A Darwinian Approach to Plant Ecology

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A DARWINIAN APPROACH TO PLANT ECOLOGY

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The theory of evolution by natural selection is an ecological theory—founded on ecological observation by perhaps the greatest of all ecologists. It has been adopted by and brought up by the science of genetics, and ecologists, being modest people, are apt to forget their distinguished parenthood. Indeed, Darwinian plant ecology has been largely neglected and a changeling child nourished and brought to adulthood by Schimper and Warming who asked geographical questions about vegetation, and answered the questions by demonstrating correlations between climate and soils on the one hand and comparative physiology on the other.

By contrast with the 'vegetationalist' and his concern to describe and interpret areas of land, Darwin's ecological observations and the questions he asked were based on a consideration of individuals and populations—a preoccupation with numbers. 'Look at a plant in the midst of its range, why does it not double or quadruple its *numbers*?' '. . . if we wish in imagination to give the plant the power of increasing in *number*, we should have to give it some advantage over its competitors, or over the animals which prey on it'. 'Look at the most vigorous species; by as much as it swarms in *numbers*, by so much will it tend to increase still further' (Darwin, *Origin of Species*, Chapter III).*

These quotations, with their emphasis on numbers, pose problems of population biology—of a demography which has never gained a momentum in plant ecology, although it has played a vertebral role in animal ecology.

Two interlinked properties of higher plants have seriously hindered the development of plant demography—plasticity and vegetative reproduction. Darwin found a 26-year-old pine tree on heathland which 'had during many years tried to raise its head above the stems of the heath and had failed'. It is clearly not fair to count such a plant as a unit equal to a full grown tree in a population census. A mature plant of an annual weed such as *Chenopodium album* may produce four seeds or 100 000 seeds, depending on the nutrient and water status of the soil. It can therefore be argued that a statement about numbers of plants implies very little about the real nature of the population. Vegetative reproduction is a further obstacle to census making, because the vegetative offspring remain to some extent a part of the parent, often for a long period. When is such a ramet to be counted as an individual? Arbitrary decisions have to be made if plant populations are to become numerable and the arbitrariness of the decisions has often discouraged attempts to count plants.

These problems are, however, not peculiar to plants and have had to be faced in animal demography where they arise in only a slightly less acute form. Plasticity in individual size and reproductive capacity have to be taken into account in population studies of fish and even of *Drosophila*. Vegetative reproduction in *Hydra*, where the 'ramets' slowly develop independence, has not prevented its use in model population studies.

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* All quotations in this paper are from Chapters III and IV of *The Origin of Species* (1859), the text being the Everyman edition of 1928. Italics are mine.

The very few population studies which have been made of plants in natural populations suggest that the difficulties are not overgreat in practice and the results can be very revealing. Tamm's study of perennial plants in forests and meadows is a classic (Tamm 1948, 1956) (Fig. 1a, b and c). Over a period of 13 years he counted 'individuals' of selected species in permanent quadrats. Many of the populations were remarkably constant in total numbers over this period and yet displayed a high turnover rate including losses both of seedlings and of mature (flowered) plants and gains from new recruits both as seedlings and from vegetative reproduction.

Tamm's study of a declining population of *Centaurea jacea* (Fig. 1c) is equally remarkable for the insight it gives to the process of disappearance of a species from a community. These data have been recalculated and presented as the change in plant numbers (as logarithms) with time (Fig. 2). The relationships are almost startlingly linear, indicating that the chance of an individual dying remains the same through the period of the study. It shows elimination as a steady, not jerky, process, with some individuals remaining vigorous enough to reproduce vegetatively to the bitter end. It suggests that the exodus of a species from a community is not due to the occasional occurrence of extreme conditions but to a slow process of elimination of which the causes act with surprisingly constant intensity. Such population changes may be characterized like the decay of a radioisotope, by a 'half-life'. The half-life of *C. jacea* calculated from Tamm's data is *c.* 1·9 years. Similar calculations made from more constant populations in Tamm's study show widely different half-life values. For example, the individuals of *Filipendula vulgaris* present at the start of Tamm's observations had a half-life of *c.* 18·4 years, and *Sanicula europaea* > 50 years (Fig. 2). In these cases the population decay was at least matched by new recruitment from seedlings or vegetative reproduction.

Sagar (1959) made a shorter but more detailed study of populations of *Plantago lanceolata* in 'permanent' grassland near Oxford which had been under essentially constant management over the preceding 10 years. Using pantograph techniques for mapping plants and seedlings and following the fates of all the seedlings and rosettes in replicate sample plots A and B, he attempted to extract life table data (Table 1).

On both of the two replicate areas sampled, the number of plants of *P. lanceolata* increased but much more strikingly in Area B than in Area A. The behaviour of those plants which were present at the start of the observations was, however, very similar on the two areas. Of the plants recruited to the population as seedlings within the 2-year period, two-thirds died when less than 12 months old. The mature plants present at the start of the period of study had a half-life of *c.* 3·2 years. This is a measure of the dynamic character of such superficially stable vegetation.

Antonovics (1966) has studied the dynamics of population of *Anthoxanthum oderatum* in the open communities of metal mine spoils—in this case marking individuals present along line transects. This was again a short-term study and typical results are given in Fig. 3. As with many of Tamm's examples (and Sagar's plantains) the new recruitment from seedlings compensated for (might indeed be determined by) the rate of loss of the initial population. Such attempts to trace the fate of individuals within populations necessarily involve detailed and frequent mapping so that a seedling which appears where another has just died is recognized as a new individual, and that individuals do not both appear and die in the interval between observations. Probably the first serious observation of this sort was that of Darwin '. . . on a piece of ground three feet long and two wide, dug and cleared, and where there could be no choking from other plants, I marked all the seedlings of our native weeds as they came up, and out of 357 no less

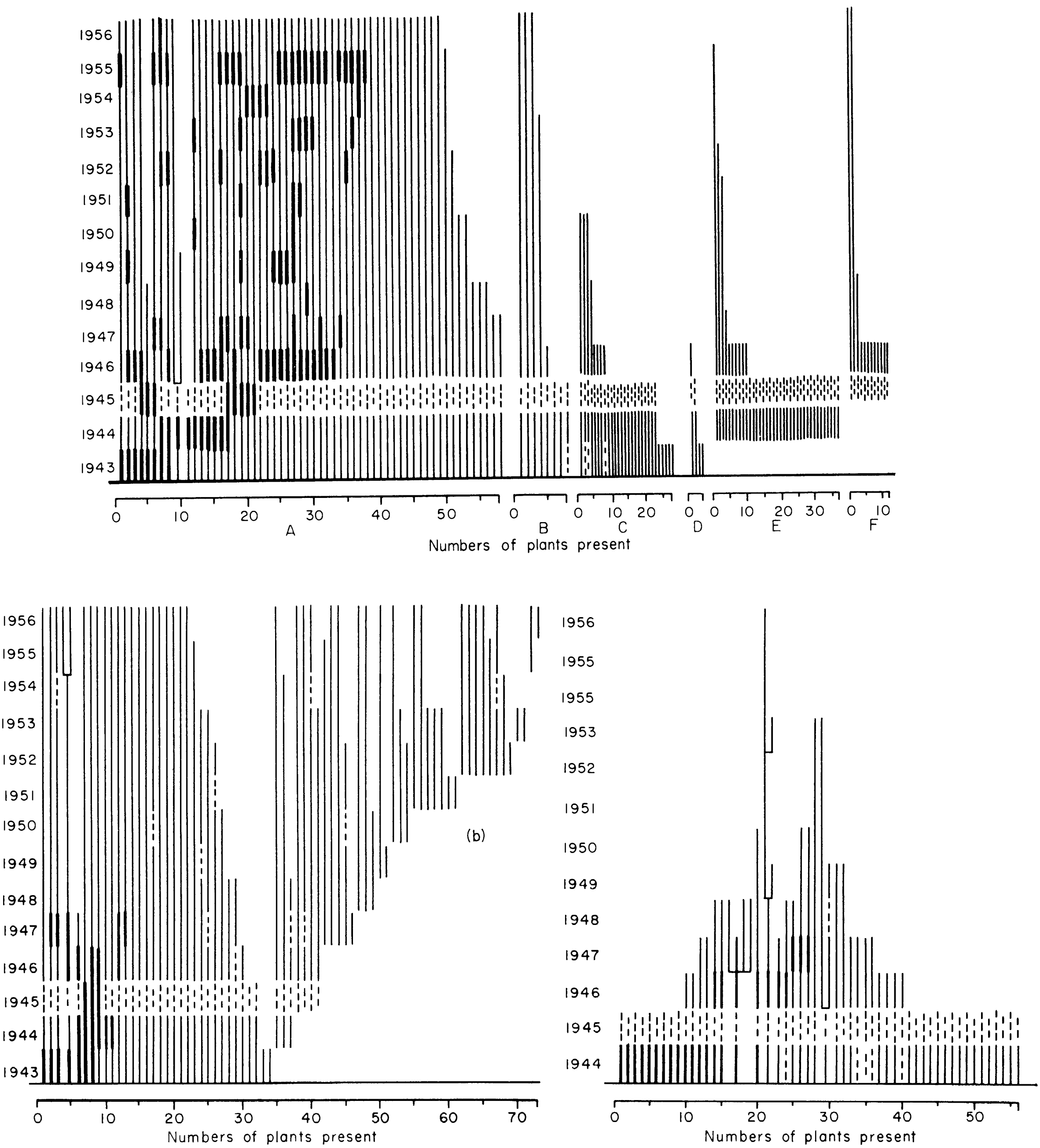

FIG. 1. The behaviour of populations of (a) *Sanicula europaea*, (b) *Filipendula vulgaris* and (c) *Centaurea jacea* within a $\frac{1}{4}$ m^2 quadrat in woodland from 1943 to 1956. Group A includes specimens that were large or intermediate in size at the first inspection, Group B rather small plants, Group C very small plants and Groups D–F different crops of seedlings. Heavy lines indicate that the plant flowered in that year. Branching of a line indicates vegetative reproduction. (Redrawn from Tamm 1956.)

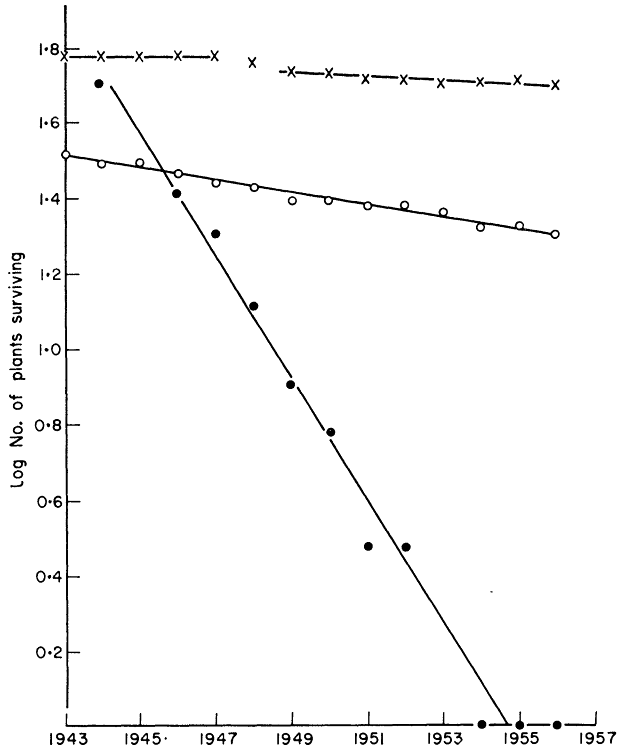

FIG. 2. The decay rate of populations of *Sanicula europaea* (×, half-life >50 years), *Filipendula vulgaris* (○, half-life *c.* 18·4 years) and *Centaurea jacea* (●, half-life *c.* 19 years) calculated from data given by Tamm (1956).

Table 1. *The behaviour of a population of* Plantago lanceolata *in an alluvial meadow near Oxford* (*adapted from Sagar* 1959)

		Area A	Area B
(a)	Number of individuals per m^2 present, April 1957	238	149
(b)	Number of individuals per m^2 present, April 1959	249	211
(c)	Net gain	+11	+62
	% gain ($\frac{c}{a} \times 100$)	4·6	41·6
(d)	New individuals appearing between April 1957 and April 1959	576	487
(e)	Individuals lost from population between April 1957 and April 1959	565	425
(f)	Individuals present at April 1957 and surviving April 1959	83	52
(g)	Individuals present at April 1957 but lost by April 1959	155	97
(h)	Percentage survival of individuals from April 1957 to April 1959 ($\frac{f}{a} \times 100$)	34·9	34·9
(i)	Calculated half-life (years) of mature plants present at start of observation	3·2	3·2
(j)	Fate of plants appearing between April 1957 and April 1959		
	(i) % dying when less than 12 months old	68·2	66·2
	(ii) % dying when 12–24 months old	2·3	1·2
	(iii) % still surviving April 1959	29·5	32·6

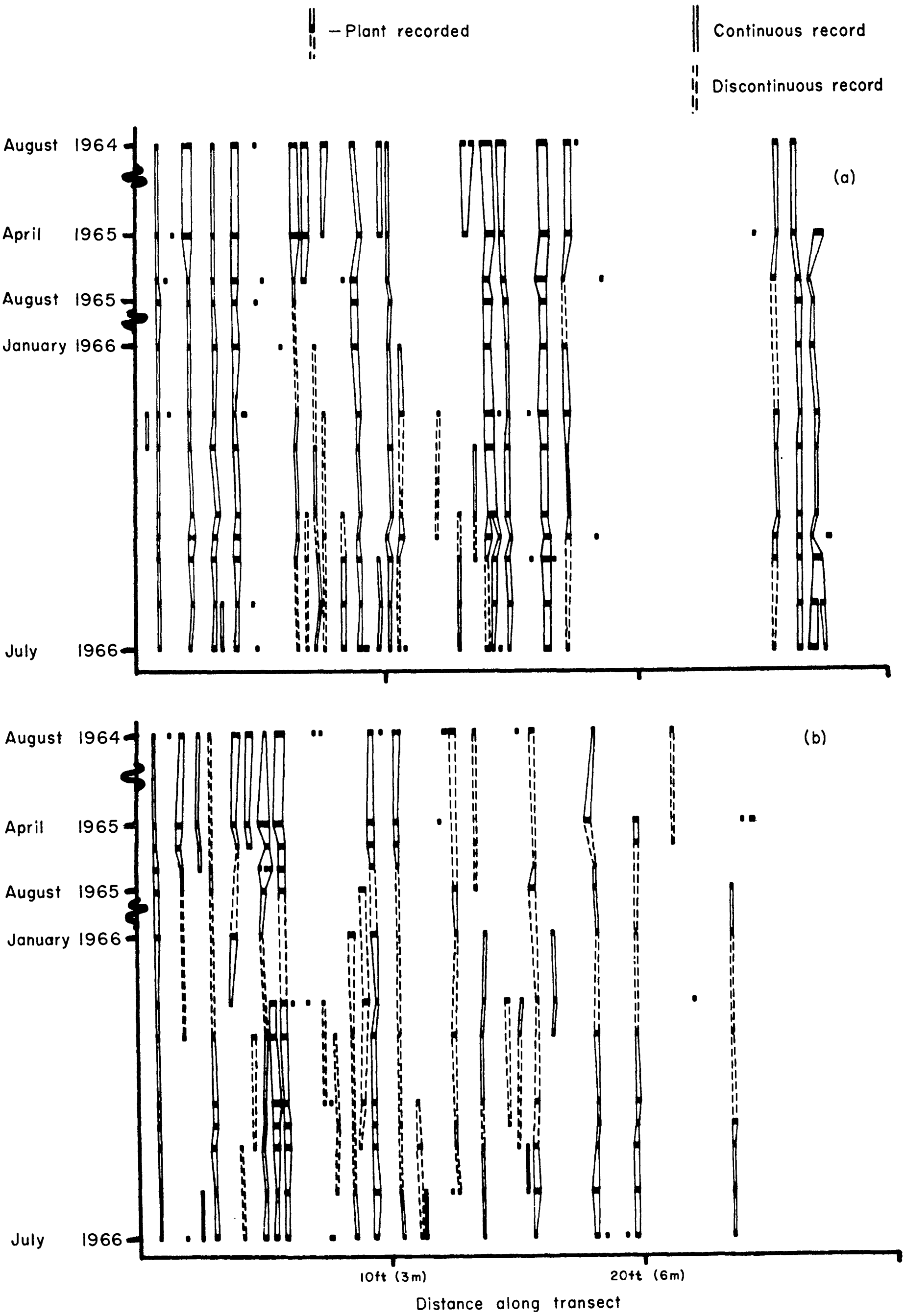

FIG. 3. (a) and (b) The pattern of change in two populations of *Anthoxanthum odoratum* over a period of 2 years in open vegetation on a copper mine site at Trelogan, Flintshire (from Antonovics 1966). Note abbreviation of time scale.

than 295 were destroyed, chiefly by slugs and insects.' Demographic study of this sort focuses attention on the life span of individuals, focuses attention on the causes as well as the time of death, and particularly on the enormous fungal and animal roles in plant mortality.

Measures of population turnover can only be obtained by the detailed observation of individuals—they are totally obscured by vegetational study and revealed by population studies only if plants are marked for repeated observations. They bring measurements of flux into ecological studies in terms which are meaningful to the selection geneticist and the evolutionist. Stable vegetation is then seen to be in a state of continuous flux in which the rates of turnover are critical characteristics of the stability.

The early seedling phases of a plant's life are usually considered the most risky, and the hazards are often strikingly exaggerated by increasing plant density; 'seedlings suffer most from germinating in ground already thickly stocked with other plants'. I have discussed the density dependent mortality of seedlings in other papers (Harper & McNaughton 1962; Harper 1960; Harper 1964a), and this self-regulating property of plant populations is becoming increasingly well documented although the ultimate causes of density-induced death are still very obscure.

One of the earliest attempts to study self-regulation of numbers in populations of plants was made by Sukatschev (1928), who sowed *Matricaria inodora* at two densities in fertilized and unfertilized soil. At the end of a season's growth the percentage loss from the population was greater at the higher density, and in the fertilized soil. (Sukatschev had also observed that the density of mature fir trunks in Leningrad forests declined steadily with *increasing* soil fertility.) Yoda *et al.* (1963) extended this type of observation on natural and artificial populations of plant species (see, for example, Fig. 4). They found that:

(a) The chance of a seed producing a mature plant declined with increasing density.

(b) That irrespective of the density of seeds sown there is a maximum population size of plants produced, and densities beyond this level cannot be realized no matter how many seeds are sown.

(c) The densities of overcrowded populations converge with the passage of time, irrespective of the differences in initial density. The converging densities are always lower on the more fertile soil.

(d) The converging (or asymptotic density) is closely correlated with plant size—so that plants having a certain average size always maintained a more or less similar level of surviving density regardless of the differences in stand age, initial density and fertilizer level.

A particular achievement of this group of Japanese workers was that they were able to formulate a hypothesis linking the numbers of plants and their weight in pure stands which could be expressed as a mathematical relationship—susceptible to experimental test—the major step in transforming a wordy descriptive science into a rigid discipline.

The empirically derived relationship of Yoda *et al.* is

$$w = Cp^{-3/2}$$

where w = mean weight per plant, and p = existing plant density or

$$y = wp = Cp^{-1/2}$$

where y = mean weight per unit area.

It remains to be seen whether this formal relationship holds good for a wider range of species than those studied by Yoda *et al.* which did, however, include such different forms as pure populations of *Betula* sp., *Pinus densiflora, Abies sachalinensis, Erigeron canadensis, Amaranthus retroflexus* and *Plantago asiatica.* It is of great interest to know how far this type of generalization, made for populations of a simple species, can be extended to include populations of several species. The studies of density-dependent mortality in *Papaver* spp. made by Harper & NcNaughton (1962) suggest that pure stands behave in essentially the same way as that suggested by Yoda *et al.*, but that in mixed stands the processes of self-thinning and alien-thinning (intra- and interspecific effects) are subtly different. A very important aspect of the work of Yoda *et al.* is that it examines both the response of numbers and of individual plant size (i.e. both mortality and plasticity) to changing density. Most previous attempts to study density effects in plant populations have looked at changes in mean plant weight while density is artificially regulated, or have examined changes in plant numbers whilst ignoring plant weight. Because of the comment made earlier that the study of plant demography is hindered by plant plasticity, the attempt by Yoda *et al.* to take plasticity into account in a generalized theory is important. Their experiments suggest that mortality is a continuing risk through the life of the plant, continually adjusting the numbers in the population in

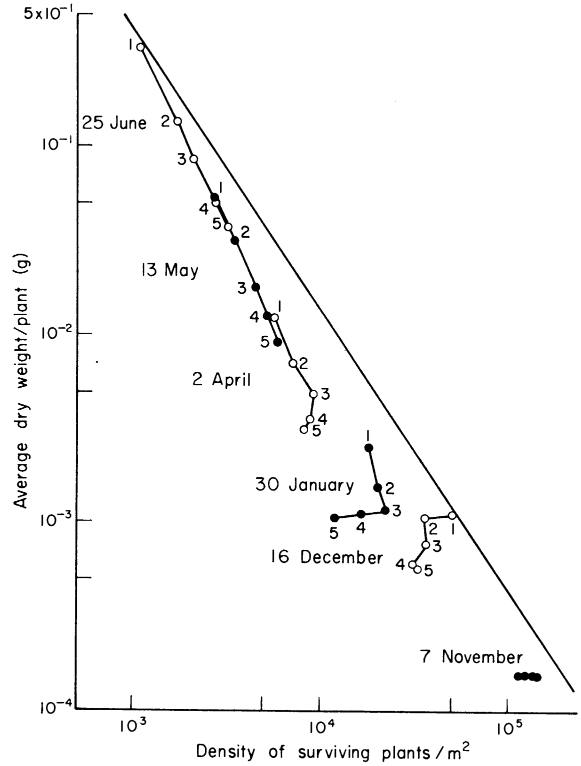

FIG. 4. Changes in numbers and individual plant weight of *Erigeron canadensis* with time. Observations on an abandoned field at Osaka, Japan. The field contained a steep fertility gradient and the plot numbers 1–5 represent an order of decreasing fertility which was exaggerated by the addition of N-P-K-Mg 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/m^2. (Redrawn from Yoda *et al.* 1963.)

relation to the increasing size of the plants. This to an extent contradicts Darwin's view that mortality is concentrated in the seedling stage, and much work is needed to clear up this point and obtain accurate life tables for a number of plant species.

'There is no exception to the rule that every organic being naturally increases at so high a rate that, if not destroyed, the earth would soon be covered by the progeny of a single pair.'

'Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount.'

'A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase.'

The manner in which potentially explosive plant populations are regulated or controlled in nature is obscure. The pattern of population growth is commonly taken to be logistic

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(\frac{K-N}{K}\right)$$

Rate of growth of population = Intrinsic rate of natural increase ×
Degree of realization of the potential increase

In environments in which there is a recurrence of natural hazards, populations may spend most of their time recovering from the hazards—increasing their population size at a rate near to the intrinsic rate of natural increase. The size of such populations may frequently be a function of the magnitude of the last catastrophe and the time available for recovery. Regulation preventing an excessive population size may then be a relatively rare occurrence. This may well be true for many annual plant species of disturbed habitats such as arable weeds. More stable environments are likely to contain populations which spend most of their time near to the K value or saturation level of the population and then density-dependent regulating processes may control population growth continuously.

The intrinsic rate of natural increase of higher plants is a function of seed output and of vegetative reproduction. These two forms of increase represent different values of r, the one appropriate for increase over a broad geographical range and the other for immediate and local colonization. The higher (seed) value of r is associated not only with high risk but also with a spread of the risk over a large, sometimes very large, number of small capital investments (or bets!). The lower (vegetative) value of r is often associated with heavy and continuous capital investment, a 'cautious' policy of placing the investments and a low risk. I know of no attempts to compare the capital investment in seed and vegetative reproduction in any species that possesses both. Comparisons of the seed output of a range of species were made by Salisbury (1942) and these are invaluable starting material for a study of the reproductive strategy of higher plants. However, numbers and seed size are not all of the qualities needed to assess or compare reproductive strategy of different species and perhaps the most important is some measure of the proportion of the annual capital increment of a plant which is invested in reproduction. Cody (1966) and R. H. MacArthur (unpublished) have argued that the way in which the resources of an organism are proportioned may be of profound ecological importance, particularly in comparative biology. Cody was concerned with clutch size in birds and argued that available energy may be partitioned between three ecologically important ends (amongst others): (a) contributions to r, the intrinsic rate of natural increase (in plants this represents energy put into seed and ramet production); (b) contributions to competitive ability, adaptations in relation to the K value (in plants this presumably represents energy spent in putting leaves higher than neighbours—long petioles, tall stems, or in possessing roots which grow and search faster and further than neighbours); and (c) contributions to predator avoidance (which in plants presumably corresponds to energy spent producing unpalatable structures, defensive chemicals, spines, stinging hairs, etc.).

Few attempts have been made to compare the ways in which different species of plant allocate their limited resources. The procedural difficulties are immense—it is necessary to estimate roots (always an ecologist's nightmare) and to estimate tissues which are shed as the plant grows; there is much difficulty in determining seed output because so many plants shed their seeds over a long period instead of being neat and tidy like crops and holding all their seeds until harvest.

Two examples of attempts to partition a higher plant's activities are shown in Figs. 5 and 6. I suggest that these represent ways of describing the behaviour of a plant which will be of great ecological interest when sufficient examples have been studied for generalizations to be made. It should then be possible to answer such ecological questions as the following:

(1) Is the proportion of a plant's output that is devoted to reproduction higher in colonizing species than in those of mature habitats?

(2) Is the proportion of a plant's output that is devoted to reproduction fixed or plastic? Is it changed by inter- and intraspecific density stress?

(3) Does the proportion of a plant's output that is devoted to reproduction differ between plants of hazardous climatic conditions and those of more stable environments such as a tropical rain forest?

(4) Do plants adapted to competitive environments devote a greater proportion of energy to non-photosynthetic organs (such as support organs)?

(5) Do plants with vegetative reproduction sacrifice a proportion of the energy which would otherwise be expended on seed? Are the two processes competitive within the plant?

(6) What is the relative energy expended in producing a vegetative propagule and a seed? Can this expenditure be related to the relative risks of establishment by the two means and the relative ecological importance of local and long-distance spread?

(7) What is the expenditure on organs ancillary to reproduction—the economic cost to the plant of attractive flowers, a pappus or the massive woody cones of conifers? Is this expenditure a measure of the selective advantages due to possessing these organs?

A whole branch of plant ecology lies almost untouched in attempts to understand the significance of the strategy of reproduction (a very different matter from the tactics—the significance of specific dispersal mechanisms, etc.).

'The only difference between organisms which annually produce eggs or seeds by the thousand, and those which produce extremely few, is that slow breeders would require a few more years to people under unfavourable conditions, a whole district, be it ever so large.'

The strategy of the life cycle itself is an ecologically fascinating but neglected subject of study. Cole (1954) and, more recently, Lewontin (1965) have examined the consequences to population growth of changes in the life cycle of plants and animals. Their studies show that a high intrinsic rate of natural increase (r) can be obtained by producing a few offspring early in life—precocious reproduction is all important. For example, a population of which the individuals produce two offspring in the 1st year of life and then die, will have a potential rate of increase as high as if the individuals produce one offspring every year for ever.

It is instructive to examine the consequences of life cycle strategy in such a species as

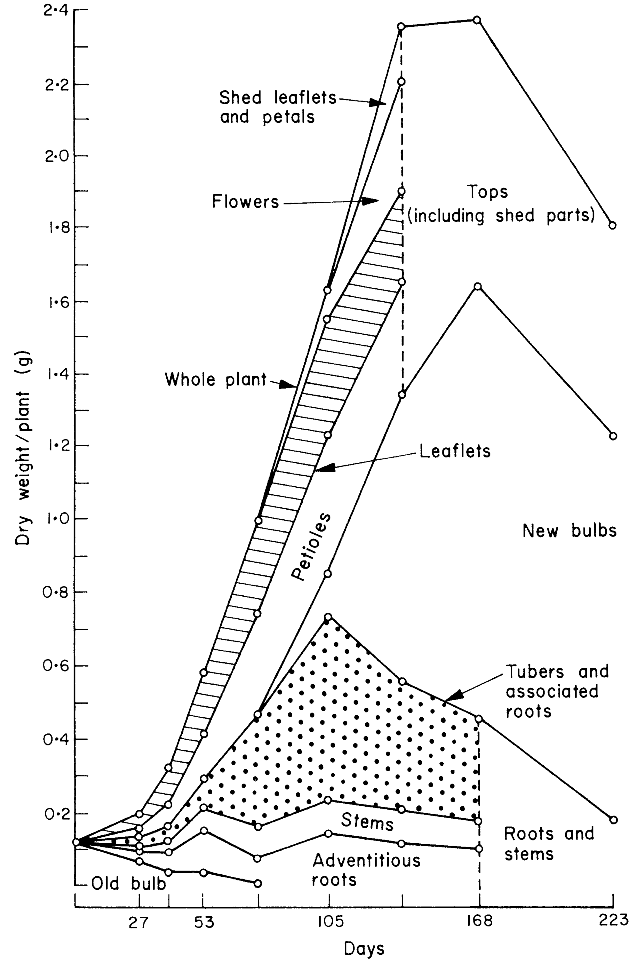

FIG. 5. The pattern of dry weight addition and distribution in *Oxalis pescaprae* L. from the time of planting of the bulb. (Redrawn from Michael 1965.)

the foxglove, which is commonly monocarpic, and under favourable conditions is biennial. In an unexploited environment an annual species producing S seeds per annum could theoretically show a population growth of 1, S, S^2, . . . , S^n in succeeding years. To achieve the same rate of population growth a biennial species would require to produce S^2 seeds at the end of each 2-year period. Thus if a biennial such as the foxglove (*Digitalis purpurea*) produces 100 000 seeds every 2 years, its annual counterpart would require to produce only 333 seeds to achieve the same population growth rate. However, if there is a significant mortality risk which is concentrated in the seed and seedling stage, the annual will experience this risk every year and the biennial only in its 1st year of growth. Thus if the 1st year mortality risk is high, a biennial with seed production $S^{<2}$ will maintain the same population growth rate as an annual with seed production S. Fig. 7 shows the calculated relationships between x, the probability of a seed producing a plant that survives through the first season, and p, the power by which the seed production S of an annual would need to be raised to permit equivalent biennial reproduction. This is shown for various values of S.

The following points emerge: (1) Where $x = 1$, and all seeds produce a mature plant, the biennial must bear the square of the number of the seeds of the annual. (2) As the chance of the plant surviving the 1st year decreases p decreases. (3) At $p = 1$ the biennial produces the same number of seeds as the annual—this corresponds to the state at which each plant, whether annual or biennial, leaves only one replacement. (4) When $p < 1$ the mortality rate exceeds the seed production and the populations decline. It is apparent that a population of annuals producing S seeds per plant will decline faster than one of biennials bearing S seeds per plant.

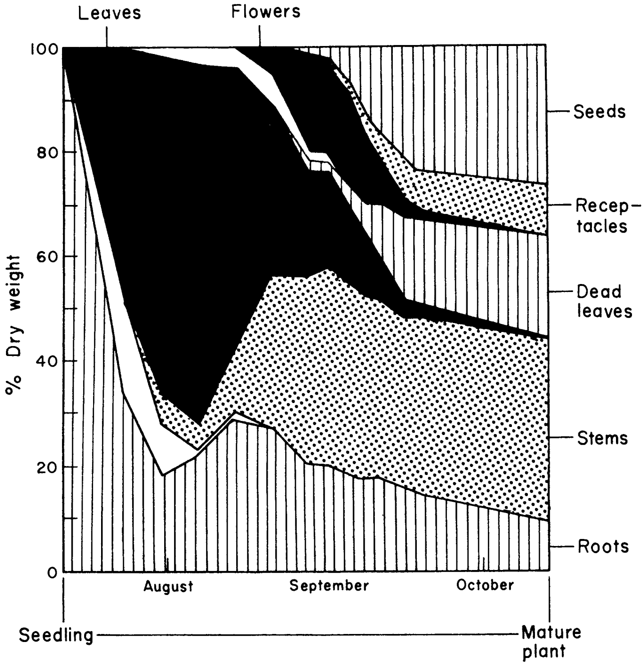

FIG. 6. The proportional distribution of the dry weight of plant parts through the life cycle of *Senecio vulgaris* (data of J. Ogden).

This sort of theoretical argument, even in the simple case argued above, emphasizes the rather subtle interplay between the strategy of the life cycle, the population parameters and the timing of the mortality risk.

Similar arguments can clearly be made for a wide variety of alternative strategies. For example: (a) If seed number is sacrificed in favour of seed size, what increase in survival value of a seed is required to maintain the same potential for population increase? (b) In the face of recurrent hazard conditions, of specified frequency and magnitude, what is the optimal fraction of seeds remaining dormant or undergoing dispersal (see Cohen 1966). (c) In what ways is the optimal strategy altered if overcrowding is a more common experience than unhindered population growth?

The great value of this type of theoretical approach lies in the extent to which it focuses attention on quantitative aspects of the life history and behaviour of species which are of acknowledged importance but have remained part of natural history rather than of science.

Even though a high intrinsic rate of natural increase is of great importance to a colonizing species—and such a high rate can be obtained by precocious reproduction—very few plants use all their reproductive output for immediate multiplication. Seed dormancy is widespread, and it is clear from an elementary consideration of life cycle strategy that a precociously produced seed loses the advantage of precocity if it is unable to start the new generation quickly. An annual colonizing species like *Avena fatua* loses much of its potential rate of population increase by the seed dormancy mechanism which ensures one to several years delay in germination. The adaptive gain from dormancy must be set against an adaptive loss in the intrinsic rate of natural increase. It is all the more interesting that *A. fatua* in the more predictable agriculture and climate of central California seems to lack seed dormancy (Harper 1965).

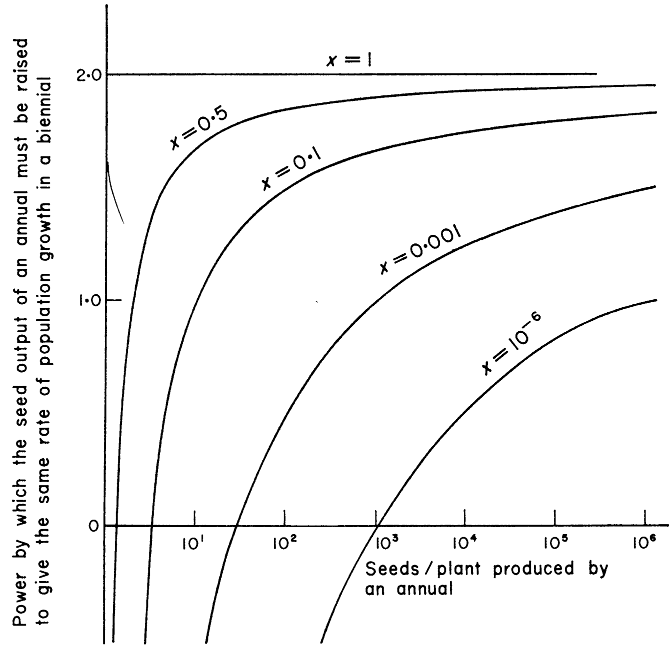

FIG. 7. The theoretical relationship between the seed output of an annual and a biennial for an equal intrinsic rate of natural increase at various values of density-independent mortality (x) where this risk is confined to the 1st year of development (data of R. Oxley).

Much of Darwin's concept of the behaviour of organisms in nature centres around the concept of struggle, '. . . as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life.'

Intraspecific struggle, in which individual development is restricted because of interference from neighbours, has been studied as an agronomic problem—what is the optimal density of plants per unit area needed to achieve maximal dry matter production per area, or maximal economic yield per unit area? At low plant densities plants may not interfere with each other, but as density increases the growth of the population becomes limited by a shortage of environmental supply factors—such as light, water and nutrients—and the growth made by the population becomes a function of the availability of supplies rather than the number of individuals. In many agronomic experiments, self-thinning is absent, so that all density stress is absorbed in the plastic development of the individuals.

Various attempts have been made to fit mathematical relationships to the yield/density responses of crop plants. Amongst the most successful of these have been various forms of the reciprocal yield law

$$\frac{1}{w} = a + bx \text{ where } x = \text{density and } w = \text{mean plant weight.}$$

Various modifications of this basic law are found in the work of Kira, Ogawa & Sagazaki (1953), and other papers of this Japanese School, De Wit (1960) and Holliday (1960). This relationship, which has wide applicability to the study of the behaviour of plants in pure stands, assumes that: (1) the increase in plant dry weight is logistic, (2) the initial growth rate is independent of plant size, (3) the final yield per unit area is constant at high density, (4) time is measured from a common time of sowing, and (5) density-dependent mortality does not occur. If it does, a model similar to that of Yoda *et al.* (1963), discussed earlier, may be preferable.

The major disadvantage of this form of description of population behaviour is that it focuses attention on yield per unit area, or on mean plant behaviour, usually measured by dividing yield per unit area by the number of plants present. This obscures the existence of plant to plant variation. When populations of plants under density stress are examined by sampling and measuring individual plants, curious effects of density on the frequency distribution are revealed. Koyama & Kira (1956) showed that populations of plants which at low density showed normally distributed plant weight, progressively developed log-normal distributions with the passage of time and with increase in density. This phenomenon is shown in Fig. 8 for populations of a variety of fibre flax (Obeid 1965). Stern (1965) has shown the same phenomenon in populations of subterranean clover. It seems that under conditions of density stress not only is there a forced sharing of limited resources with a compensating plastic reduction in individual development, but that a hierarchy emerges amongst the individuals in the population. This hierarchy consists of a few large individuals and an excessive number of small. Such a hierarchy develops in natural habitats as well as in the model crop experiments. R. Oxley has recently shown strikingly log-normal distributions for capsule number per plant in *Digitalis purpurea* in natural habitats and R. Bunce for hazel shoot length in coppices. Apart from the significance of these observations to the interpretation of population samples (in a log-normal distribution the mean plant is *not* the most representative) they show that dominance and suppression may develop within a single species stand. The direct consequences of density stress on a plant population are therefore three-fold: (i) to elicit a plastic response from the individuals as they adjust to share limiting resources, (ii) to increase mortality, and (iii) to exaggerate differentials within the population and encourage a hierarchy of exploitation.

Just as in a population of a single species the stress of density intensifies the expression of small differences (genetic or environmental) between individuals, so in mixed populations density stress may exaggerate and exploit interspecific differences. The experimental models of De Wit (1960) are superbly designed to study the behaviour of two species in mixture and so to begin the exploration of natural diversity. In these models two species are sown together in varied proportions while the overall density of the sown or planted mixture is maintained constant. The behaviour of a species can then be compared in pure stand with its performance in variously proportioned mixtures, and the mutual aggressiveness of two forms may be measured.

Fig. 9 illustrates the use of such an experimental design for the study of the interaction of *Chenopodium album* with barley and with kale. The results of experiments designed in this way may also be conveniently expressed as 'ratio diagrams' relating the sown proportions of two species to the harvested proportions. Such a diagram has considerable value in understanding both the progress of extinction of one species by another and the processes by which an equilibrium between species may be produced. Fig. 10 illustrates some idealized forms of ratio diagrams which are considered in more detail in De Wit (1960).

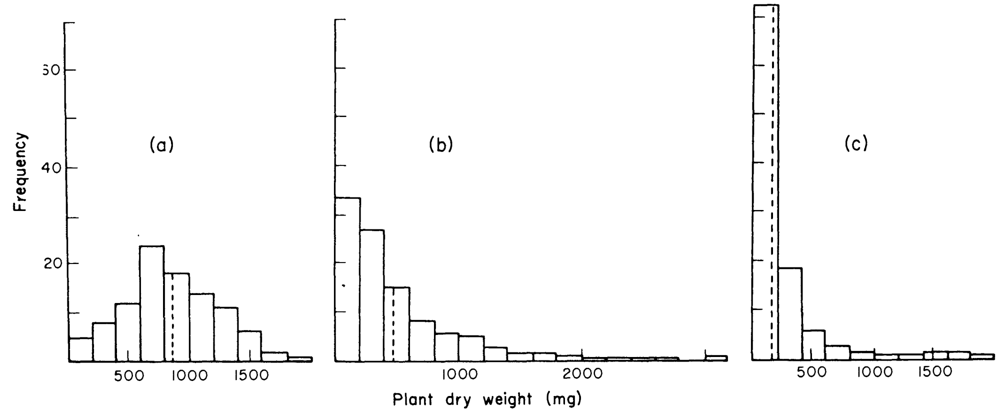

FIG. 8. The influence of density on the frequency distribution of individual plant dry weight in *Linum usitatissimum* sown at densities of (a) 60/m², (b) 1440/m² and (c) 3600/m², and harvested at seed maturity (from Obeid 1965).

Darwin was clearly aware that in nature there is a frequent ousting of one form by another, either over long periods as witnessed in the palaeontological record, involving extinction, or over short periods, involving successional changes of vegetation and purely local elimination. At times he gives the impression that the struggle for existence between forms must lead to a winner and a loser. He sees this as particularly likely between closely related species or varieties. 'In the case of varieties of the same species, the struggle will generally be almost equally severe (*cf. members of the same species*). and we sometimes see the contest soon decided.' But he is also aware that in nature diversity is everywhere, and far from this involving perpetual struggles to extinction 'Battle within battle must be continually recurring with varying success; and yet in the

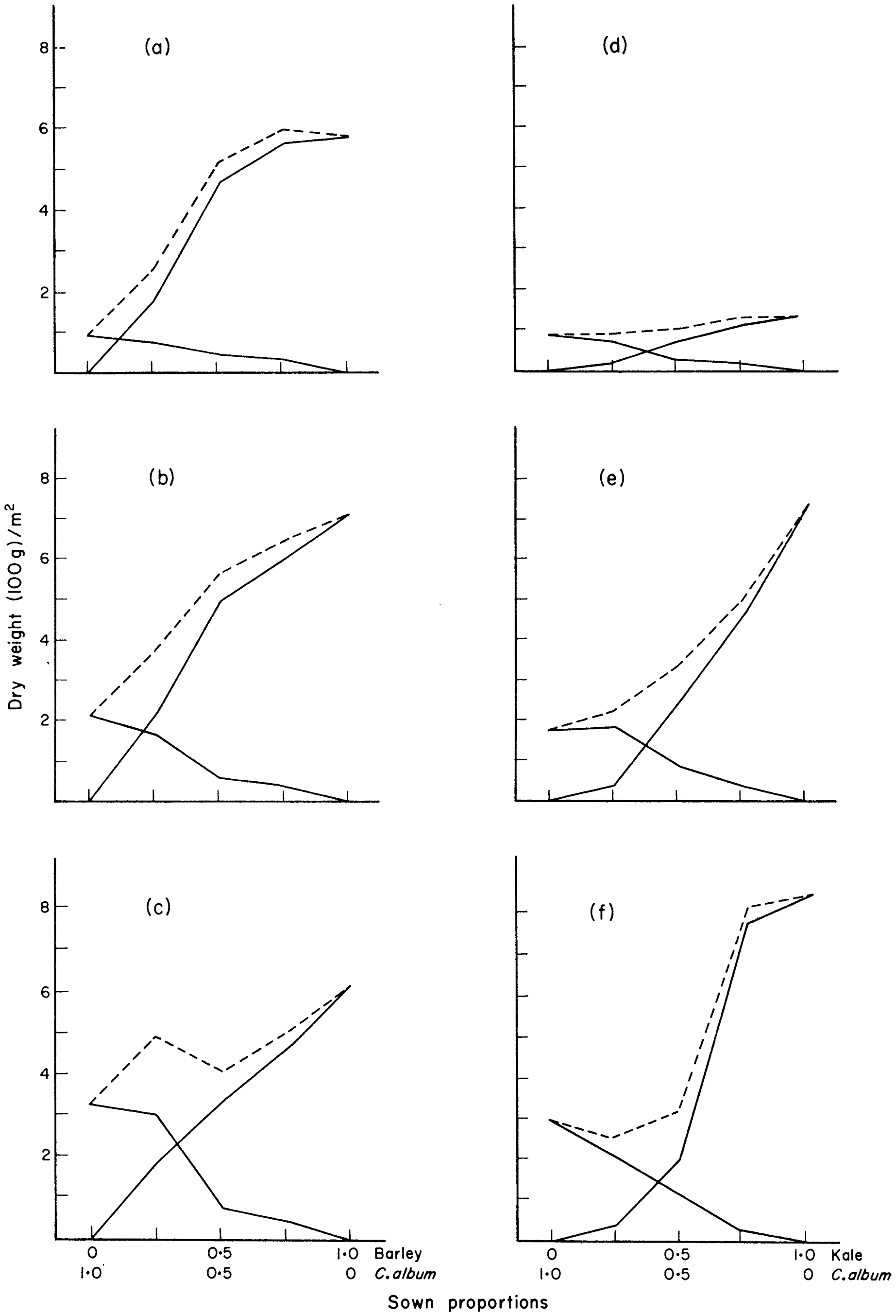

FIG. 9. The influence of proportion of two plant species in mixture at constant density on dry weight per unit area of each component and combined yield (– – – –). (a), (b) and (c) *Chenopodium album* and barley at three successive harvest dates. (d), (e) and (f) *C. album* and kale at three successive harvest dates (from Williams 1964).

long run the forces are so nicely balanced that the face of nature remains for long periods of time uniform, though assuredly the merest trifle would give the victory to one organic being over another.'

The existence of natural diversity implies that the struggle for existence is not regularly forced to decide between stronger and weaker brethren—and that the struggle between some forms living in the same area is either evaded or does not occur. This poses the question which has worried so many zoologists, most notably Gause (1934), Gause & Witt (1935) and Hutchinson (1966) and his various colleagues, what are the characteristics of species which permit them to co-occur in the diversity of nature? This has been examined in great and fascinating detail in experiments and theoretical models and a conclusion is conveniently expressed by Hutchinson in the modified logistic equation of growth for two species living together:

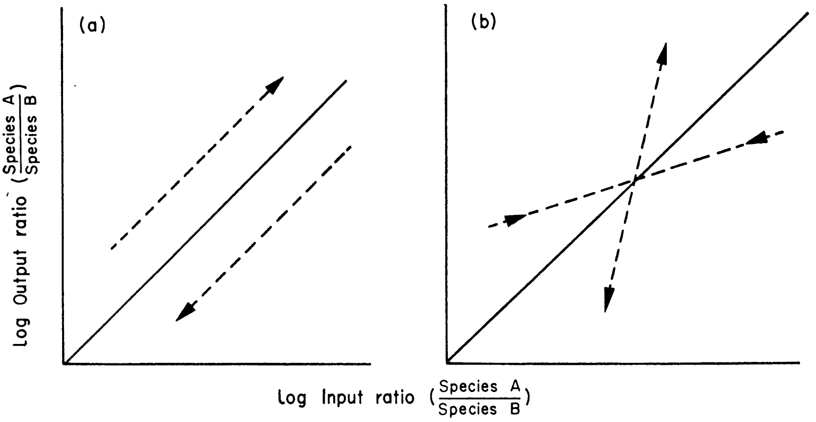

FIG. 10. Theoretical relationships between the input (sown or planted) ratio between two species and the output (seed harvested) ratio. (a) Frequency independence in which the empirical relationship has unit slope (– – →) lying above or below the continuous line which represents input ratio = output ratio. Such situations lead to the progressive extinction of one or other component of the mixture. (b) Frequency dependence in which the empirical relationships have a slope > or < unity (– – →) and intersect the line of input ratio = output ratio. A slope of > 1 implies that the population moves towards the extinction of the minority component. A slope of < 1 implies equilibration and stabilization of the mixed condition.

$$\mathrm{d}N_1 = r_1 N_1\left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)$$

$$\mathrm{d}N_2 = r_2 N_2\left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right)$$

where N_1 and N_2 are the numbers of individuals of species S_1 and S_2.

The conditions under which both S_1 and S_2 survive is that $\alpha < K_1/K_2$ and $\beta < K_2/K_1$, or that the growth of each species population inhibits its further growth more than it inhibits that of the other species. This solution assumes a linear competition function, and there are likely to be further solutions where the function is not linear. This solution generalizes a host of differences between organisms which may permit them to evade a struggle to the death and so permit diversity. In animals it is easy to see that differences in food taken or in feeding habits, differences in habitat preference, differences in prey (or in predators) may prevent an exclusive struggle by focusing the intensive battles within rather than between the species. In plants it is less easy to see how a group of species which all require the same basic food requirements—light, water and mineral nutrients—may possess sufficiently diverse biologies to prevent a best species from excluding all others. There are, however, a number of experiments which show that mixtures of two plant species may form stable associations and indeed possess self-stabilizing properties.

Van den Bergh & De Wit (1960) grew *Phleum pratense* and *Anthoxanthum odoratum* together in field plots at a range of proportions and compared the ratio of tillers of the two species after the first winter with the ratio after the second winter (Fig. 11). In plots in which *A. odoratum* had been in excess, the proportion of *Phleum pratense* increased. Where *P. pratense* was in excess, *Anthoxanthum odoratum* increased. Thus the mixture possessed self-stabilizing properties—the stable mixture under this set of environmental conditions being the point at which the experimentally obtained ratio line A–B on Fig. 11 intersects with the line of unit slope C–D (cf. Fig. 10). In a similar experiment performed in a controlled environment chamber, *A. odoratum* was at a slight advantage over *Phleum pratense* at all relative frequencies, and at all proportions and the population changed regularly towards increasing dominance by *Anthoxanthum*.

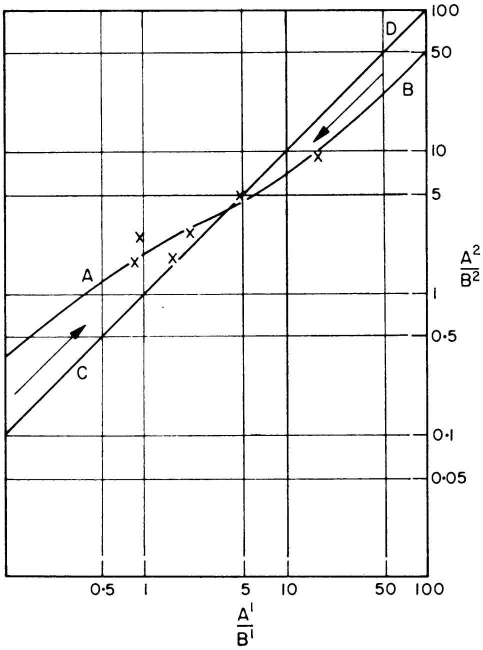

FIG. 11. The relationship between the ratio of the number of tillers of *Anthoxanthum odoratum* (A) and *Phleum pratense* (B) after the first winter (A^1/B^1) and after the second winter (A^2/B^2). (Redrawn from Van den Bergh & De Wit 1960).

A stabilizing situation is also found in mixtures of *Lolium perenne* and *Trifolium repens*. Lieth (1960) has described how in pastures these two species form a moving mosaic in which patches of the mosaic dominated by grass tend to be invaded by clover, while patches dominated by clover are overrun by grass. Ennik (1960) grew *Lolium perenne* and *Trifolium repens* in mixtures of varying proportions in controlled environments at high and low light intensities. Ratio diagrams relating the proportion of the two species at the beginning and end of the treatment are shown in Fig. 12. At high light intensity the populations changed regularly towards extinction of the grass. At low light intensities the populations equilibrated, those with excess clover tending to increase their grass content, and those with excess grass tending to increase in clover. In this example the ecological differentiation between the species which permits this stabilization is almost certainly due to differences in their nitrogen nutrition.

A further example of stabilizing action in mixture has been demonstrated by P. D. Putwain for the sexes of the sexually dimorphic *Rumex acetosella*. In permanent grasslands this species only rarely reproduces by seed and the main means of spread is by root buds. In dense stands the two sexes are therefore the equivalent of two species with different biologies, one having the whole task of seed production and the other the apparently light responsibility of producing pollen. It might be expected that two such forms would differ in aggression in the community and that in old pastures the 50 : 50 sex ratio of seedlings would become biased. In fact, natural populations have been shown by Löve (1944) and many others to have a sex ratio not departing significantly from equality.

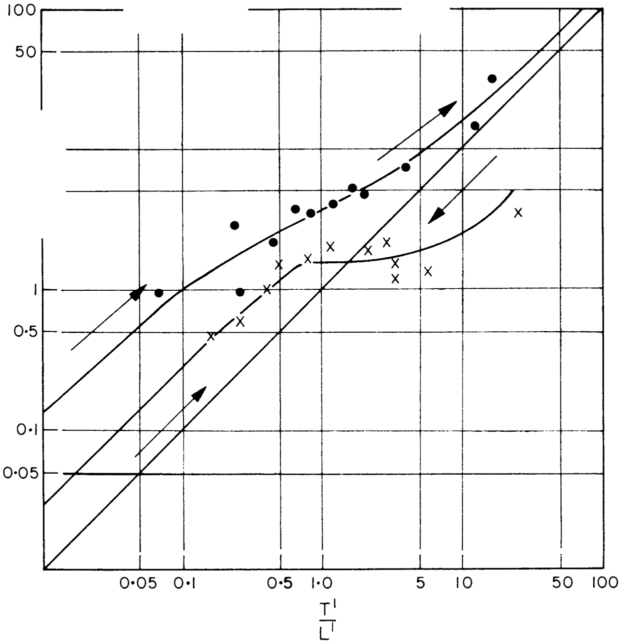

Fig. 12. The ratio of the length of stolons of *Trifolium repens* (T) and the number of tillers of *Lolium perenne* (L) in the first winter (T^1/L^1) plotted against the same ratio in the second winter (T^2/L^2). ●, At high light intensity; ×, at low light intensity. (Redrawn from Ennik 1960.) The same data are presented with calculated linear regressions in De Wit *et al.* (1960).

An experiment was designed on the 'De Wit' model to study the population balance of the sexes in this species. Clonal populations of males and of females were obtained from root fragments and were grown at various proportions at low and high densities. The results of the high density treatment are shown in Fig. 13. Populations with an excess of males increased the proportion of females, and those with excess females increased the proportion of males. Experimental distortion of the sex ratio from equality led to readjustment towards equality as a result of the more vigorous reproduction by the minority sex.

In the three experiments described above, reproduction was clonal and the adjustment of balance between the species (or sexes) was by differential vegetative reproduction. All these examples illustrate the essential criterion for a balanced 'co-occurrence' of two species—that the minority component should always be favoured.

A similar model was shown by Harper & McNaughton (1962) for the survival of *Papaver* spp. sown in mixture. In this case each individual of a species in a mixture of two species had the greatest likelihood of becoming an adult plant when it was in the minority. In the discussion of the poppy experiments we contrasted 'self-thinning' (the reaction of a species to an increase in its own density) with 'alien-thinning' (the reaction of a species to the density of its associated species). These experiments suggested that each species in a mixture suffered more severely from intra- than from interspecific interference. It was argued that this was a necessary condition for stable diversity. It is interesting to find that a similar differentiation between self- and alien-thinning occurs in mixtures of *Medicago sativa* and *Trifolium pratense*. Black (1960) sowed these two species in variously proportioned mixtures, and recorded plant survival. From his data it is possible to calculate the chance of a seed forming a plant and this is shown for two ranges of density in Fig. 14. The nature of the differences between poppy species and between *Medicago sativa* and *Trifolium pratense* which alleviate interspecific interference are obscure. It is presumably an understanding of these critical differences between species that will provide the 'explanation' of stable diversity in nature.

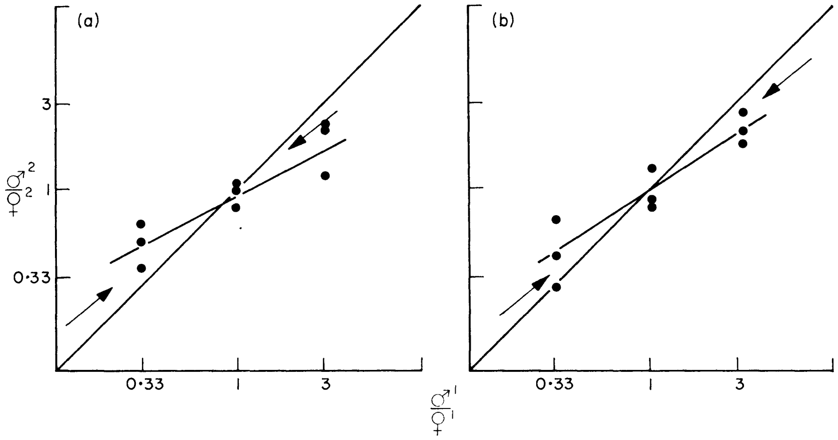

FIG. 13. The ratio of male to female plants of *Rumex acetosella* planted in the spring ($♂^1/♀^1$) plotted against the same ratio in the autumn ($♂^2/♀^2$). (a) Dry weight of above ground parts, (b) number of inflorescences (data from P. D. Putwain). Values for three replicates are shown individually.

In the various models of the behaviour of two species in mixture, the existence of a stable equilibrium depends on *frequency-dependent* 'competition'. This phenomenon has recently been recognized by Pavlovsky & Dobzhansky (1966) in *Drosophila* cultures, and, as they point out, it plays havoc with the Sewall Wright concept of adaptive values.

Selection genetics is therefore forced to take account of fundamental ecological phenomena and the convergence of population genetics and population ecology provides one of the most exciting fields of development in modern biology.

Recently there has been growing interest in the genetic consequences of a struggle for existence between two populations and the ecological significance of these changes. The experiments have all involved flies, and in a lecture on plant ecology I have assumed that *Drosophila* (by usage) and all flies (by analogy) are appropriate objects for botanical study!

Pimentel *et al.* (1965) allowed populations of blowflies and houseflies to multiply with a controlled food supply in a network of interconnected population cages. He observed oscillation in the populations of the two species. By sampling and testing his two populations against each other at intervals he was able to show that there was an oscillation in the 'competitive ability' of the two species. He argued that in a mixture the minority species faces predominantly interspecific interference, and is therefore under selection to improve its performance relative to the majority species. The majority species, however, experiences predominantly intraspecific interference and hence selection within it is concentrated on qualities important in the intraspecific struggle. The minority species eventually gains the majority because of its newly selected qualities, and interspecific selection immediately concentrates on the new minority species. The two species thus oscillate in relative abundance. Pimentel shows that the amplitude of oscillations may become progressively damped and he suggests that the two species are attaining an equilibrium.

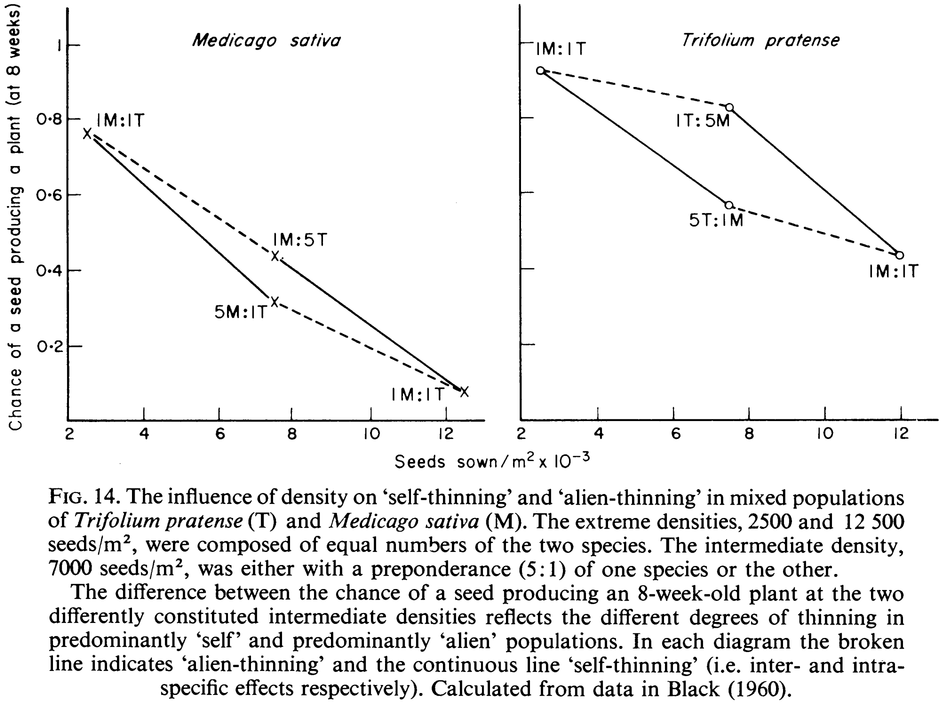

FIG. 14. The influence of density on 'self-thinning' and 'alien-thinning' in mixed populations of *Trifolium pratense* (T) and *Medicago sativa* (M). The extreme densities, 2500 and 12 500 seeds/m^2, were composed of equal numbers of the two species. The intermediate density, 7000 seeds/m^2, was either with a preponderance (5:1) of one species or the other.

The difference between the chance of a seed producing an 8-week-old plant at the two differently constituted intermediate densities reflects the different degrees of thinning in predominantly 'self' and predominantly 'alien' populations. In each diagram the broken line indicates 'alien-thinning' and the continuous line 'self-thinning' (i.e. inter- and intraspecific effects respectively). Calculated from data in Black (1960).

Seaton & Antonovics (1967) reared wild type and 'dumpy' *D. melanogaster* in milk bottle cultures. The two forms were reared in mixtures, but care was taken that mating did not occur between them (by removing virgin females and mating them with males of the same type from their own culture). Each succeeding generation was started with six wild type and six dumpy flies from the preceding experiment, and the food supply was limited. After four generations the two mutually selected populations were tested against each other and against stock populations using a 'De Wit' model for the experimental testing. The results are shown in Fig. 15.

The results of mutual selection were at first sight surprising. Instead of one type of fly acquiring increased success in a struggle for existence the selection process seems to have resulted in an ability of the wild type and the 'dumpy' fly to avoid interference from each other. At the end of the experiment neither wild type nor dumpy had as depressive effect on the other, as did mutually unselected strains. Moreover, the mutually selected strains grown together achieved a greater output of offsprings than did either of the stock types grown in pure culture.

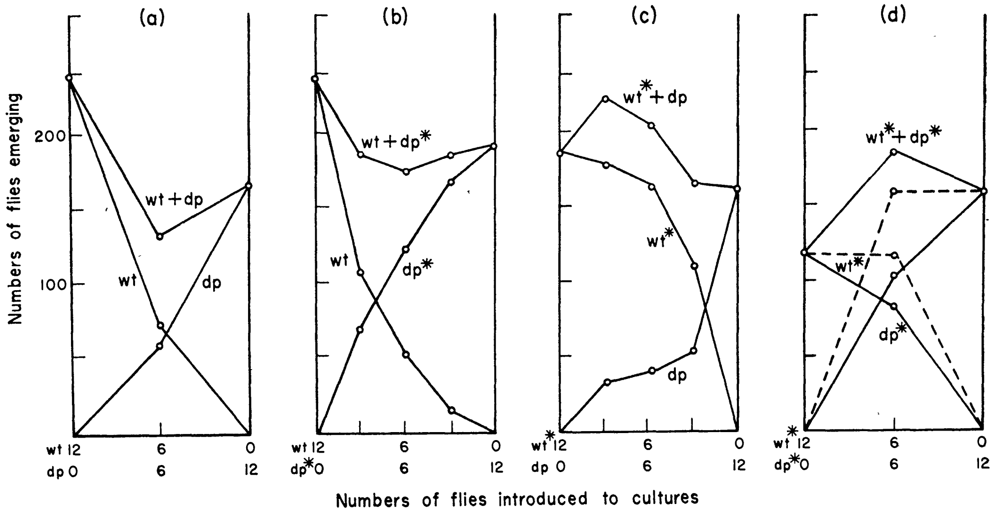

FIG. 15. The results of a replacement experiment (cf. Fig. 9) involving wild type and dumpy *Drosophila melanogaster* grown in pure cultures and mixtures. The two forms were prevented from mating with each other.

The success of each component in mixture and pure culture was assessed as the number of offspring hatched in the first generation of progeny. (a) Stock 'wild type' with stock 'dumpy'. (b) Stock 'wild type' with selected 'dumpy'. Selected 'dumpy' had experienced four repeated generations in mixed culture with 'wild type'. (c) Selected 'wild type' with stock 'dumpy'. Selected 'wild type' had experienced four repeated generations in mixed culture with 'dumpy'. (d) Selected 'wild type' with selected 'dumpy' (after one further generation of relaxed selection). – – –, Replicate experiment; wt, Stock wild type; wt*, selected wild type; dp, stock dumpy; dp*, selected dumpy. (From Seaton & Antonovics 1967.)

This would appear to be a case of direct selection for some difference in niche occupancy, the evolutionary process which Ludwig (1950) has called 'annidation'.

The experiments of Pimentel and of Seaton & Antonovics illustrate three different evolutionary solutions to the problem of intergroup struggle for limited resources: (i) extinction of one group, (ii) mutual oscillating inter-group selection leading to increased stability of the mixture (the Pimentel solution), and (iii) mutual divergence in behaviour leading to the avoidance of inter-group struggle (the Seaton–Antonovics solution).

Both (ii) and (iii) imply that in the process of natural selection the reaction to the other species may be a critical force '. . . . the structure of every organic being is related, in the most essential yet often hidden manner, to that of all the other organic beings, with which it comes into competition for food or residence, or from which it has to escape, or on which it preys.' Goodall (1966) has recently argued a similar point, though he despaired of the chance of demonstrating such coadaptive evolution in action.

The concept of natural selection operating between groups of organisms and adjusting their mutual strategies to permit increasing diversity and more efficient environmental exploitation strengthens the image of the community as an integrated whole rather than a Gleason-type assemblage of individuals.

The logical extension of the view that community stability and diversity depend on niche specialization, is that complex ecosystems are more efficient than simple in using environmental resources. Yet the rigid demonstration that mixtures of plant species outyield pure stands seems not to have been made. Darwin wrote 'It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater dry weight of herbage can be raised in the latter than in the former case.' More than 100 years later, the Director of the Grassland Research Institute writes 'No research, as far as I am aware, has yet shown that a mixture of two or more grass species, when sown together, will outyield the crop that can be obtained from a single bred variety' (Woodford 1966). Perhaps the answer to this contradiction lies in the degree to which the forms that are grown together have been mutually selected. It may be too much to hope that any pair of species grown together will already possess the precise biological differences needed to interniche or annidate effectively. Perhaps special breeding programmes are needed to develop 'ecological combining ability' (Harper 1964b) in agricultural crops.

With the exception of examples of mutual exploitation of the light environment shown by the studies of Salisbury (1916) in woodland—there are few demonstrations that stable mixed vegetation is compounded of ecologically complementary species. Recently, a number of experimental designs have been suggested which permit the 'ecological combining ability' of groups of species to be examined, in the same way that a plant breeder explores the 'genetic combining ability' of a range of genotypes (Sakai 1961; Williams 1962; McGilchrist 1965; Harper 1964b; Norrington Davies 1967). These are all based on diallell analysis, in which a number of species are grown in all possible combination of pairs and their yield as mixtures is contrasted with the yield of pure stands. In this way the ecological equivalents of the genetic concepts of dominance, recessiveness, overdominance and interaction can be detected and—more important—measured. These techniques seem likely to bring to experimental synecology a refinement and subtlety appropriate for a science which has outgrown its qualitative and descriptive youth.

It is impossible in the time of one lecture to do justice to the range of ecological thought and the stimulus to modern experimental ecology to be found in just two chapters of *The Origin of Species*. I have wholly omitted the fascinating matter of animal–plant interactions that play so large a part in Darwin's ecology. I am not amongst those very few ecologists since Darwin who are intellectually equipped to deal with the plant–animal interface. My aim has been to try to show that much of what is exciting to me in the science of plant ecology in the late sixties has a highly respectable origin in the ecological thinking of Darwin. 'It is never safe for a biologist to announce a discovery if he has not read and mastered *The Origin of Species.*' (Keith 1928). A presidential address is a rare opportunity for a personal expression of belief. My own is that *The Origin of Species* states precise questions which plant ecologists can usefully spend the next hundred years answering.

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