass ($F_{1,101} = 1{\cdot}948$, $P > 0{\cdot}05$). It was therefore concluded that the region left for a border, in combination with the shading cloth used around each pot, was sufficient to absorb any edge effect on plant growth.

DISCUSSION

Self-thinning and the intensity of competition

The evidence from the *Ocimum* populations points to a lowering of the thinning line as nutrient level is reduced, confirming the findings of Furnas (1981) and Morris & Myerscough (1985). More data points would be required to delineate conclusively the regions of non-thinning with biomass increases, thinning with biomass increases, and thinning with static biomass described in the Introduction. The main finding is clear, however, irrespective of the exact choice of points to calculate thinning lines (Fig. 2, Table 1). In other cases, populations at lower levels of nutrient supply followed substantially the same line (White & Harper 1970; Bazzaz & Harper 1974).

The intensity of competition in the *Ocimum* stands varied with the level of nutrient supply. At each harvest, the greatest mortality was observed in the high-nutrient populations of *Ocimum*, so in this sense competition was most intense in the resource-rich populations (Grime 1979). However, the populations grown at lower nutrient levels were not merely subject to a slowed-down version of the same competitive process found at the nutrient-rich level, they were subject to more-intense competition at a given mass. More plants died in the lower-nutrient stands to achieve a given biomass, and conversely the survivors required greater ground area per individual to support that biomass (Fig. 2). This is true for shoot biomass and total biomass (although less so for root biomass.) In this sense, therefore, the plants grown at low nutrient levels appeared to forage further afield to capture given resources, and in so doing have encountered and competed with their neighbours to a greater extent than plants in high-nutrient populations (Newman 1973; Grubb 1985; Tilman 1987). However, this intensified competitive process has developed at a slower rate than that in the resource-rich stands.

As resource levels decline, competition may be (i) slowed down without being intensified (on a mass basis) or (ii) intensified. This intensified competition may develop faster than, at the same rate as, or slower than the competitive process occurring in the stands at higher resource levels.

How is competition intensified?

Competition between plants involves the acquisition of resources by one plant and the denial of those resources to a neighbour. A precondition for this to occur is that the zones of resource uptake of the plants must overlap. At lower resource levels the extent of this overlap in combination with the rate of development of such overlap may determine whether competition is intensified or not. What is critical is the degree of overlap of zones of uptake in order to achieve given mass. Greater overlap

to achieve given mass at lower resource levels would intensify competition compared to controls (described as 'altered-form competition' by Morris & Myerscough 1984). If the degree of overlap of zones of uptake is essentially the same at a given plant mass (irrespective of resource level), competition may occur more slowly in lower-resource stands, but develop in the same way in all stands (termed 'altered-speed competition' by Morris & Myerscough 1984).

Whether intensification or slowing down of competition is occurring can be tested by examining the degree of overlap of zones of resource depletion of competing plants. Overlap of resource depletion may occur in the rooting medium or in the canopy of stands.

Depletion of aerial resources will depend on the leaf area borne by plants, and how this leaf area is arranged in a canopy. In *Ocimum*, both were affected by nutrient supply. At the lower nutrient levels, plants had less radial extension of the canopy for a given height (Fig. 3c); moreover, they carried less leaf area within those canopies (Fig. 5b). It can be argued from these changes (in conjunction with the plant spacing that developed) that the individual canopy volumes of plants overlapped less at low than at high nutrient levels.

These changes to canopy shape also have implications for the thinning lines that the stands should traverse, if canopy interactions determine self-thinning. If a canopy of given mass becomes relatively taller as the height:canopy-width ratio increases, more plants should fit into unit area, and the thinning line should rise (Givnish 1986; Hardwick 1987; Norberg 1988). In *Ocimum* the ratio of height to radial extension of the canopy would be higher in the populations grown at lower nutrient levels. This was most apparent in plants grown at the 30% nutrient level and sown at the lower density; they showed very little change in leaf extension over the course of the experiment, even though they self-thinned. Effectively they grew as cylindrical plants. (Ellison (1984) noted that *Salicornia europea* plants growing at densities above $10\,000\,m^{-2}$ grew effectively as cylinders, and showed no self-thinning.) Whether or not changes in canopy shape lead to a shift in thinning lines, however, depends on how much biomass is packed into that canopy shape (biomass–packing relationship).

The measurement of biomass packing as calculated by Lonsdale & Watkinson (1983) is based on the population-level measurements of canopy height and biomass per unit area (B/V ratio). The B/V measurements for *Ocimum* showed that differences in this ratio did contribute slightly to the differences in biomass–density thinning lines in the same way observed for the shaded *Helianthus* populations of Hiroi & Monsi (1966) (analysed by Lonsdale & Watkinson (1983)). The $V-N$ thinning lines were somewhat closer than the $B-N$ lines, and this can be attributed to more biomass being packed into given canopy volume in the populations grown at full nutrients than those grown at lower nutrient levels, at comparable thinning densities.

However, the concept of biomass-packing can also be approached at the level of the individual plant. On the assumption that the volumes occupied by the individual plants in the canopy can be represented by cylinders (defined by the mean height and radial extension of the plant (Weller 1987b)), it was shown that the plants grown at lower nutrient levels carry more biomass in unit canopy 'volume' (Fig. 3d). (The assumption of cylindrical shape was most valid at the lower nutrient levels. At higher nutrient levels, the canopy typically showed tapering towards the top and bottom. Measurement of e at randomly selected nodes on the stem (as performed here) would average out this taper. Thus v' would approximate v (true canopy volume)

in this case.) This is the opposite of what population-based measures of biomass-packing indicate. Moreover, plants that pack more biomass into a given canopy volume at a given thinning density should have a higher thinning line than those that do not (Lonsdale & Watkinson 1983).

Thus canopy shape, overlap of canopy volume and biomass-packing in the canopy volume of individual plants changed with nutrient level. If canopy interactions were driving self-thinning (i.e. canopy overlap had been the same in all self-thinning stands), a higher thinning line would be expected in the lower-nutrient populations. The reverse was observed; indeed the wide spacing between plants in the low-nutrient treatments led to lower B/V values in these stands than in high-nutrient stands at given densities, despite the individual biomass of each plant being fitted into a smaller canopy volume. This suggests that something other than canopy packing was determining plant spacing in the nutrient-poor stands; it seems that the major interactions between plants in these stands were not above ground.

In the rooting medium, Nye & Tinker (1977) list two options for plants in crowded populations to increase their uptake of mineral nutrients: (i) Make more root and explore a greater volume of soil. This would be likely if soil diffusion of nutrients was limiting uptake, e.g. on a nutrient-poor soil. (ii) Increase the absorbing power of the root, for example by increasing physiological uptake, increasing root radius (mainly for mobile nutrients at higher concentrations), increasing the proportion of root along which uptake occurs, altering the number, size or shape of root hairs, utilizing mycorrhizal or bacterial effects or expanding the effective concentration of nutrients exploited (exudation of chelating agents or other root exudates.)

Option (ii) can be examined to a certain extent in the *Ocimum* experiment. No mycorrhizal fungi were found on the plants. No tests were made to detect chelating agents, exuded substances, or increased physiological uptake. As nutrient level declined, root hairs occupied a smaller proportion of lateral root length, and were shorter, than on the plants grown at full nutrients. This, if anything, is a shift in the opposite direction to that required by option (ii).

This leaves option (i), the making of more root and exploration of more soil. This option by itself may or may not lead to increased overlap of depletion zones and so intensified competition, depending on the architecture of the root system, and what extra soil volume is explored. Placement of the extra root in a soil volume already occupied by the plant itself, or in soil unoccupied by other plants, would not lead to increased overlap with neighbours. Thus competition would not be intensified. Placement of the extra root in soil already occupied by a neighbour's roots could intensify competition, however.

There is evidence that plants in the lower-nutrient regimes were making relatively more root weight than the stands grown at higher-nutrient levels (Fig. 5a). The same shift to relatively more root growth was seen in *Trifolium* (Morris & Myerscough 1985). (This extra root biomass was absent in the 'altered-speed' cases at different nutrient levels examined by Morris & Myerscough (1985)). This extra weight was equivalent to extra length, as the root-length–root-biomass relationship remained largely unaffected by nutrient level. Nutrient uptake is a function more of root length than root biomass, however. The length of root required to support given leaf area and shoot yield increased as nutrient level fell (Fig. 5).

Just under half of the root length was consistently found in the surface root zone, representing 16% of soil volume, at all nutrient levels. The rooting densities achieved

were very high, being comparable with the highest values recorded under grass swards (Barber 1984). The inter-root distances in such a dense root mat mean that the potential for overlap of zones of depletion for mobile ions such as nitrate is very high; for relatively immobile ions like phosphate, potential overlap is probably much less (Fusseder & Kraus 1986; Caldwell 1988; Beck, Fusseder & Kraus 1989). Although this is not direct evidence that there was increased overlap of depletion zones by plants in order to achieve a certain plant biomass, it is evidence that the conditions necessary for this to occur have been met.

Thus we would predict that the following of either different lines or a common line by populations grown over a range of nutrient supply could be explained in terms of the overlap of nutrient-depletion zones between neighbours to achieve a given plant mass. However, other explanations must be considered. There is a consistent difference between the two patterns of thinning observed over a range of nutrient levels: a soil–peat–sand growth medium was used in the cases where a common line was followed, and sand or perlite media in cases where different lines were observed. Different species have been used in each case. Differences could be due to differences in the thinning patterns shown by the species used, or differences in the supply of nutrients by the different media and rooting patterns of plants on the media. Comparison of thinning in the one species grown on both media is needed, as well as study of the supply of nutrients to plants and rooting patterns of plants on both media. This would discriminate between alternative explanations for the different patterns of thinning observed over a range of nutrient levels.

Mineral reserves and populations at low nutrient levels

The divergence in the biomass–density paths followed by the populations at the 30% nutrient level and sown at low or high density was most apparent for shoot and root biomass (Fig. 2). A similar divergence between low- and high-density populations at low nutrient levels has appeared in earlier experiments (Morris & Myerscough 1985), where it was suggested that the mineral reserves contained in the initial seed capital might represent a substantial part of the total nutrient supply of the high-density populations during the experiment, effectively putting these stands at a higher nutrient level. Analysis of the seed mineral content for the major macronutrients confirms that in *O. basilicum*, the population sown at the higher density and grown at the 30% nutrient level did receive an input of minerals in the seed capital that represented a substantial proportion of the total nutrients supplied in solution (Table 5). Because these populations self-thinned from the first harvest onwards, recycling of the nutrients from dead individuals to the survivors could have kept a large part of the seed capital in the pot system. This would lead to the high-density population being at a higher nutrient level than the low-density population at the same nominal nutrient level, and would account for the different thinning paths seen in the two treatments.

Nutrients and individual plant growth

The precise mechanism by which increased overlap of nutrient depletion zones occurs does not matter in one sense: it is the effect of the nutrient shortage so induced that does matter. The discussion so far has been in terms of the mean

plant response; but it is at the level of the individual plant that competitive effects occur. Some recent models of plant growth (Hirose 1987, 1988) have addressed the linkage between low nutrient levels, absorption of nutrients, root–shoot division and RGR. The models and experimental evidence suggest a negative feedback of nutrient shortage on overall growth, coupled with a shift in root:shoot ratio; this negative feedback becomes relatively more intense as nutrient level falls. The *Ocimum* data are in qualitative agreement with these models.

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