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CORRELATED CHANGES IN PLANT SIZE AND NUMBER IN PLANT POPULATIONS

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INTRODUCTION

The capacity of plants to react to the competitive stress of their neighbours by means of phenotypic plasticity has been shown in a large number of experimental investigations. However, the commonest fate of plants under natural conditions is to die before reaching reproductive maturity; this is a basic tenet of Darwinian natural selection theory, but one which has not received much attention, beyond the casual observation that not all seedlings survive to reproduce themselves. Harper & McNaughton (1962) showed that the number of mature plants of *Papaver* species, sown in pure and mixed populations, becomes independent of the number sown above a certain density. The capacity of plants to absorb density stresses may, on the other hand, be very high, so that while *Papaver* species seemed to have a limit of about 1000 plants/m², *Agrostemma githago* has been found to suffer no density dependent mortality at densities as high as 2300 plants/m² (Harper & Gajic 1961). *Agrostemma* absorbs the density response in individual plasticity to a greater extent than *Papaver*. Sukatchew (1928), one of the first to study the thinning phenomenon experimentally, found that *Matricaria inodora*, sown at two densities on fertilized and unfertilized soils, suffered mortality; this mortality was greatest at the higher density and in the fertilized soil. Several passing references are made by various authors to mortality in experimental plots, but the first formal analysis of the thinning process appeared in a series of examples cited by Yoda *et al.* (1963). They examined thinning in overcrowded pure populations of several species on soils of varying fertility and found that the number of surviving plants could be related to their mean weight as $w = C.p^{-3/2}$, where p is the density of surviving plants and w their corresponding mean weight; the value of C varies with the species. The gradient of the line relating p to w remains constant with time while thinning proceeds. They concluded from observations made under natural and cultivated conditions that 'whatever the factors responsible for plant size may be, age, edaphic or other habitat conditions, the possible maximum density for plants of a given average size w , brought about by self-thinning, is expected to be equal to $(C/w)^{2/3}$. If the age of stands were uniform, stands on soils of different fertilities would be arranged along the line having the gradient value of $-3/2$ on \log/\log co-ordinates, those on the more fertile soil exhibiting lower plant density and larger plant size.'

In this paper the above generalization is extended to several other species, using data derived from experiments under cultivated conditions and from forestry management tables. Firstly an experiment specifically designed to observe thinning is reported in some detail. This is followed by analyses of data from other published studies which contain sufficient relevant information to construct the necessary density/mean dry weight graphs. As a preliminary example the archetype of these experimental studies is shown

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in Fig. 1 for *Erigeron canadensis*, a pure population of which declined from 122 400 to 1060 plants/m² in 9 months. A fitted regression line for all points except those of the first harvest has a slope of -1.66 .*

MATERIALS AND METHODS

Raphanus sativus L. (radish) and *Brassica napus* L. (rape), commercial cultivars giving rapid and even germination, were grown in pure populations and mixtures on soils of different fertilities. Plastic pots of 20 cm diameter were filled to within 2 cm of the top

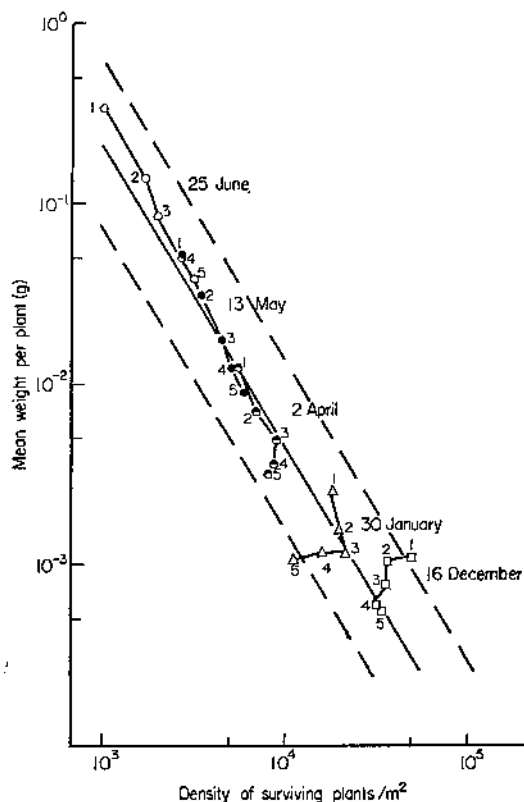


FIG. 1. Changes in numbers and individual plant weight of *Erigeron canadensis* with time; observations taken on an abandoned field at Osaka, Japan. The field contained a steep fertility gradient and the plot numbers 1-5 represent an order of decreasing fertility which was exaggerated by the addition of N-P-K-Mg fertilizer in the ratio 5:4:3:2:1 on the plot numbers 1-5. Seed of *E. canadensis* was distributed evenly over the ground, 1.2×10^5 seeds/m². Redrawn with calculated regressions from data of Yoda *et al.* (1963). Dashed lines denote confidence limits ($P = 0.05$) (first harvest, November 7, omitted).

with John Innes Compost (7:3:2, loam:peat:sand by volume). Three fertility levels were established, J.I. No. 3 (most fertile), J.I. No. 1 and J.I. and lime but without additional fertilizer (least fertile). Seeds (passed through sieves to ensure uniformity of size) were sown randomly, on the levelled soil surface in each pot and covered with 0.5 cm

* This is less than 3° greater than the gradient of -1.5 drawn as an asymptotic line in Yoda's figure. It may be noted, for subsequent comparisons, that lines 5° on either side of the -1.5 gradient have values of -1.25 and -1.83 .

of sand. Pure stands were sown with 180 seeds of each species; one of the mixtures contained 120 seeds of rape and sixty seeds of radish, the other sixty seeds of rape and 120 seeds of radish. After 2 weeks the number of established seedlings was counted; not all had germinated and the basic number per pot was reduced to 150 (equivalent to 4.8×10^3 seeds/m²). The mixtures were thereby slightly altered in composition to 66% rape/34% radish and 37% rape/63% radish.

The experimental design was a randomized block of four combinations of species at three fertility levels with three replicates at each of three harvests. Harvests were taken at 6½, 13 and 17 weeks after sowing. The plants remained in a vegetative condition throughout the growing period. Since the seeds had been sown randomly it was impossible to leave an outer edge of plants at each harvest, but the pots were closely packed and were re-randomized every fortnight.

At harvest the plants were washed to remove soil, cut into roots, leaves and petioles and dried in a forced air oven at 75° C for 3 days and weighed. There was little or no stem on either species that could be separately determined as the leaves remain radical until a flowering shoot emerges.

RESULTS

The relationship between the mean weight per plant and the surviving density (expressed as the mean of the three replicates for each harvest) is given in Fig. 2 on log/log co-ordinates. The calculated regression line is $\log w = 2.28 - 1.45 \log p$, or $w = 190 p^{-1.45}$, which shows a close similarity to the 3/2 power law of Yoda *et al.* Only two points, those for pure stands of rape and radish at the second harvest, appear to be anomalous. It is apparent that greater thinning occurred on the more fertile soils, a feature common to all treatments except the two mentioned above. At the first harvest there was a slight increase in the extent of thinning from radish alone, to the mixture with excess radish, to the mixture with excess rape and to rape alone: this was not apparent at later harvests. Rape and radish seem to have reacted to each other in mixture in much the same manner as they reacted to their own density in pure stands (their general growth habit is quite similar). As may be seen in Fig. 3, however, radish tends to suffer the greater mortality as does the mixture in which it is the major component. The time sequence of thinning shown in Fig. 3 indicates a rather constant death rate over the period of the experiment. In every case the populations on the most fertile soil have suffered the greatest thinning, as noted previously, although the rates of thinning are not greatly different on any soil. The self-thinning of rape and radish in pure stands at the lowest fertility level in the second harvest is unexpected (as noted in Fig. 2) and obscures the pattern in Fig. 3 (a and b).

The calculated regressions of log plant weight on log plant number are given in Table 1. Each combination of the two species has a regression equation which gives a coefficient of p within 3° of -1.5 . Most of the variance is accounted for by these equations and the additional variance included by a second degree polynomial is not significant in any instance. Radish in both mixtures has a lower exponent of p (-1.2) than rape. It may also be noted from Table 1 that whereas the values of C are of comparable order of magnitude for the various treatments involving rape and radish, they differ quite considerably from that obtained with *Erigeron canadensis* by Yoda *et al.*; the coefficients of p remain similar.

Not only does the relationship between the number of plants and mean weight per

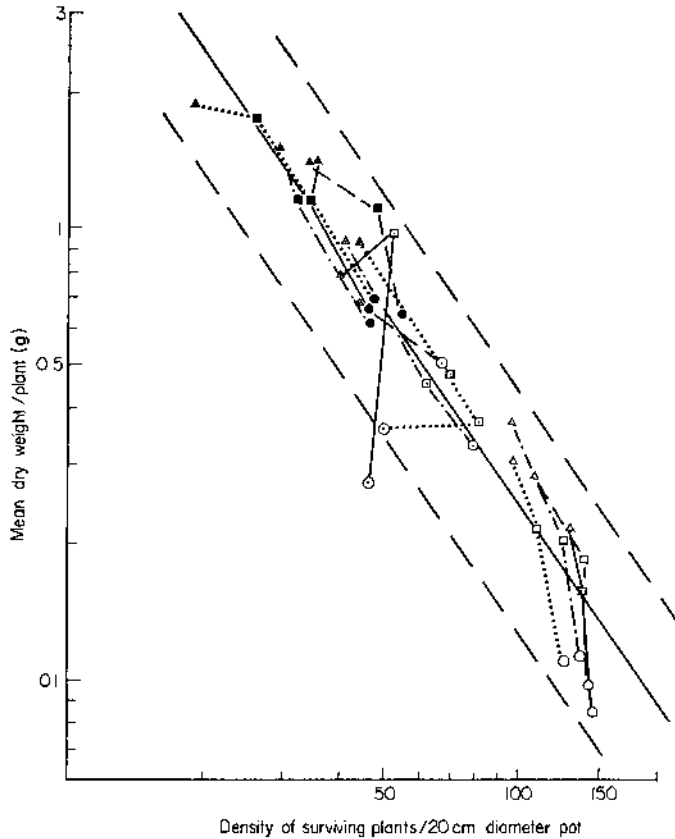


FIG. 2. Changes in numbers and individual plant weight with time of *Brassica napus* (—) and *Raphanus sativus* (.....) in pure stands and in mixtures; the mixtures consisted of 37% *Brassica*/63% *Raphanus* (- - -) and 66% *Brassica*/34% *Raphanus* (—) 2 weeks after sowing, before changes in numbers occurred. Three fertility levels (○, low; □, medium; △, high) were imposed on the populations. Harvests were taken at 6½ (○), 13 (◐) and 17 (●) weeks after sowing. Confidence limits are drawn at $P = 0.05$. Regression equations are given in Table 1.

Table 1. Relationship between mean weight per plant (w) and surviving plant density (p) for populations of rape and radish undergoing thinning, as shown in Fig. 2 (data of Yoda *et al.* (1963) on *Erigeron canadensis* are included for comparison)

Treatment	Regression	% of total variance accounted for by equation	Additional % variance accounted for by a second degree polynomial
All data (totals)	$\log w = 2.28 - 1.45 \log p$	88.7	0.5
All data (leaves, petioles and stems)	$\log w = 2.09 - 1.41 \log p$	88.6	0.3
All data (roots)	$\log w = 1.91 - 1.60 \log p$	83.0	1.3
Rape alone (totals)	$\log w = 2.19 - 1.43 \log p$	80.9	0.1
Radish alone (totals)	$\log w = 2.18 - 1.42 \log p$	90.7	0.7
37% rape/63% radish mixture (totals)	$\log w = 2.23 - 1.42 \log p$	94.8	0.1
Rape in this mixture	$\log w = 1.53 - 1.43 \log p$	74.9	0.1
Radish in this mixture	$\log w = 1.63 - 1.21 \log p$	90.9	0.7
66% rape/34% radish mixture (totals)	$\log w = 2.74 - 1.67 \log p$	94.4	0.6
Rape in this mixture	$\log w = 2.47 - 1.70 \log p$	89.0	0.2
Radish in this mixture	$\log w = 1.36 - 1.23 \log p$	70.8	6.0
Data of Yoda <i>et al.</i> excluding the initial harvest	$\log w = 6.99 - 1.66 \log p$	93.2	3.2

plant hold for whole plants, but it seems to be valid also for components of yield, as may be seen from the equations relating numbers of plants to mean weights per plant of leaves and petioles (and stems, which are underdeveloped), and of roots. The coefficients of p are within 2° of the -1.5 gradient obtained for whole plants.

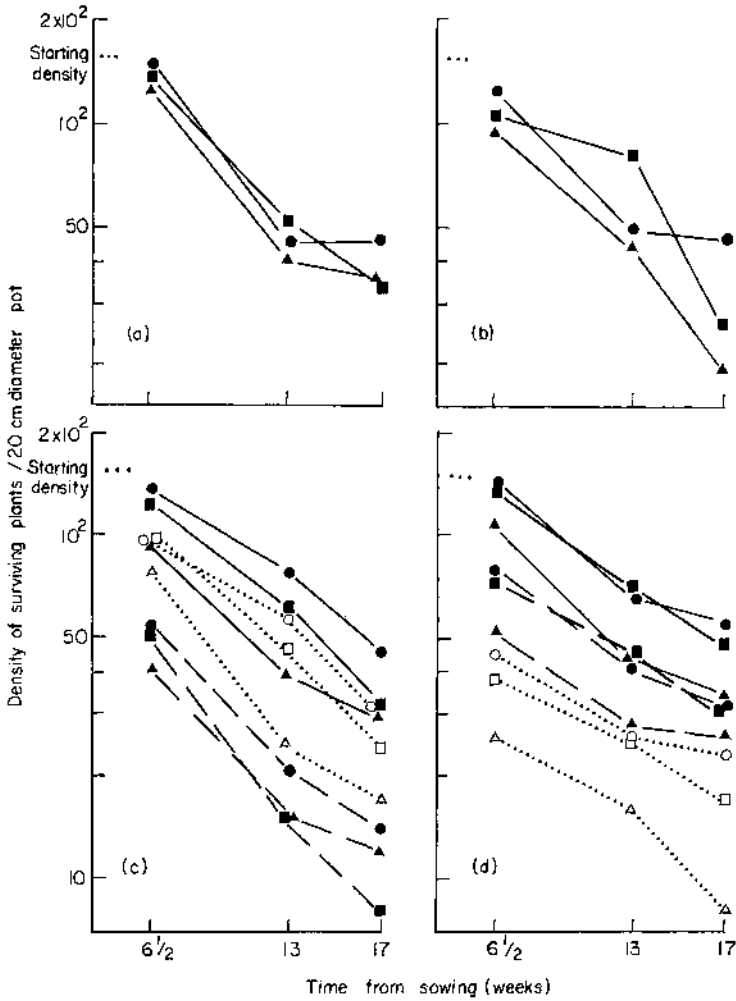


FIG. 3. Time trends of thinning for pure stands and mixtures of (a) *Brassica* and (b) *Raphanus* at three fertility levels, low (●), medium (■) and high (▲). (c) 37% *Brassica*/63% *Raphanus* and (d) 66% *Brassica*/34% *Raphanus* show the decline in total numbers (—) and of the component species of the mixtures, *Brassica* (---) *Raphanus* (.....).

EVIDENCE FROM PUBLISHED SOURCES

The conclusions reached in the above experiment are so closely parallel to those of Yoda *et al.* to prompt the suggestion that the $3/2$ power law has a more universal validity than hitherto generally realized. An examination of the literature on plant competition reveals that mortality is not uncommon in controlled experiments, in which for example the reactions of plants to varying density levels are being tested. In most cases, unfortunately, these observations are casual and do not include sufficient data for deriving a

relationship such as described in the previous section. Three examples which permitted further analysis are given below.

Hiroi & Monsi (1966) grew *Helianthus annuus* at varying densities and light intensities and recorded the mortality and total dry weight of surviving plants at successive harvests. In an experiment conducted in 1962, *Helianthus* communities were grown at 100, 60 and

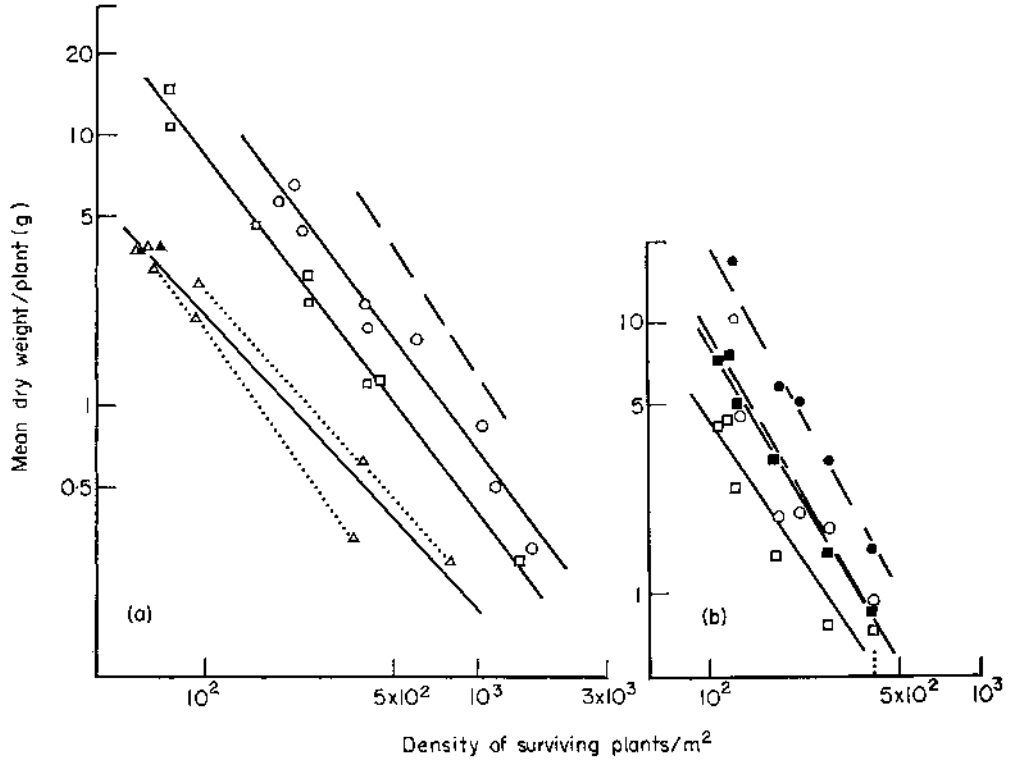


FIG. 4. Changes in numbers and individual plant weight of *Helianthus annuus* communities with time. The communities were grown at 100% (○), 60% (□) and 23% (Δ) light intensity at densities of 1600, 400 and 100 plants/m². (a) Shows the changes in numbers and plant weight over 10 weeks; plant weight includes dead and shed material, the only data given. The larger open symbols refer to a starting density of 1600 plants/m², the smaller to 400 plants/m². Thinning was also observed at 100 plants/m² at the lowest light intensity (▲). The broken line on the right of (a) shows a gradient of -1.5 for comparison. (b) Gives data for a separate experiment with observations taken over 8 weeks at a starting density of 400 plants/m². Data are given for plant dry weight which excludes (open symbols) and includes (closed symbols) dead material at 100% (●, ○) and 60% (■, □) light intensity. Regression equations are given in Table 2. Data recalculated from Figs. 1 and 5 and from Table 2 of Hiroi & Monsi (1966).

23% L.I. at densities of 1600, 400 and 100 plants/m² and at similar light intensities and densities of 400 and 100 plants/m² in another experiment the following year. The observations were made over a growing period of 10 weeks.

The relevant data are shown after recalculation in Fig. 4 (a and b). The regression equations given in Table 2 indicate that with one exception the slopes of the lines are close to -1.5. It may be of significance that the gradients are in every case slightly less steep at the lower light intensities falling to -1.08 at 23% L.I. In the second experiment the data for the treatment at 60% L.I. which exclude dead and shed material are better

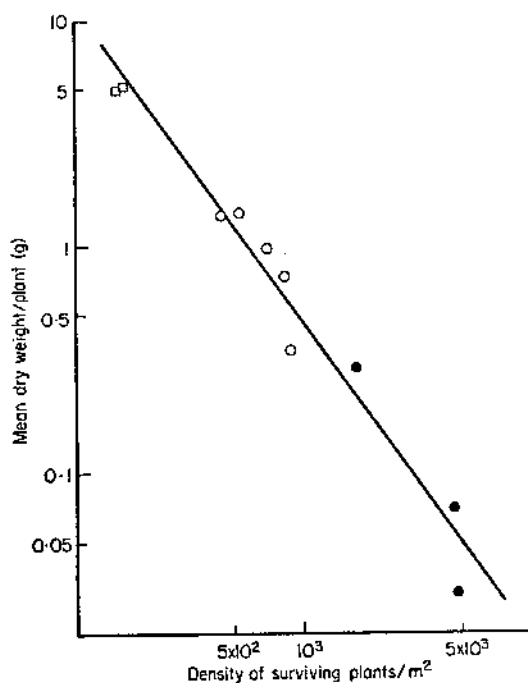


FIG. 5. Changes in numbers and individual plant weight of wheat undergoing self-thinning with time. Initial starting densities were approx. 5400 (●), 1078 (○) and 184 (□) plants/m². Thinning begins earlier in the stands of higher density. Regression equation is given in Table 2. Data of Puckridge & Donald (1967), and some supplied by Dr Puckridge.

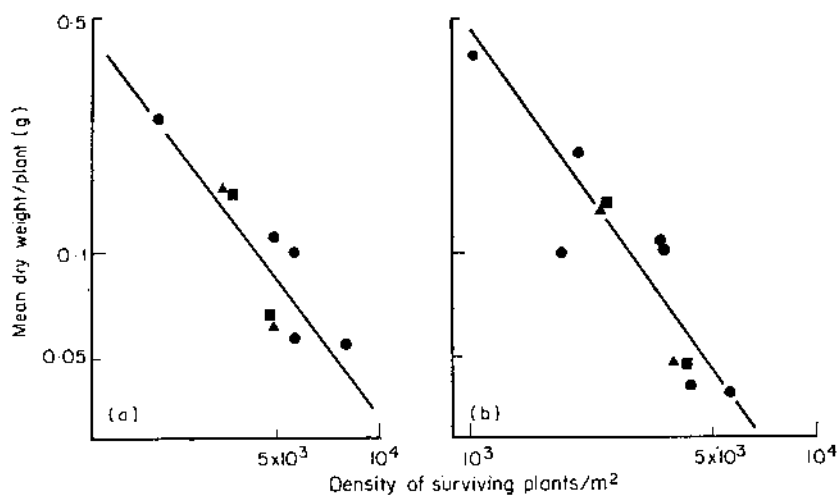


FIG. 6. Changes in numbers and individual plant weight of (a) *Trifolium pratense* and (b) *Medicago sativa* over 8 weeks, in pure stands (●) and in mixtures with an excess of the one species over the other (■ 6250/50; ▲ 6250/250). Mixtures were regarded as almost pure stands, to provide sufficient data, since there were only two harvests taken 2½ weeks apart. Regression equations are given in Table 2. Data recalculated from Tables 1 and 2 of Black (1960).

fitted by a second degree polynomial, $\log w = 24.6 - 19.7 \log p + 3.9 \log p^2$. A third degree polynomial reduces the total variance only by a further 0.4% and is not significant.

The second example is derived from data of Puckridge & Donald (1967), who studied the growth of wheat plants at a range of sowing densities from 1.4 to approximately 5400 plants/m². At the two highest densities mortality occurred, reducing the numbers from 1078 to 447 in 26 weeks in the one treatment, and from 5400 (approximately) to 1766 in 14 weeks in the other (after which it was abandoned). At a lower density (184 plants/m²) some mortality had occurred by 20 weeks and by 26 weeks the density had fallen to 154/m². The data and calculated regression are shown in Fig. 5. The regression

Table 2. Relationship between mean weight per plant (w) and surviving plant density (p) for populations undergoing thinning (the data for *Helianthus annuus* have been recalculated from Hiroi & Monsi (1966), those for wheat from Puckridge & Donald (1967) and for *Trifolium pratense* and *Medicago sativa* from Black (1960))

	Regression	% of total variance accounted for by equation	Additional % variance accounted for by a second degree polynomial
<i>Helianthus annuus</i>			
Experiment I			
100% light intensity	$\log w = 3.84 - 1.33 \log p$	96.8	0.3
60% light intensity	$\log w = 3.53 - 1.30 \log p$	96.4	0.6
23% light intensity	$\log w = 2.50 - 1.08 \log p$	95.6	0.3
Experiment II			
100% light intensity*	$\log w = 4.96 - 1.84 \log p$	96.8	0.01
60% light intensity*	$\log w = 4.34 - 1.70 \log p$	97.9	0.4
100% light intensity†	$\log w = 4.24 - 1.66 \log p$	80.4	5.6
60% light intensity†	$\log w = 3.62 - 1.49 \log p$	85.7	9.6‡
Wheat	$\log w = 3.83 - 1.39 \log p$	96.4	0.6
<i>Trifolium pratense</i>	$\log w = 3.86 - 1.33 \log p$	76.2	1.3
<i>Medicago sativa</i>	$\log w = 3.93 - 1.42 \log p$	88.8	2.0

* Includes dead and shed material.

† Excludes dead and shed material.

‡ This is the only example of significant variance accounted for by second degree polynomial.

equation is $\log w = 3.83 - 1.39 \log p$. This graph in particular emphasizes a conclusion of Yoda *et al.* that 'densities in heavily overcrowded plots tend to converge with the lapse of time on the same level, irrespective of the difference in initial density'. The stands of highest density are the first to thin, followed by the less dense; those with few plants may not thin at all.

An analysis of data published by Black (1960) provides a further example of the thinning law. *Trifolium pratense* L. and *Medicago sativa* L. were grown in pure stands and in mixtures at eight densities, from 50 to 12 500 plants/m². Heavy mortality was recorded at the three highest densities at two harvests taken 7 and 9½ weeks after sowing; total dry weight of the surviving plants was also recorded. Mortality at the remaining five densities was negligible. Since there are only two items of data for any given treatment (those of the two harvests) a number of treatments have been combined graphically to follow the density/mean weight relationship and to reduce error. In Fig. 6(a) the data

for *Trifolium* (T), grown in pure culture and the mixtures in which it was planted in excess of *Medicago* (M), are given; these mixtures contained 6250T-50M and 6250T-250M, both virtually pure stands of *Trifolium*. In Fig. 6(b) are shown the relevant data for pure stands of *Medicago* and the mixtures with 6250M-50T and 6250M-250T. Other mixtures which had a large excess of one species over another (e.g. 1250T-50M) were not included because they had suffered very little mortality by 9½ weeks from sowing. The populations included in the analysis had declined in number by more than 15% within the period of the experiment. The relationships between the number of surviving plants and their mean dry weight are shown in Fig. 6(a and b). The thinning lines are 3¼° and 1½°, respectively, lower than a -1.5 gradient (Table 2).

Interesting sources of information on thinning are contained in the large literature amassed by foresters although none of the observations appears to be used with the intention of establishing thinning laws of the Yoda-type. A paper by Mackenzie (1962) contains sufficient data for analysis of the kind described above. Although unaccompanied by any observations of naturally thinned stands, it records the effects of four

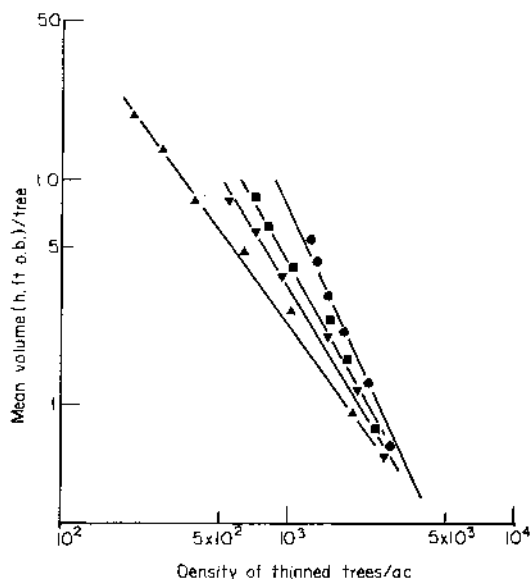


FIG. 7. Changes in numbers and mean volume per tree of *Picea abies* under four thinning regimes over a period of 30 years. The treatments were light (●), moderate (■), 'light crown' (▼) and heavy (▲) thinning (see text) which result in gradients of -2.18, -1.77, -1.63 and -1.39 respectively. Data recalculated from Mackenzie (1962).

thinning regimes on Norway Spruce from 1930, when the trees were 20 years old, until 1960. The trees were thinned at 5-yearly intervals. There were four thinning levels:

- B. Light, removing badly suppressed, dead and dying trees.
- C. Moderate low thinning.
- D. Heavy low thinning, only best trees (mainly dominant) left and given space for full crown development.
- L.C. 'Light' crown thinning—resembles D except that suppressed and subdominant trees are left to fill the spaces between the best dominants. It is the 'bad' dominants and co-dominants that are removed.

(As the tables in Mackenzie's paper give the numbers and volumes of trees after thinning, a correction was made to obtain an estimate of the mean volume per tree before thinning. The total volume remaining after thinning at year t was added to the volume of thinnings removed at the next thinning period (year $t+5$) and the resultant total divided by the number of trees present at year t . It was hoped thereby to estimate more accurately the carrying capacity of the plots than by using the raw data which gave the volume per tree immediately after thinning, when more space had become available for each.)

The gradients of the lines in Fig. 7 are -1.39 (D), -1.63 (L.C.), -1.77 (C) and -2.18 (B) from left to right respectively. The three heavy grades of thinning, C, D and L.C., show close agreement with the natural self-thinning relationship described by Yoda *et al.* (and found also by them to apply to forest trees thinned naturally). The lightest thinning treatment (B), which can be regarded as almost natural, unexpectedly shows least conformity with the -1.5 gradient, although the thinning line nevertheless remained straight over the 30-year period of observations.

EVIDENCE FROM FOREST MANAGEMENT TABLES

Yoda *et al.* (1963) quote evidence that 'empirically established standards of thinning in tree plantations, such as the stem volume-stand density relations given in yield tables, gave a curve on the log/log diagram more or less parallel to the $3/2$ th power law line specific to the tree species concerned'. They expressed the belief that the $3/2$ th power law 'can serve as the basis for establishing a reasonable system of plantation management'. This belief seems to have been so far little realized, possibly because of the comparative neglect of their work on self-thinning (Harper 1967).

The Forest Management Tables published by the Forestry Commission (Bradley, Christie & Johnston 1966) contain a wealth of information on thinning practices for a large number of tree species. Thinning in forestry terms may be defined as 'a technique or series of techniques which aim at providing suitable physiological conditions for tree growth and for improving the quality of trees' (Taylor 1964), or 'a silvicultural practice carried out partly to remove hazards and uncertainties from the process of population reduction as it would occur in untended stands and partly to produce a particular pattern of tree in the final crop and so of economic produce' (Day 1966). Bradley (1967) has described the method of determining the normal thinning yield for forest trees in Britain. The yield tables are 'based on a thinning regime which, with the initial planting distances commonly used in this country, provides the greatest girth increment, consistent with maximum volume production'. They are intended for use with fully stocked stands, that is, those in which near maximum growth per acre is maintained. The thinning intensity is 'based on an annual thinning yield during early life which is equal to 70% of the maximum mean annual volume increment which the crop is capable of producing. Although this is an arbitrary standard, it represents the best estimate which conventional thinning research has been able to provide of an economic compromise between maximum growth per tree and per unit area' (Bradley 1967). 'This constant ratio of 70% of the maximum m.a.i. was found, by a process of trial and error, to be the most appropriate to hold good for all species and yield classes' (Bradley 1966). Yield classes indicate the maximum m.a.i. a stand is capable of producing. The type of thinning is varied in accordance with the characteristics of the different species. Crown-thinning is adopted for first thinnings in the more tolerant or shade-bearing species, while for the intolerant or light-demanding species a thinning which

removes most of the trees in the lower canopy classes (as well as removing trees in the upper canopy classes to favour selected trees) is used.

By use of the normal yield tables provided by Bradley *et al.* (1966) the predicted mean volume per tree has been plotted against the surviving density after the recommended thinning regimes for several species. The results are shown in Figs. 8 and 9. Sets of data for two or three of the yield classes are given for each species. These represent stands of trees with varying levels of actual or potential maximum m.a.i., and as such reflect the

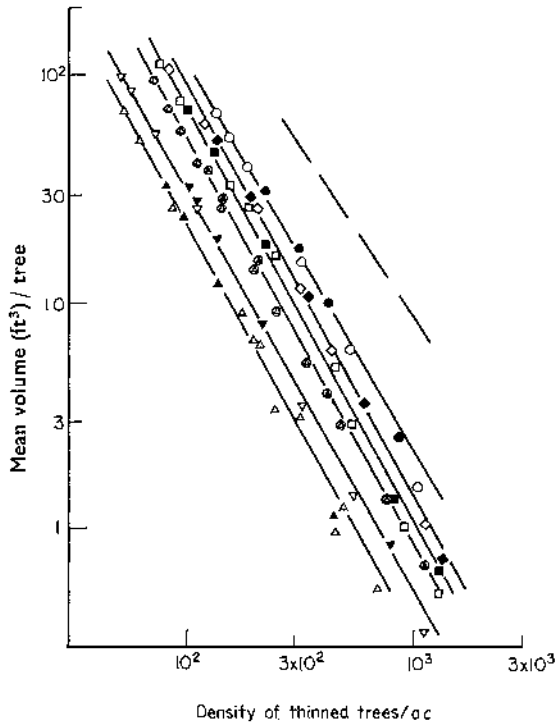


FIG. 8. Relationships between density and mean volume per tree in fully stocked stands for up to 100 years after planting, drawn from data in Forestry Management Tables (Bradley *et al.* 1966). The relationships are based on data which predict yields obtained in accordance with the thinning practices advocated in the management tables. Two or three sets of yield class (Y.C.) data are given for each species: Noble fir, Y.C. 240 (○), Y.C. 160 (●); western hemlock, Y.C. 260 (◇), Y.C. 180 (◆); Sitka spruce, Y.C. 260 (□), Y.C. 200 (■); Scots pine, Y.C. 160 (△), Y.C. 100 (▲); European larch, Y.C. 140 (▽), Y.C. 80 (▼); sycamore/ash/birch (joint tables), Y.C. 120 (△), Y.C. 80 (▲). The data for the separate yield classes lie along common thinning lines, whose gradients range from -1.72 to -1.82 . A slope of gradient -1.5 is shown at right for comparison.

fertility levels of different sites. The recommendations extend for periods of 20–100 years after planting. All the lines shown in Fig. 8 have gradients between -1.72 and -1.82 , all 4° or 5° higher than the idealized -1.5 gradient reported by Yoda *et al.* The different yield class data for each species lie along a common line. It is readily apparent that the thinning treatments proposed by Bradley *et al.* and based upon ‘an arbitrary standard’ to ‘maximise growth per tree and per unit area’ follows closely the empirical conclusion of the Japanese workers—‘there is a maximum asymptotic density at each stage of growth and densities beyond this level cannot be realised, however high the initial density was, because of the regulation by self-thinning’.

Fig. 9 gives the data for beech and oak derived from the thinning tables. Separate relationships of volume with number of stems were used in constructing the tables for each yield class (Y.C.). The gradients of the lines range from -1.48 to -1.62 , as indicated in the Figure. The points of maximum m.a.i. for beech are 80–90 years for Y.C. 100, 95–100 years for Y.C. 60; and for oak at 80 years for Y.C. 60 and 100 years for Y.C. 40. Above these points the gradient of the line changes such that the final point shown lies

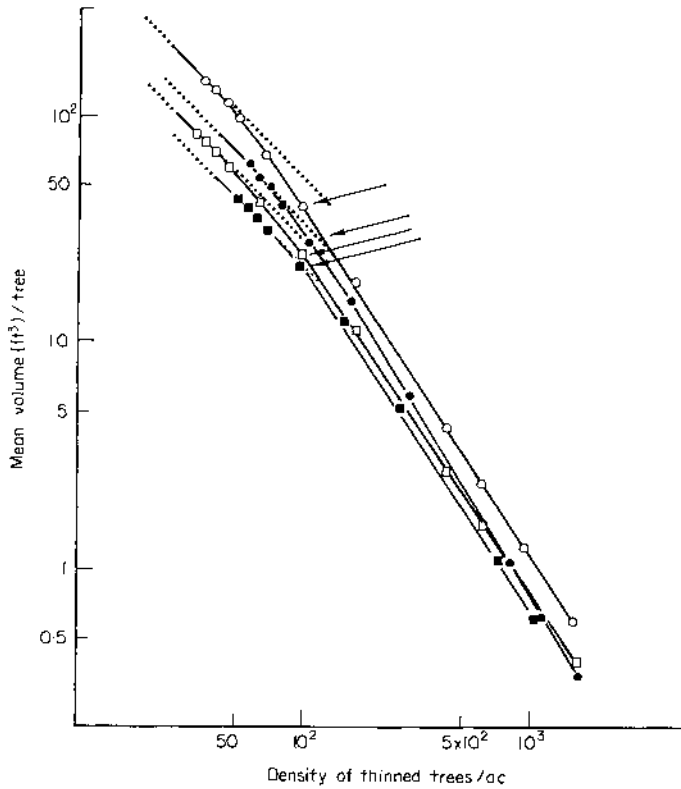


FIG. 9. Relationships between density and mean volume per tree for beech and oak in fully stocked stands for up to 150 years of age. The data have been recalculated from Forestry Management Tables (Bradley *et al.* 1966) which predict yields obtained in accordance with the thinning practices advocated. Two sets of yield class data are given for each species: beech, Y.C. 100 (○), Y.C. 60 (●); oak, Y.C. 60 (□), Y.C. 40 (■). At points of maximum mean annual increment (indicated by arrows for each yield class) the slopes change from a gradient of -1.5 to -1 .

along a gradient of -1 (-45° slope). The final three points for beech which lie along this -45° slope are for 130, 140 and 150 years of age for both yield classes. The final five points for oak cover 100–150 years of age at both yield classes. The consequences of this change in the gradient of the recommended thinning line are of some interest. While thinning proceeds along the -1.5 gradient, the relationship

$$w = Cp^{-1.5} \text{ holds, or its corollary } y = wp = Cp^{-0.5}$$

which shows that the total plant yield (y) increases with the progress of self thinning in spite of the decrease in plant number. But when the gradient changes to -1 , the relation-

ship of y to p becomes $y = Cp^0$, that is, the total yield has become constant. For plant populations sown at a wide range of densities in which no mortality occurs the line of gradient -1 is an asymptotic value, reached sooner by the stand at the highest density and successively reached by those stands at successively lower densities (Shinozaki & Kira 1956). Evidently, after oak and beech have passed their period of maximum m.a.i. the thinning practice advocated in the yield tables will not greatly increase the total yield from the site, although the trees left after thinning continue to grow.

A similar analysis of the yield table given by Joyce & Gallagher (1966) for *Pinus contorta* in Ireland gives a slope of -1.8 . The data of Duff (1966) for *P. contorta* in New Zealand also give a slope of -1.8 . This gradient is constant in both cases over the periods of 20–50 years of age recorded, although it is several degrees higher than the ideotype of Yoda *et al.*

There are undoubtedly many further examples in the literature of the type cited above; those analysed were readily available and contained sufficient relevant data for computation.

DISCUSSION

The results of the experiments quoted, and of the management methods adopted by foresters, seem to strengthen the generality of the $3/2$ power law of Yoda *et al.* (1963). The law holds, with very slight deviations, for species other than those mentioned by the Japanese workers and can apparently be further applied to mixtures and to vegetative components of plant yield as for whole plant yield.

The law may be derived, as Yoda *et al.* have done, from a simple geometrical model. The average ground area(s) occupied by a plant will be proportional to a linear dimension of the plant (L) as $s \propto L^2$. The weight (w) of a plant will be proportional to its volume, which in turn is proportional to the same chosen linear dimension as before (L), e.g. height of plant, diameter of stem or crown, etc.: that is, $w \propto L^3$. Therefore, $s \propto w^{2/3}$. s is also proportional to density (p), assuming that thinning occurs when the total stand cover exceeds 100% and operates to maintain 100% cover, as $s \propto 1/p$. From the above argument the relationship $w = Cp^{-3/2}$ is readily derived. This model is offered by Yoda *et al.* as 'a crude approximation'.

The connection between the $3/2$ power law and an equation for distance to nearest neighbour as a measure of spatial relationship in populations given by Clark & Evans (1954) is of some interest. They considered the pattern of distribution to be a fundamental characteristic of a population and, following earlier workers, they used distances between nearest neighbours to obtain measures of departure from random distribution. They derive the equation $r_e = 1/2\sqrt{p}$ to describe the relation between expected mean distance between nearest neighbours in a randomly distributed population (r_e) of density p (expressed as numbers per unit area). (The mean distance between nearest neighbours is maximized in a hexagonal distribution, where each point has six equidistant nearest neighbours. Here the constant distance between nearest neighbours (r_A) is $2^{1/2}/3^{1/2} p^{-1/2}$.)

Without making any assumptions about the degree of departure from randomness in the sort of plant populations described in previous sections one might assume $r = c.p^{-1/2}$, where c is a constant depending on the pattern of distribution, and r is the mean (linear) distance between plants (nearest neighbours). In a stand of plants where the total cover does not fall below 100% (the assumption of the Yoda *et al.* model), or

where the space available per plant* is such that competition is occurring and zones of influence overlapping, it may be assumed that r is not only the expected mean distance between plants, but is also a function of the mean area of (ground) space available to each plant, or of the mean volume of plant material occupying that ground area. (This volume would include both aerial and underground parts of plants.) Hence, $r^3 \propto v$, where v is the mean volume of space per plant. The definition of this space in simple terms of regular geometric volumes (such as cones, spheres or cylinders) would be rather difficult. It might, however, be possible as greater insight is gained into canopy structure (cf. Monsi 1968, for example) or root structure (cf. Kutschera 1960).

The original equation of Clark & Evans might now be rewritten in the form $k_1 v = c.p^{-3/2}$, where k_1 is a constant depending on the shape of the space occupied by the plant. The space occupied by a plant will determine its weight at any given time, so that $k_1 v = k_2 w$, where w is the mean weight per plant, related to the volume by a further constant, k_2 . This leads to a statement, $k_2 w = k_3 p^{-3/2}$, or $w = K.p^{-3/2}$, an equation formally identical to that of Yoda *et al.* K is thus a constant depending on the space available to each plant, *under competitive conditions*. As such, it will depend on planting pattern, on density per unit area and on the genetic properties of each plant. These genetic characteristics determine, subject to environmental constraints, a plant's pattern of development, its structure, its ability to use the resources available to it and its ability by plasticity of phenotype to absorb the physiological (and physical) pressures exerted upon it by neighbours. When K reaches its maximum value for the species concerned, thinning ensues and the plant population adjusts itself in numbers, thereby altering w and p , but not K .

It would be of great theoretical interest, and of no little practical significance, to determine the parameters of K for even a single species. A measure of how plants use the space available to them would be required. An approximation might be provided by geometrical definitions of canopy structure, since it has been shown that some components of plant yield (the aerial part of the plant for example) conform to the 3/2 power law in a manner similar to that of whole plants. The definition of the elements of K which relate to the shape of the geometric space occupied by the aerial part of a plant might simplify the determination of the other elements, which depend on pattern and density, *inter alia*. Density determines the *rate* at which the population reaches its K value—this is strikingly confirmed by the analysis of the data from Puckridge & Donald (1967). Pattern may have other effects not yet known. As thinning proceeds, pattern will change, so that a dynamic concept of pattern will be required. The effect of geometric shape of (for example) the aerial part of a plant on K is not readily comprehensible, since it subsumes a large number of meteorological variables: canopy structure may be expected to be not independent of the intensity and quality of light, of temperature, of CO_2/O_2 profiles, etc. The data of Hiroi & Monsi (1966) show the effect of varying light intensities on K (*vide supra*). Canopy structure is related also to size and age of leaves and to population density, as Nichiporovitch (1961), Loomis *et al.* (1968), de Wit (1965) and others have shown.

The cause of the thinning phenomenon in plant populations is not clear, but it would seem that it can partly be understood by considering the population as a 'hierarchy' of resource exploitation, which results in differential growth rates among its members. This leads to a development of pattern of dominance and suppression. Slight differences

* Space may be interpreted *sensu* de Wit (1960) to denote 'growing factors' or 'requisites' like water, minerals, light, etc.

in seed size, in soil microtopography, in the microclimatology of the stand will 'generate differentials within a population which time and density may be expected to exploit, to skew an initially normal frequency distribution' (Obeid, Machin & Harper 1967). Koyama & Kira (1956), Obeid *et al.* (1967) and others have shown that the frequency distribution of plant weights changes from normal to log-normal as density stress develops in a population and that this change occurs more rapidly the higher the density; the most abundant class is that which contains the plants of lowest weight. It may be expected, then, that in populations which are undergoing thinning the relative skewness of the individual plant weights is quite high and that it will be the smaller individuals which die. This would appear to be true from casual observation but there are no available data which give measures of skewness for populations in the process of thinning. However, in an experiment performed simultaneously with the first one reported in this

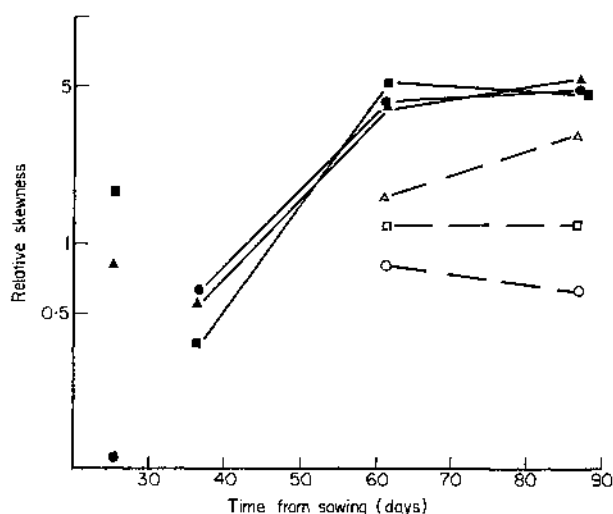


FIG. 10. Change of relative skewness with time of *Brassica napus* (●) and *Raphanus sativus* (■) and a mixture of both (▲) in competition at low (open symbols) and at high (closed symbols) density. At first harvest at the higher density there was a spread of skewness values which is unaccounted for. At high density slight mortality was observed by the third harvest and became greater by the final harvest, but with only a small increase in the relative skewness of the populations. No plants died at the lower density during the experiment.

paper, using the same two species in a de Wit (1960)-type analysis of their competitive relationships, individual plant weight was measured over four harvests at two densities; further, at higher density mortality occurred at the penultimate harvest and its continuation was recorded at the final one, 3 weeks later.

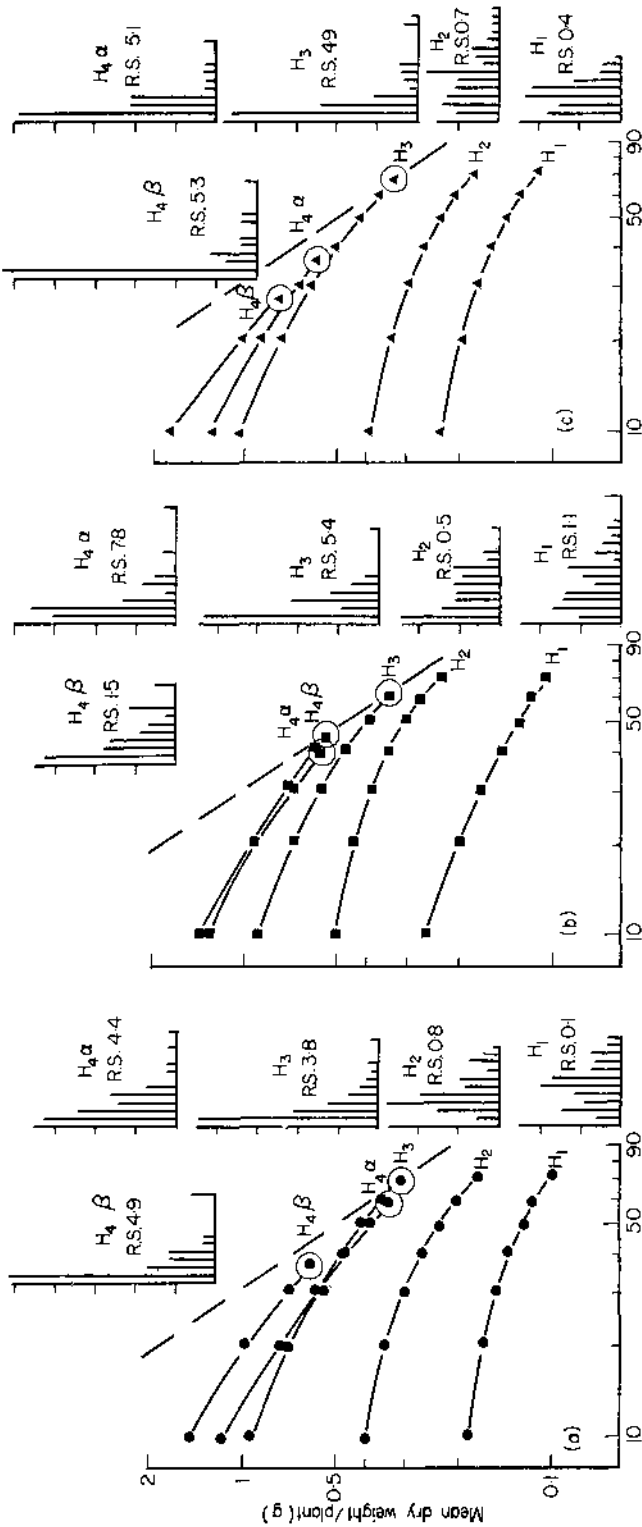
Fig. 10 shows the increase in skewness over the period of the experiment for rape and radish and for a fifty/fifty mixture of each at low (twenty-eight plants per unit area) and high (seventy-two plants per unit area) density. At low density, the populations after 12 weeks had a relative skewness no greater than 0.63 for rape and 1.21 for radish in pure stands, although the value for the mixture reached 3.0 without mortality. At the higher density, rape, radish and the mixture reached values of relative skewness of 4.0–5.4 by the third harvest, just at the onset of mortality; numbers were reduced from seventy-two to seventy (rape), sixty (radish) and sixty-seven (mixture) at this time, 9 weeks after sowing. By 12 weeks the numbers were further reduced, but the skewness values remained

almost unchanged. (At the first harvest, $3\frac{1}{2}$ weeks after sowing, there was a spread of skewness values which is not accounted for.) Thus, it appears that when a certain imbalance in the size structure of the population is attained mortality occurs and the degree of skewness then remains fairly stable. It may be assumed that the smallest plants are most readily thinned but this has rarely been demonstrated. For example, Black (1958), growing large and small seeds of a *Trifolium subterraneum* cultivar in mixture, found that the plants derived from the larger seeds maintained a superiority which enabled them to intercept 97% of the incident light after 12 weeks, allowing less than 3% to the suppressed plants from the small seeds; the suppressed plants suffered heavier mortality. Even in isogenic populations where no conscious selection is imposed with regard to seed size or capacity for rapid growth, plants are likely to evolve a 'hierarchy', however slowly, in which some will monopolize incident light at the expense of their neighbours. From a competition experiment with a pure line of subterranean clover, in which the performance of individual plants was measured, Stern (1965) observed a pattern of dominance and suppression developing, which was accentuated by density and accelerated with time. Although mortality is recorded in one treatment, there is no evidence that it is the smallest plants in the population which die.

Tentative evidence for the assumption that the smallest plants die first may be obtained from a consideration of the data mentioned above which recorded the development of skewness in rape and radish populations over a three-month period of four harvests. In Fig. 11(a) the mean dry weight per plant at successive harvests (H_1 – H_4) is shown for rape on log/log co-ordinates. The extreme right-hand point at each harvest gives the mean dry weight for the intact population. Successive points to the left give the corrected mean weight per plant of the population remaining when successive groups of ten smallest plants are removed. The extreme left-hand point shows the mean weight per plant of the ten largest plants in the population. The relative skewness of the population is shown by the accompanying histogram. (The dry weight data are means of three harvests, except at the last harvest, when there were two replicates, each shown separately. The histograms of frequency distribution of dry weights relate in every case to a single replicate but are typical of the harvest they accompany; at the fourth harvest, they are drawn for both replicates. The histograms show the shape of the distribution subject to a limit of sixteen intervals imposed in the computation. The actual values for dry weights have been omitted for clarity.) As the plants in the populations grow, the difference between the mean dry weight of the ten largest plants and of the population as a whole is accentuated—the slopes steepen. By the third harvest there is a very slight reduction in numbers. This is more evident at the final harvest, where one replicate has thinned to a much greater extent than the other. Meanwhile the mean dry weight of the ten largest plants has continued to rise to a greater extent than that of the total population. The relative skewness does not rise appreciably, however (*vide* Fig. 10), indicating a self-adjustment towards stability of population structure. This adjustment can be achieved under these conditions only by removal of the smallest plants.

The same trend is confirmed by data obtained from radish in pure stands and from a rape–radish mixture (Fig. 11b and c). The final values of relative skewness for rape are widely disparate however and do not conform to the pattern seen in (a) and (c).

The mean dry weight per plant of the intact populations shown in Fig. 11 increased between the first two harvests. At the third harvest this mean weight has further increased but the number of plants have fallen, by two for rape, by twelve for radish and by five for the mixture. On the log/log co-ordinates it might now be expected from the 3/2



Nos. in intact or adjusted populations

Fig. 11. Changes in the relationship between mean dry weight per plant and the frequency distribution of individual plant weight with time (12 weeks) for *Brassica napus* (●), *Raphanus sativus* (■) and a mixture of both (▲). The right-hand point in each curve represents the mean weight of the intact population, encircled if natural thinning has occurred. Each point to the left gives the corrected mean weight per plant of the population remaining when successive groups of ten smallest plants are removed; the extreme left-hand point shows the mean weight per plant of the ten largest plants. A thinning line of gradient -1.5 is drawn through the point where the population first shows signs of thinning; populations subsequently adjust their numbers and mean weight such that the line is not transgressed. The histograms give the corresponding frequency distribution of plant weights at each harvest (H_1-H_4), the relative skewness (R.S.) of each being indicated. Each of the two replicates for the final harvest (H_4) is shown separately. The ordinates in each histogram are subdivided into units of ten. On the abscissa the lowest weight classes are on the left.

power law that these thinned populations lie along a line of gradient -1.5 and that their subsequent growth would be restricted in their plant weight/plant number relationship by such a slope. In fact, no point rises above it—the mean dry weight of the plants is now laterally rather than vertically displaced. The encircled points in Fig. 11 show naturally thinned populations, self-adjusted in a manner which does not allow transgression of the thinning line. Extrapolation of the lines, as drawn, gives a value for $\log C$ (in the $w = Cp^{-3/2}$ relationship) of 2.20 in all three cases, which corresponds almost exactly to that given in Table 1 for the parallel experiment with the same species specifically designed to test the thinning hypothesis. This seems to attest further to the validity of the law; initial thinning as recorded in the third harvest in Fig. 11 occurs at precisely the same value of C as in the example quoted extensively at the outset. At the final harvest the populations seem to have over-compensated slightly for the density stress, but it is significant that none of the points rises above the thinning line.

Thinning in accordance with the $3/2$ power law is therefore compatible with frequency distributions of populations in which thinning begins with the smallest individuals and progressively includes larger ones, removing as many small individuals as are required to restore equilibrium. Hozumi, Shirozaki & Tadaki (1968) have shown theoretically that the constant C of the thinning equation controls the frequency distribution of plant weight in stands undergoing thinning. The data of Figs. 10 and 11 seem to confirm this; as a result of thinning the relative skewness of the rape and radish populations tends to be stabilized.

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SUMMARY

The $3/2$ power law, established by Yoda *et al.* (1963) and which relates the number of surviving plants in a population undergoing self-thinning to their mean dry weight, has been confirmed and extended to several other species. Root and shoot components of plant yield appear to follow the same law. Stands of the same species starting growth simultaneously at different densities are shown to follow a common thinning line, the stands of highest density thinning first. Varying light regimes appear to affect the constant of the $w = Cp^{-3/2}$ equation (where w is mean plant weight and p the corresponding density) but not the $-3/2$ gradient. The 'arbitrary standards' of foresters in constructing yield tables coincide closely with the law also.

A possible alternative derivation of the law is recorded based on distance to nearest neighbour measurements. The assumption sometimes made that the smallest plants in a population are the first to thin, leaving the larger ones to grow more rapidly, is shown to be valid, by measurements of individual plant weight over a series of harvests.

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