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The Population Dynamics of Plants [and Discussion]

Michael J. Crawley and G. J. S. Ross

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The population dynamics of plants

MICHAEL J. CRAWLEY

Centre for Population Biology, Department of Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, U.K.

SUMMARY

Long-term studies of plant populations are reviewed, and their dynamics summarized in three categories. Many short-lived plants have ephemeral, pulsed dynamics lasting only a single generation, with recruitment determined almost entirely by germination biology and by the frequency and intensity of disturbance. Such populations are not amenable to traditional population models. At the other extreme, some long-lived plants have such protracted tenancy of their microsites that it is impossible to establish what pattern of dynamics (if any) their populations exhibit. A relatively small number of species show what we would traditionally regard as population dynamics at a given point in space (i.e. reasonably predictable trajectories that can be modelled by $N_{t+1} = f(N_t)$). A major difficulty in generalizing about plant dynamics is that the majority of species are successional; their recruitment depends upon the death, through senescence or disturbance, of the dominant plants. Where we do have data spanning several generations, it is clear that: (i) the populations are regulated by density dependent processes; (ii) in contrast to some animal populations, numbers appear to vary less from year to year in places where mean density is higher, and less from place to place in years when mean density is high than when density is low; (iii) few, if any, plant populations show persistent cyclic or chaotic dynamics, but (iv) there are several robust generalizations that stem from the immobility and phenotypic plasticity of plants (the law of constant yield; self-thinning rules, etc.). These generalizations are analysed in the context of simple theoretical models of plant dynamics, and the patterns observed in long-term studies are compared with similar data from animal populations. Two important shortcomings of traditional plant demography are emphasized; (i) the dearth of simple manipulative experiments on such issues as seed limitation, and (ii) the tendency to locate study plots around existing mature individuals (the omission of 'empty quadrats' may introduce serious bias into the estimation of plant recruitment rates).

1. INTRODUCTION

The idea of counting plants has never had widespread appeal. There are two main reasons for this. First, the longevity of plants is such that one individual may survive for many human lifetimes. Second, the phenotypic plasticity of plants is so great that the fecundity of the same individual genotype may vary by four orders of magnitude, depending upon the circumstances of its cultivation. There is a further general problem about what precisely to count. In animal ecology is taken as axiomatic that counting refers to individual, free-living genets (Harper 1977). Plants, however, are modular in construction and for most practical purposes it may make more sense to estimate the plant biomass rather than to count the number of individual genotypes. Again, it is unclear whether a count of the numbers of shoots per genet, or of the number of modules per shoot is the most appropriate currency for assessing plant abundance. The traditional distinction in population biology between plants and animals is not really taxonomic, but based on a comparison of mobile unitary organisms with sessile, clonal organisms. The population dynamics of sessile animals (like corals or sponges) and of mobile plants (like diatoms and non-rooted aquatics) have received very little attention.

(*a*) *History of plant dynamics*

The first published counts of plants refer to rarities, and to the documentation of the demise of much-loved species (e.g. successive presidents of the Tyneside Natural History Society, Carr (1848) and Burdon (1856), described the decline of the lady's slipper orchid in Castle Eden Dene, County Durham, to its local extinction in about 1850).

The idea of counting common plants is very much a 20th century pursuit. Work in the arid S.W. of the U.S.A. during the first decade of this century enumerated the decline of conspicuous plants like the saguaro cactus (*Carnegiea gigantea*) and the increase of invasive woody plants like mesquite (*Prosopis glandulosa*) with the advance of cattle ranching. The first permanent quadrats in which plants were routinely counted were set up by V. M. Spalding in 1906 at the Carnegie Institute's desert laboratory at Tumamoc Hill in Arizona (Hastings & Turner 1965). Results from these quadrats documented the gradual increase of grazing sensitive and the decrease of uncompetitive plants following fencing to exclude the cattle (Goldberg & Turner 1986). The discrete morphology and wide spacing of these desert plants may have been conducive to counting. None of the species exhibited any dramatic ups or downs, and none showed any signs of cycling.

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The famous Park Grass and Broadbalk experiments at Rothamsted, England, were set up much earlier than this (in 1840s and 1850s), but they were concerned with changes in plant biomass rather than with the determination of plant population density (Williams 1978).

(*b*) *Plant population biology*

It is worth cataloguing some of the important attributes of plant morphology because their impact on population dynamics is so profound. (i) Plant size is extremely plastic, as we have already seen. (ii) The sedentary, rooted habit means that neighbour relations are vital. Plant performance can often be accurately predicted simply from knowledge of the number of neighbouring plants that are bigger than the plant in question (Hutchings 1986). (iii) Successional change in plant communities may be the rule (rather than the exception as is implicitly assumed in many animal population models). Thus the probability of recruitment may change systematically through time, independent of the reproductive performance of the plant species in question. (iv) Recruitment may be infrequent and unpredictable. Some plant species, like seed-bank annuals, may have population dynamics that are determined more by their germination biology (the duration of dormancy and the stimuli necessary to break dormancy) than by the number of seeds produced in the previous generation. (v) Competition is asymmetric. Larger plants influence the growth and reproduction of smaller ones, but small plants rarely have measurable impact on the performance of larger ones. (vi) Mortality is size dependent. The plants that die as a result of plant competition come exclusively from the smallest size classes. (vii) The death of large plants from old age, accident, or herbivore attack, may open up conditions for recruitment (Grubb 1988).

2. PATTERNS OF DYNAMICS

There is no typical pattern of plant dynamics. Instead, we observe a continuum from virtual stasis (e.g. very long-lived desert shrubs that have shown no recruitment since records began) to violent year-to-year fluctuations in abundance (e.g. desert annuals whose recruitment is controlled by the intensity of rainfall). Within this continuum, there are habitat differences (associated with the frequency and intensity of disturbance) and differences associated with plant life history (principally longevity and the degree of iteroparity). The degree to which plant dynamics are affected by internal, over-compensating density dependent processes of the kind that might lead to cycles or to chaotic dynamics is unclear, and examples are few.

The role of herbivores in affecting plant abundance and the stability of plant populations is potentially great, and appears to be related to the body size, mobility and degree of monophagy of the herbivores involved. For example, large, mobile, polyphagous vertebrate herbivores tend to have more impact on plant dynamics than small, sedentary, monophagous insect herbivores (Crawley 1989).

(*a*) *Episodic recruitment*

Many plant populations consist of only one or two age classes, and any given age class may cover areas of many square kilometres. The forces responsible for creating these large, single-aged patches include fire (Noble 1989), tropical storms (Whitmore 1989), volcanic eruption (Mueller-Dombois 1981), drought (Hubbell & Foster 1990), unusually heavy rains (Epling *et al.* 1960), and epidemic disease among keystone herbivores (Crawley 1983).

Many annual plants of arable land will not produce any seedlings at all unless there is cultivation or other soil disturbance sufficiently severe to open up large gaps in the perennial plant cover. These annuals typically possess long-lived seed banks, and some of them have very precise germination requirements, such that the weed flora that develops in the first year after cultivation depends critically upon the timing of soil disturbance.

The agricultural practice of fallowing is intended to cause mass germination of dormant seeds, then to kill the plants by cultivating again before any of them have set seed. Fallowing has varying degrees of success with different species of annual weeds. Some like the poppy *Papaver rhoeas* have such large seed banks, that one year's germination causes no significant decline in seed bank numbers. Others like the grass *Alopecurus myosuroides*, have their numbers substantially depleted by fallowing, but are so fecund in the low competition environment that occurs after a successful fallow, that the few surviving plants grow so large that the seed bank is replenished in a single year (Brenchley & Warrington 1930).

(*b*) *Ephemeral populations*

John Harper has remarked that it is the fate of most populations studied by plant ecologists to go extinct during the course of the study. This is graphically shown on the cover of the thesis by de Jong & Klinkhamer (figure 1), and documented by the local demise of *Vulpia membranacea* (Watkinson 1990) shown in figure 2. In such cases, the conditions favouring plant recruitment are not met within the quadrats where the initial cohort of adult plants was selected. The only solution to this problem is to ensure that 'empty quadrats' are included from the outset of the project (i.e. potentially habitable sites from which the adult plants are currently missing). Ideally, the quadrats should be placed at random within suitable habitats, but this is rarely done in practice.

The notion of potentially habitable sites begs several questions. A sample of unoccupied sites is almost certain to contain an unknown proportion of potentially occupiable but currently unoccupied sites, plus a proportion of genuinely uninhabitable sites. If, for simplicity, we were to assume that plants were distributed over the suitable sites in a Poisson manner, then the whole set of quadrats would represent a

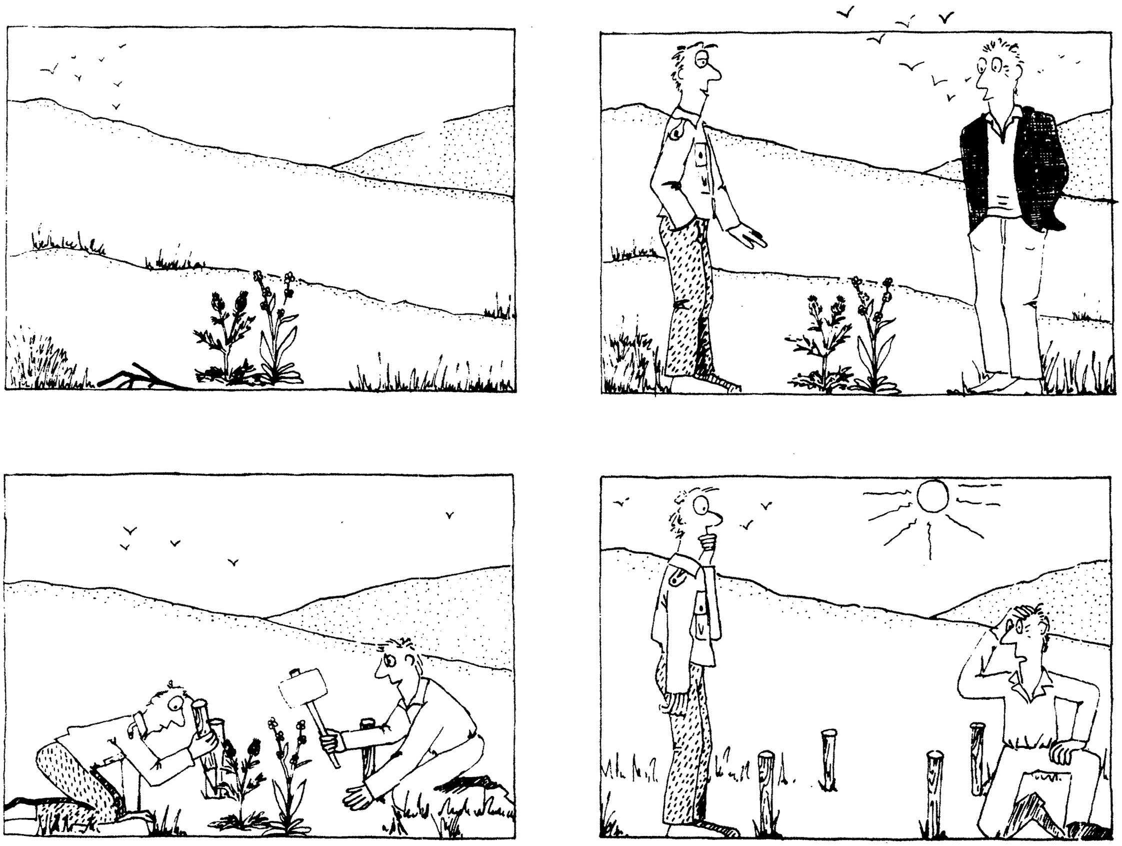

Figure 1. The cover from the doctoral thesis of Tom De Jong and Peter Klinkhamer (1986), showing the demise of plant populations singled out for detailed study.

'Poisson plus added zeros' and would be bound to exhibit an artificially aggregated pattern (Pielou 1977). Again, a quadrat that is empty of adult plants may contain countless dormant seeds within the seed bank beneath it, so 'local extinction' in these cases should strictly be read as 'current absence of vegetative plants'.

(*c*) *Self-replacing, equilibria*

Seed-limited dynamics have been studied by a number of theorists (Watkinson 1986; Pacala & Silander 1985) and described from a few field systems (Symonides *et al.* 1986) and experimental trials (Pacala & Silander 1990). One strong generalization appears to be that populations can get to their carrying capacity extremely quickly, and often in as little as one or two generations (e.g. the annual grass *Poa annua*; Law 1981). Slower increases may be indicative of microsite limitation rather than seed limitation (Rabinowitz *et al.* 1989). In many cases, the carrying capacity itself will fluctuate from generation to generation, so that the resulting dynamics may reflect more about shifts in recruitment and microsite availability than any internally generated, cyclic tendencies.

(*d*) *Model populations*

The model of plant population dynamics that forms the central organizing theme of this paper was described by Crawley (1986). We depict the rate of change in plant numbers, $\mathrm{d}N/\mathrm{d}t$, as a function of six controlling processes, and we require that the rate of change is positive, at least when the plant is rare:

$$
\begin{aligned}
\mathrm{d}N/\mathrm{d}t = {} & \text{intrinsic rate of increase of the plant} \\
& -\text{resource-limitation effects} \\
& -\text{interference effects} \\
& -\text{herbivore and pathogen effects} \\
& -\text{mutualist-limitation effects} \\
& +\text{refuge effects}
\end{aligned}
$$

The intrinsic rate of increase is known for rather few plant species. The potential fecundity of plants is extremely high, of course, but the minimal level of mortality that is to be expected under the best possible conditions is unknown (see Crawley 1989). The intrinsic rate of increase of crop plants has been known since Biblical times to be between 30-fold and 100-fold per generation (St Matthew 13). There is no information at all on the intrinsic rate of increase of longer lived plants like trees, although some simple approximations may be possible (Crawley 1983, p. 28).

The effects of competition for light, water and nutrients have been studied intensively, and competition-based models of dynamics are quite numerous (Watkinson 1986; Pacala & Silander 1985; Crawley & May 1987). It has long been implicit among plant ecologists that asymmetric interspecific competition for light is the driving force in the dynamics of most plant communities (and competition for water in desert environments).

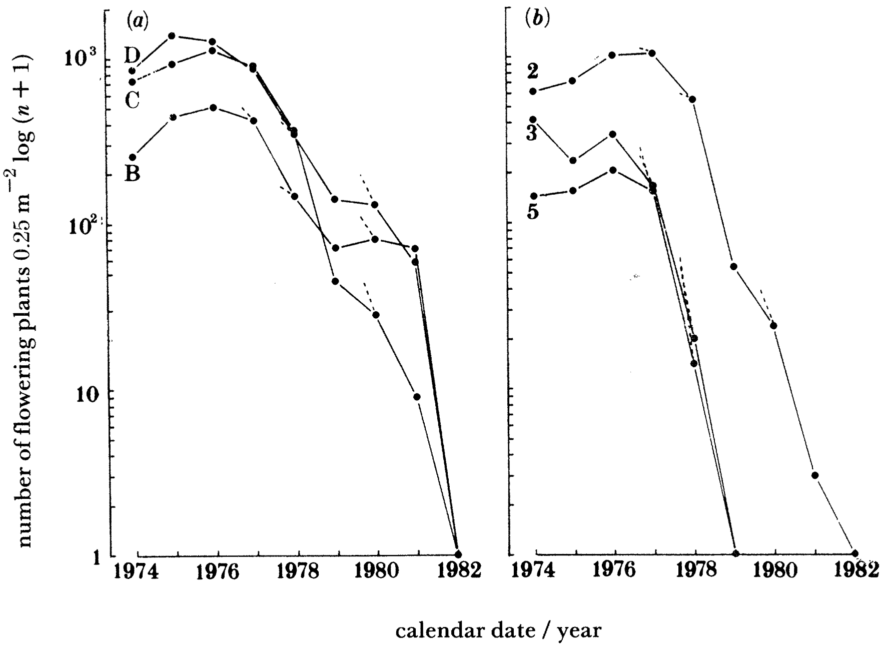

Figure 2. The demise of local populations of the annual grass *Vulpia fasciculata* on sand dunes in North Wales. Conditions for recruitment deteriorated over the course of the study period as a result of changes in the pattern of movement of surface sand (from Watkinson 1990). The number of flowering plants of *Vulpia fasciculata* on (*a*) plots *B*, *C* and *D* at Aberffraw and (*b*) plots 2, 4 and 5 at Newborough Warren between June 1974 and June 1982. The number of individuals dying at the stage of inflorescence development is shown by the dashed lines.

Behaviourial interactions between plants in the form of chemical warfare (allelopathy) have been as comprehensively ignored by modellers as they have been enthusiastically documented by field workers (Rice 1984). There has been a view (Harper 1977) that it is so difficult to show the importance of allelopathy unequivocally under field conditions, that it can safely be ignored. While it is true that allelopathy experiments need be carefully designed to eliminate other possible causes of differences in plant performance (herbivory, resource competition), the role of allelopathy in plant dynamics, and in successional dynamics in particular, deserves a reassessment.

The effects of herbivory on plant dynamics are reviewed elsewhere (Crawley 1983, 1989). The important point is that relatively small changes in competitive ability may be sufficient to tip the balance in favour of one plant species over another, and that selective herbivory (taking 5–15 % of leaf tissue) may be just the kind of mechanism to bring about such changes (Crawley & Pacala 1990). The relative importance of vertebrate and invertebrate herbivory is readily seen from a comparison of fencing exclosures against vertebrates and insecticide spraying against invertebrates. Crawley (1989) found that the identity of the dominant plant was almost always changed after the exclusion of vertebrate herbivores, and that measurable change in plant relative abundance occurred in more than 90 % of studies. Of the 30 or so studies of insect exclusion in natural vegetation, only half produced measurable impact and the effects on plant abundance were often subtle. Thus, while fence-lines excluding vertebrate of often conspicuous landscape features, the edges of insecticide-sprayed plots are seldom so clear-cut. Plant pathogens can inflict highly selective mortality on seedlings, and may have a substantial impact in determining the identity of recruits, especially in tropical plant populations (Burdon *et al.* 1981: Augspurger & Kelly 1984). Long-term data on pathogen-exclusion trials in natural vegetation are not yet available.

Mutualists are often omitted from models of plant dynamics. This is despite the fact that a number of convincing data sets show that recruitment may be limited by a shortage of pollinators (see below). The absence of specific mycorrhizal fungi may be the reason that orchids have such low rates of establishment in many habitats. In general, it is preferable to include mutualism in models as a negative rather than a positive factor, since the benefits of mutualists saturate very quickly. This avoids, in Bob May's graphic phrase, the 'orgy of mutual benefaction', that would result from including mutualists and hosts as being reciprocally beneficial in a Lotka–Volterra-style model of mutualism.

Refuge effects include a variety of stabilizing influences that provide a positive input of propagules, even when the local above ground plant population has gone extinct. There may be subterranean reserves of ungrazable meristems (Noy Meir 1975), long-lived seed banks (Roberts 1981) or immigration of wind borne or animal carried seeds from elsewhere (Rabinowitz *et al.* 1989). In some cases, recruitment from these refugia may be greater than from current reproduction, so that traditional models of the form $N_{t+1} = \lambda N_t f(N_t)$ become wholly inappropriate.

(*e*) *Dynamics*

For the species and the environment in question we have defined that $dN/dt > 0$ when rare, so that exponential increase in plant abundance is to be expected. The question of interest, therefore, is what determines the average level of abundance, and what determines the pattern of fluctuation about that average? What is the role of endogenous, time-lagged density dependent processes within the plant population (e.g. the tendency to cyclic or chaotic dynamics), and what is the relative importance of exogenous variation in producing catastrophic plant mortality or causing random fluctuations in plant recruitment (environmental stochasticity)?

Two aspects of plant population biology have a profound bearing on these questions. First, the size-specific fecundity of plants is such that in most reported cases, seed production is directly proportional to shoot mass, and there is no evidence for a threshold plant size below which reproduction is impossible (Rees & Crawley 1989) (figure 3*a*). This means that substantial changes in the size structure of the plant population (e.g. as a result of intraspecific competition) have no measurable effect on total seed production (see below for exceptions to this). Secondly, intraspecific plant competition tends to take the form of a contest rather than a scramble for resources (figure 3*b*). Thus the number of plants surviving intense self-thinning is more or less independent of the precise form of the size distribution (J. Weiner & S. Pacala, unpublished results).

Taken together, these two processes mean that the number of recruits is independent of the size of the parent plant stock over a wide range of plant densities. This effect is embodied in one of plant ecology's most robust empirical generalizations; the Law of Constant Final Yield (Harper 1977).

3. RECRUITMENT

The biology of recruitment has been understood since biblical times (see The Parable of the Sower; St Matthew 13: 4–8). The 'fowls of the air' (herbivory), 'stony places' (unsuitable microsites) and the 'thorns which sprang up and choked them' (interspecific plant competition) accounted for most of the seeds, most of the time. However, the question as to whether or not plant recruitment is seed-limited remains controversial.

(*a*) *Seed-limited recruitment*

It is important to establish whether or not recruitment in a given plant population is seed-limited or not. If it is not seed limited, then herbivores that cause only moderate reductions in plant fecundity may have no measurable impact on plant abundance or on population stability. It is curious that the simple experiment of sowing extra seeds and recording the numbers of recruits has been carried out so seldom. If a population is not seed-limited, then recruitment may be limited by microsite availability, by competition with mature plants of the same or of other species, or by seed and seedling predators. In very few cases have the necessary factorial experiments been carried out to discover which of these factors limits recruitment in a given circumstance. Presumably, the result will depend both upon the kind of habitat (e.g. seed-limited recruitment will be more likely in plant communities that have high equilibrium proportions of bare ground, and competition-limited recruitment will be more likely in forest than in grassland communities), and upon the growth form of the plant species (e.g. its longevity, its fruiting pattern and the degree of iteroparity exhibited).

M. Johnston (unpublished results) sowed 1000 seeds per square metre of 20 plant species growing in acid

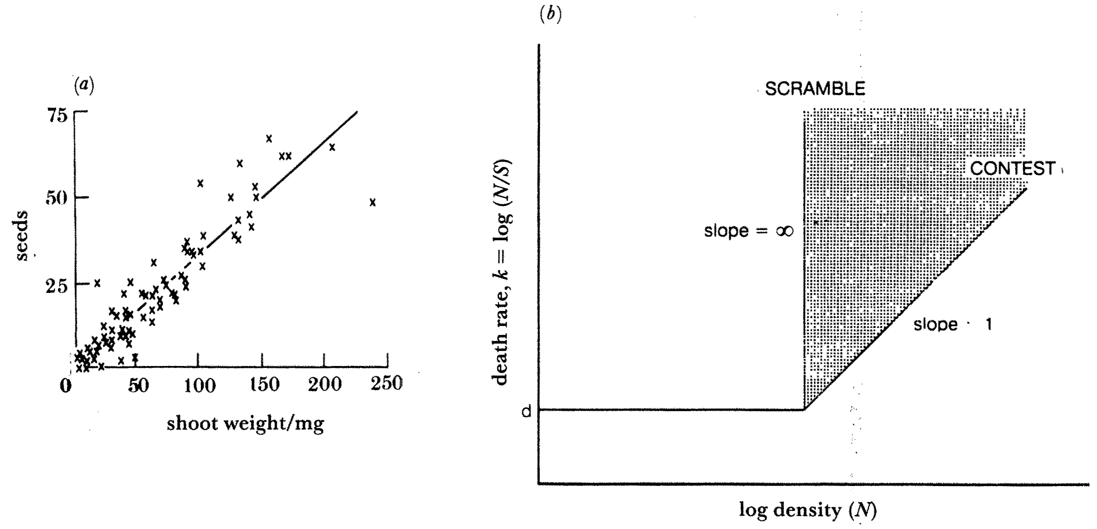

Figure 3. (*a*) The relation between shoot weight and fecundity in the annual crucifer *Thlaspi arvense*, showing direct proportionality and no threshold size prior to reproduction. (*b*) The relation between mortality (k) and log population density for plants that compete by scramble or contest; most plants have slopes close to 1, suggestive of contest competition.

grasslands in Nash's Field, Silwood Park. Only two species produced any seedlings at all; the large-seeded legume *Lotus corniculatus* and the sheep's sorrel, *Rumex acetosella*, both appeared to be seed limited, but the remainder were not. He has yet to establish the factors limiting the recruitment of the other 18 species.

(*b*) *Experimental protocol*

In order to establish the factors responsible for the limitation of recruitment requires a very simple experimental protocol. The 4 potential limiting factors (seed, competition, microsites and herbivores) are varied in factorial combinations and the resulting plant recruitment is monitored. In the simplest case, each factor just has two levels. Extra seed is sown or not, the ground is cultivated or not, competing vegetation is clipped or not, and herbivores are excluded or not.

The role of seed recruitment in perennial herbaceous vegetation is controversial. Some authors argue that seed recruitment is rare in general, but this view is disputed by Erkison (1989). He found that in a review of more than 60 studies, seedlings were present in 40% of cases. Of course, the fact that seedlings are found within populations of mature plants does not mean that recruitment is necessarily seed limited.

Within any one year, recruitment may be seed limited in some microhabitats but not in others (e.g. Keddy 1981). This argues for spatially replicated, long-term studies of the kind so rarely carried out (e.g. they are logistically impossible for Ph.D. students working on their own).

(*c*) *Data on recruitment limitation*

We have done the recruitment-limitation experiment on four species so far: the crucifer *Cardamine pratensis* (Duggan 1986), the umbellifer *Heracleum sphondylium* (Sheppard 1987), the composite *Senecio jacobaea* (Crawley & Nachapong 1985) and the oak tree *Quercus robur* (Forrester 1990). All the studies were done in acid grasslands in Silwood Park, Berkshire.

Cardamine pratensis growing in wet grassland was found to be competition-limited, with slugs and rabbits acting as important factors in reducing recruitment following cultivation. Recruitment was increased by seed addition only on the cultivated plots protected from herbivory (Duggan 1986).

Ragwort *Senecio jacobaea* showed no recruitment in grassland when extra seeds were sown, but recruitment was seed-limited following cultivation. Ragwort produces smaller seeds on regrowth shoots (following defoliation and destruction of the primary flower heads by cinnabar moth). Large seeds from primary capitula were capable of recruitment when sown into grassland cut to 2 cm in height, whereas the smaller seeds from regrowth shoots produced no recruits in cut grassland. Small and large seeds were equally likely to produce recruits in cultivated ground (Crawley & Nachapong 1985).

When the acorns of oak *Quercus robur* were placed on the surface of grassland, they were all consumed within a matter of days by mice, rabbits and larger seed-feeding birds (jays and wood pigeons). If piles of 1000 acorns were put out, only the dozen or so weevil-containing acorns were left after 48 h (M. J. Crawley, unpublished results). If the acorns were buried beneath the grassland, however, their survival rate was very high, and the seedlings were competitive with intact grassland canopy, whether or not they were exposed to rabbit grazing. The large acorn gives them both substantial competitive ability and substantial powers of regrowth (Forrester 1990). Recruitment of the oak, therefore, is seed-burial limited. Recruitment is herbivore-limited if the acorns are placed on the ground surface, and only seed-limited if the seeds are buried. Levels of oak recruitment from acorn caches buried by jays and squirrels are sufficiently high for the plant to be considered a flower-bed weed in gardens frequented by domestic cats. Apparently, the cats reduce the cache retrieval efficiency of the jays and squirrels, so that tree recruitment in this case is predator-mediated. This parallels the kind of three-trophic-level effect that led to the regeneration of large areas of oak woodland following the extermination of the rabbit population after the introduction of the myxoma virus (above).

The umbellifer *Heracleum sphondylium* is the only species so far that has proved to be seed-limited (and then in only one site out of two). Adding hogweed seeds to moist grassland in 1981 initiated a population which has persisted and is still expanding in 1990. Adding seed in a drier part of the same grassland led to no recruitment even after cultivation, and it appears that in this second site recruitment was limited by a shortage of water.

Fowler (1986) was able to increase recruitment in the grass *Bouteloua rigidiseta* by a factor of 3.4 when she sowed seeds at a rate of 4500 m^{-2} in arid grasslands in the southern United States.

4. EXAMPLES

The search for general principles of plant population dynamics is unlikely to produce robust generalizations unless we distinguish the habitat and the life forms involved. Hairston (1989) has reviewed the limitation of plant populations in a range of habitats (forests, successional communities, deserts, freshwater and marine environments), and I shall concentrate here on differences between plant growth forms. These, of course, are often closely correlated with habitat differences (trees in forests, shrubs in deserts, annuals in early successional communities, herbaceous perennials in grasslands, and so on).

(*a*) *Trees*

As a consequence of their great longevity, we have little direct evidence on tree population dynamics. Most studies have relied on indirect data, of the kind that are obtained from age structure studies (based on ring-counts from increment borers; Ogden 1985), or by observation of the relative abundance of saplings of different species beneath various canopy species (Horn 1975). The assumptions of constant recruitment and

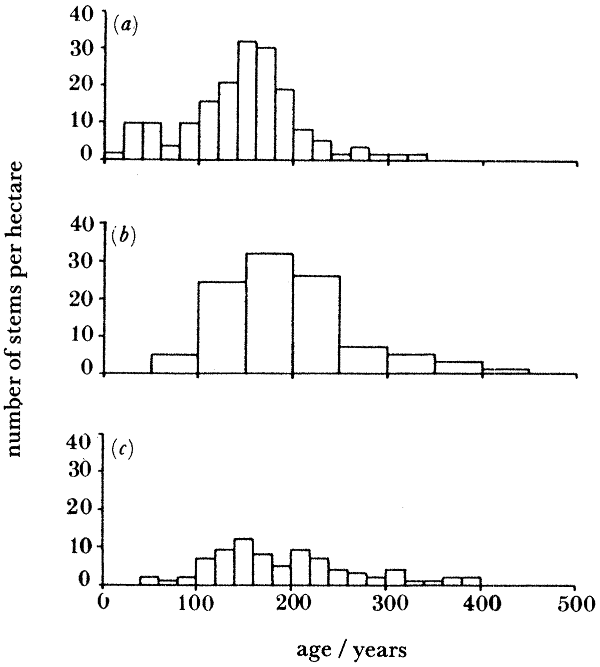

Figure 4. The age structure of three populations (*a*–*c*) of Japanese beech, *Fagus crenata* (from Nakashizuka 1987), showing a complete absence of recruitment in recent years.

time-invariant survivorship that underlie many of these reconstructions of forest dynamics are unlikely to be realistic in the majority of cases.

For example, the Japanese beech *Fagus crenata* exhibits large patches of uniform age, resulting from disturbance from typhoons, and dominance of large areas of the forest floor by dwarf bamboos (*Sasa* spp.), with the result that most age structure diagrams lack any recruiting juvenile age classes (figure 4). The absence of recruits in this case is due to asymmetric intraspecific competition between seedlings and adult trees and to intense interspecific competition with the perennial ground cover bamboos (Nakashizuka 1987).

Wildfire and wind are the major disturbances in the coniferous forests of the N.W. United States. There have been 16 major fires in Mount Ranier National Park since the year 1260 (Hemstron & Franklin 1982) with an average fire rotation of 434 years. The largest fire destroyed over 150 square miles, almost half the area of the Park.

Hubbell & Foster (1990) re-surveyed their permanent plot on Barro Colorado island in 1985, 5 years after the initial survey. They discovered greater than 10% change in the absolute abundance of more than 40% of the plant species. Catastrophic mortality of moisture loving species occurred during the drought year of El Nino. Rare species suffered greater declines, and common species more increases, than would be expected by chance alone. Hubbell & Foster conclude that the present forest is not an equilibrium assemblage, but that drought caused differentially high mortality among the smallest, shallowest rooted under-story plants, and the most intensely irradiated, emergent trees.

In a 21-year study of the Kolombangara rain forest in the Solomon Islands (Whitmore 1990) with 22 plots each of 0.63 ha† all trees greater than 30 cm girth were measured and all individuals counted for the 12 dominant species. This study stressed the importance of cataclysmic destruction in tropical forest dynamics. It catalogued the differences on permanent plots through time and from place to place, within and between floristic types of forest, and related these to canopy disturbance. Successional elimination of light-demanding tree species occurs under the present canopy disturbance régime; the more shade tolerant species increase in numbers until a sufficiently extensive canopy disturbance occurs to allow the establishment of more light-demanding species.

Coining the phrase 'shifting mosaic steady state' (Bormann & Lichens 1979) described the pattern of recruitment dynamics for deciduous forest in the N.E. United States. The average canopy turnover of 1–2% per year obscured big spatial variations of up to 10% in a single year.

While episodic disturbance appears to regulate recruitment in the majority of forest types, there are some relatively undisturbed forests that appear to have equilibrium species assemblages, in which the relative abundance of mature trees can be predicted on the basis of tree replacement probabilities. These are judged simply by counting the numbers of saplings of different species beneath the canopy of each kind of mature tree. The probability of replacement of canopy dominant of species A by a sapling of species B is taken to be the proportion of all saplings belonging to species B (of course, the equilibrium dominant species will have a high probability of self-replacement). Horn (1975) has documented the existence of such forests in the N.E. United States. There is no circularity in these predictions, since data gathered on replacement probabilities in one site can be used to predict the equilibrium tree assemblage in another site.

On balance, it appears that tree dynamics within most forests are governed by disturbance-limited recruitment, rather than by equilibrium successional dynamics. The impression gained from long-term study plots in tropical forests like Whitmore's (1989) long term study in the Solomon Islands and Hubbell & Foster's more recent work on Barro Colorado Island, is of much higher levels of dynamism and turnover than was previously believed. The fact that some of the individual trees are long-lived, does not mean that turnover within forests is slow.

While it is often assumed that the keystone herbivores in forest communities are the invertebrates feeding in the canopy, it is clear from recent work that seed and seeding-feeding mammals may be influential in determining the identity of the species that survive to the sapling stage, and eventually form the canopy dominants (Forrester 1990; C. D. Pigott, personal communication).

Stable age structures will not be found in the majority of tree populations because: (i) recruitment is too episodic; (ii) plant size has more impact on demography than plant age (sapling banks with negligible growth rates); (iii) predominance of strong

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† 1 hectare = 10^4 m^2.

age classes in many populations; (iv) we know virtually nothing about the history of recruitment, but what little we do know suggests that recruitment is most unlikely to be constant from year to year.

(*b*) *Shrubs*

The dynamics of shrub populations have received rather little attention, except in desert regions where long-term studies have been carried out since the early years of this century (Goldberg & Turner 1986). A variety of recruitment limitation mechanisms has been reported, including insect herbivory (Parker & Root 1981), rainfall (Prentice 1986), limited seed dispersal (Brown & Archer 1897) and direct seed limitation (Louda 1982), but too few studies are available for any broad patterns to emerge.

Vegetation dynamics in some heathland shrubs are cyclical, driven by changes in the age structure of relatively large patches of the dominant plant (e.g. the so-called stand cycle of *Calluna vulgaris*; Watt 1964). Even with species that may exhibit local internal cycles, however, the more typical pattern of recruitment may be dominated by external, relatively large scale disturbance. Regeneration of heather *Calluna vulgaris*, for example, can occur from seed or by layering, but the relatively large scale patterns of recruitment tend to be dominated by fire (Hobbs & Gimmingham 1987).

(*c*) *Herbaceous perennials*

Herbaceous perennials may be evergreen or deciduous, mobile or fixed, tussock-forming or straggling, bulbous or rhizomatous, geophyte or hemicryptophyte, and all these different features of their growth form are likely to influence their population dynamics. They will affect their characteristic patterns of survivorship (depending upon the longevity of their perennating tissues and the ability to produce vegetative offshoots under a range of competitive conditions) and fecundity (whether they are monocarpic or polycarpic, alternate bearing or masting, etc).

We have detailed demographic information on only a small sample of herbaceous perennials. Several authors have published long-term studies on the dynamics of terrestrial orchids (Inghe & Tamm 1985; Wells 1981; Hutchings 1987). These studies show: (i) periodic recruitment; (ii) unequal age structures with strong age classes; (iii) irregular flowering. Orchids also exhibit the irritating tendency to come back from the dead. Plants that have disappeared for one or more years may reappear above ground, having spent the intervening period underground either dormant, or living a parasitic existence, obtaining sustenance from mycorrhizal fungi. This means that losses can not be equated with death until many years have elapsed without evident vegetative growth.

An interesting twist to orchid dynamics comes from Gill's (1989) 10-year study of the pink lady's slipper *Cypripedium acaule* in Virginia. Despite their extremely ornate flowers, these flowers appear to be virtually useless at attracting insect pollinators. The flowers 'cheat' the insects by producing neither nectar nor fragrance, and the insects appear to have learnt to avoid them. Cross pollinations by hand produce perfectly satisfactory seed set, and Gill's study provides one of the most convincing examples of pollinator-limitation of plant population density. More plants are produced if more seed is set, and more seed is set if more pollinia are transported to receptive stigmas. In only 1 year out of 10 did more than 5% of the plants produce seed and in 4 years out of 10 there was complete reproductive failure.

The question of how often long-lived herbaceous plants recruit from seed has been the subject of some debate. Everyone agrees that recruitment from seed is uncommon in these plants, but the impression has been given by some authors that seedlings are never found at all. Eriksson (1989) reviewed studies of 68 species and found that seedling recruitment in established populations was actually observed in 40% of cases. Seedling recruitment was more likely in grassland than in woodland species, in above-ground rather than below-ground clonal species, and in species lacking long-distance seed dispersal mechanisms. Seedling recruitment is obviously more likely in communities that have high average proportions of bare ground than in communities with high average cover values (Crawley 1986). Even when seedling recruitment does occur in these clonal communities, the death rate of seedlings is typically much higher than the death rate of daughter ramets. Even though the sample sizes are small, it appears that the possession of seed banks in herbaceous perennials is correlated with the turnover rate of ramets; plants with high turnover (like *Ranunculus repens*) tend to rely relatively more on seedling establishment and to possess seed banks, whereas the slow turnover species (like *Potentilla anserina*) have no seed bank and show little seedling recruitment

Table 1. *Depletion data for long-term studies on herbaceous perennials, showing the estimated half-life. Note that for some of the forest herbs, the plants may live through several generations of the dominant trees. Many of the orchids disappear temporarily then reappear in later years, making estimation of their half-lives more difficult. Data from Inghe & Tamm* (1985) *and references therein*

species	half-life/years
Hepatica nobilis	360
	59
	32
Sanicula europaea	221
	74
Primula veris	50
	6
	3
Dactylorhiza sambucina	20
	10
Dactylorhiza incarnata	
original cohort	5
1966–67 cohort	3
Orchis mascula	5
Listera ovata	56

(Eriksson 1986). In Tamm's long term study plots (above), there was no relation between the numbers of seedlings recruiting in any year, and the magnitude of seed production in the previous season (Inghe & Tamm 1985), suggesting that although seedlings were found in most years, seedling recruitment was not seed limited.

Clearly, these kinds of studies need to be done over protracted periods, especially in circumstances where microsite availability is likely to be episodic (e.g. in arid systems). It is entirely plausible, for example, that recruitment could be seed limited in that rare year in which a combination of adequate rainfall and sufficient disturbance to create plentiful microsites means that recruitment is possible.

Most of the information on clonal plants comes in the form of depletion curves, in which the mortality of permanently marked clones is monitored (table 1). It is striking that the half-lives of several woodland perennials are long enough that one genet of *Hepatica nobilis* or *Sanicula europaea* might outlive two or more generations of the dominant canopy trees (Inghe & Tamm 1985).

(*d*) *Annuals in dunes and deserts*

More is known about the population dynamics of annuals than about any other group of plants. Several data sets exist in which the dynamics have been followed for more than five years and a few data sets of 10 or more years have been collected. We need to distinguish the dynamics of desert and sand dune plants in which conditions for recruitment are available more or less constantly, providing there is sufficient rain to allow germination, with early successional communities, in which only one or two years following disturbance are suitable for recruitment. In both cases, we need to consider the relative importance of long-term seed dormancy (the size of the 'seed bank'; Leck *et al.* 1989) and of long-distance seed dispersal.

Given that they have the longest runs of data, they also have the widest variety of dynamic behaviours. Perhaps the commonest pattern is that exponential increase is so rapid that all microsites are occupied after only one or two generations (e.g. *Poa annua* on waste ground; Law 1981). Alternatively, long-term successional changes in the distribution and abundance of perennial plants may so change the local microsite conditions that recruitment becomes impossible, and the population declines to local extinction (e.g. *Vulpia* in sand dunes, figure 2; Watkinson 1990).

In a few cases, cyclic dynamics have been reported. In one case, the skeletons of dead *Salicornia* were thought to occupy microsites in sheltered places for a year after their death, taking up space that would be occupied by recruits in more exposed places, where the skeletons would be washed away. In the second year, the microsites became available, and a two-year cycle in population density was initiated (Wilkon-Michalska 1976, in Symonides (1984)). In a second case, Symonides (1984) described how the tiny annual crucifer *Erophila verna* underwent a two-point cycle in inland dunes in Poland. Fecundity was overcompensating, so that a single plant produced more seed per unit area than did a large number of small plants. At very high densities, many of the rosettes failed to flower, or flowered very late, so that their leaves had not withered at the time of fruit maturation. This meant that much of the seed was intercepted by the upper surface of leaves and desiccated or was eaten by seed predators before it could germinate. Thus extremely low recruitment followed extremely high adult-plant densities, but the large plants that grew at these low densities produced sufficient seed to ensure exceptionally high densities in the following year. She suggests that this is the origin of the observed two-year cycle. A climatic cause of the cycles is ruled out by the fact that different patches within the same dune system are one step out of phase with each other, so that high and low density patches can be found in any given year (Symonides 1984). Only some of the study plots exhibited these cycles, and there is no suggestion that cyclic behaviour is characteristic of *Erophila verna* populations in general.

Both these cases are unusual in that the physical presence of dead or dying parts of mature plants in high density populations ensured that only a small number of plants become established in the following year. It is more common that annual fluctuations in plant abundance are caused by variations in the weather conditions affecting seedling recruitment, and density-dependent variations in fecundity are rarely sufficiently intense as to cause seed-limitation in the years following high density.

(*e*) *Annuals in early successional communities*

The majority of early successional annuals possess long-lived seed banks (Roberts 1981; see also D'Angela *et al.* (1988) for exceptions). Those early successional ruderals that lack dormancy rely upon high fecundity and wide seed dispersal for their persistence (Egler 1954). The two types of plant have quite different dynamics.

In the case of seed bank annuals, there is virtually no relation between population density and seed production in the previous year. This means that classical population dynamics models are virtually useless. The factors determining the relative abundance of these plants in any given year depend almost entirely upon the extent and the precise timing of soil disturbance. We have found that the dominant weed in Pound Hill Field in Silwood Park can be altered from *Myosotis discolor* to *Solanum nigrum* solely by altering the timing of cultivation (M. J. Crawley, unpublished results). In the absence of disturbance these plants will not recruit at all.

Many species will not germinate beneath a canopy of green leaves, while others require several gap-sensing stimuli (e.g. white light and fluctuating temperatures) to initiate germination (Leck *et al.* 1989). In diverse communities of ruderals, a knowledge of the germination biology of the component species is vital to an understanding of their coexistence. For example, despite over 120 repeated annual cultivations, the species richness of the weed flora of the

Broadbalk experiment has not declined, and there is no evidence of competitive exclusion (Crawley 1986).

We know much less about the population dynamics of 'dispersal ruderals', mainly because their occurrence in permanent quadrats is sporadic. There is a well developed theory for the persistence of this kind of annual (Crawley & May 1987; Kadmon & Shmida 1990). Briefly, their fecundity must exceed the reciprocal of the equilibrium proportion of gaps in the canopy (the proportion of the total area over which seed is distributed that constitutes a suitable microsite). The smaller the number of gaps, the higher the fecundity must be to ensure persistence. It is axiomatic that dispersal must be sufficiently efficient to 'find' the available gaps with Poisson (or better) probability.

In a nine-year study of common and sparse prairie grasses, Rabinowitz *et al.* (1989) found that the uncommon species had lower variation in reproductive output and were less likely to show reproductive failure than the common species. The correlation between rainfall and reproductive output was good for the common grasses, but poor for the sparse species, suggesting that the pattern of environmental fluctuations buffers the reproductive output of the sparse species.

5. SPATIAL DYNAMICS

In concluding his paper on the population dynamics of invading *Poa annua*, Law (1981) wrote: 'It may prove to be more enlightening to take spatial pattern as an essential component of plant demography, rather than as an unfortunate barrier to reliable population estimates'. Rather few data sets are sufficiently extensive that they allow simultaneous estimation of spatial and temporal variance in population density in such a way that the relative magnitudes of spatial and temporal variance can be compared.

There are some fundamental problems in obtaining precise, unbiased estimates of spatial variance. Most plant ecologists place their long-term study quadrats around existing aggregates of plants (see above). This means that plant recruitment into previously unoccupied quadrats is rarely estimated in an unbiased way. It has the other undesirable property that most studies are of declining populations and tend, therefore, to give negative estimates of the intrinsic rate of increase. Studies in which the quadrats are placed within suitable habitat at random, and in which the 'empty' quadrats are given as detailed attention as the occupied quadrats, are very rare. I present two examples: one of the annual *Salicornia brachystachys* from Dutch salt marsh and the mobile perennial *Glaux maritima* from meadows on the shores of the Swedish Baltic.

There are several technical problems in any comparison of spatial and temporal variances. While it is relatively clear that one year is a sensible time unit for calculating the variance in population size of an annual plant, it is by no means clear what quadrat size should be used in calculating spatial variance. Plant ecologists have long known that the variance obtained depends upon the size of the quadrat employed, and that the same plants can exhibit spatial patterns on several scales simultaneously (Kershaw 1964).

Again, Hanski (1987) has pointed out that the slope of Taylor's Power Law for plots of spatial variance against spatial mean density is influenced by the degree to which the dynamics of local populations are correlated over large spatial scales. Do all local populations experience the same 'good years' or is there relatively low cross-correlation between local dynamics?

Note, however, that temporal variance is bound to be calculated for quadrats of a given size, and that changing quadrat size would alter the estimate of temporal variance. Quadrat size, therefore, is not just an issue for considerations of spatial variance, but is central in any discussion of plant population dynamics.

(*a*) *Salicornia dynamics*

These data relate to a study from 1977 to 1989 (with gaps in 1981 and 1988) along a transect of 42 quadrats, each measuring 50 × 50 cm (B. Koutstaal & A. Huiskes, unpublished data). The time series shows a fluctuating pattern of abundance that might best be described as a damped decline. There is evidence for density dependent regulation, and a plot of the change in log population size against population density has a significant negative slope (figure 5). Population variability is measured by the standard deviation of log population size. This population fluctuated 12-fold over the 13-year period, and gave a standard deviation (s.d.) in log density of 0.717.

Averaged over 13 years it is quite clear that there are good sites and bad sites for *Salicornia* along the transect (figure 5). Taking the total over all years, we can calculate the s.d. in log population size from quadrat to quadrat along the transect (s.d. = 1.481). It is clear that the population is more variable in space than in time.

Another way of presenting data on population density variation is in the form of plots of log variance against log mean density (Taylor's Power Law). *Salicornia* has a temporal power law slope of 1.24 and a spatial slope of 1.24. The intercept is also significantly higher in the spatial plots.

(*b*) *Glaux dynamics*

A 7-year study by Jerling (1988) involved the repeated census of 13 permanent quadrats, each measuring 2 × 2 m. The time series shows wide fluctuation, but no obvious upward or downward trend (figure 6). There is evidence of density dependent regulation, and although the scatter of points is greater than in the case of *Salicornia* there is a significant negative relationship between change in log population size and population density.

The spatial variation is shown in figure 6, and as with *Salicornia*, it is greater than the temporal variation. The power law plots have slopes of 2.09 for the temporal and 4.74 for the spatial variance.

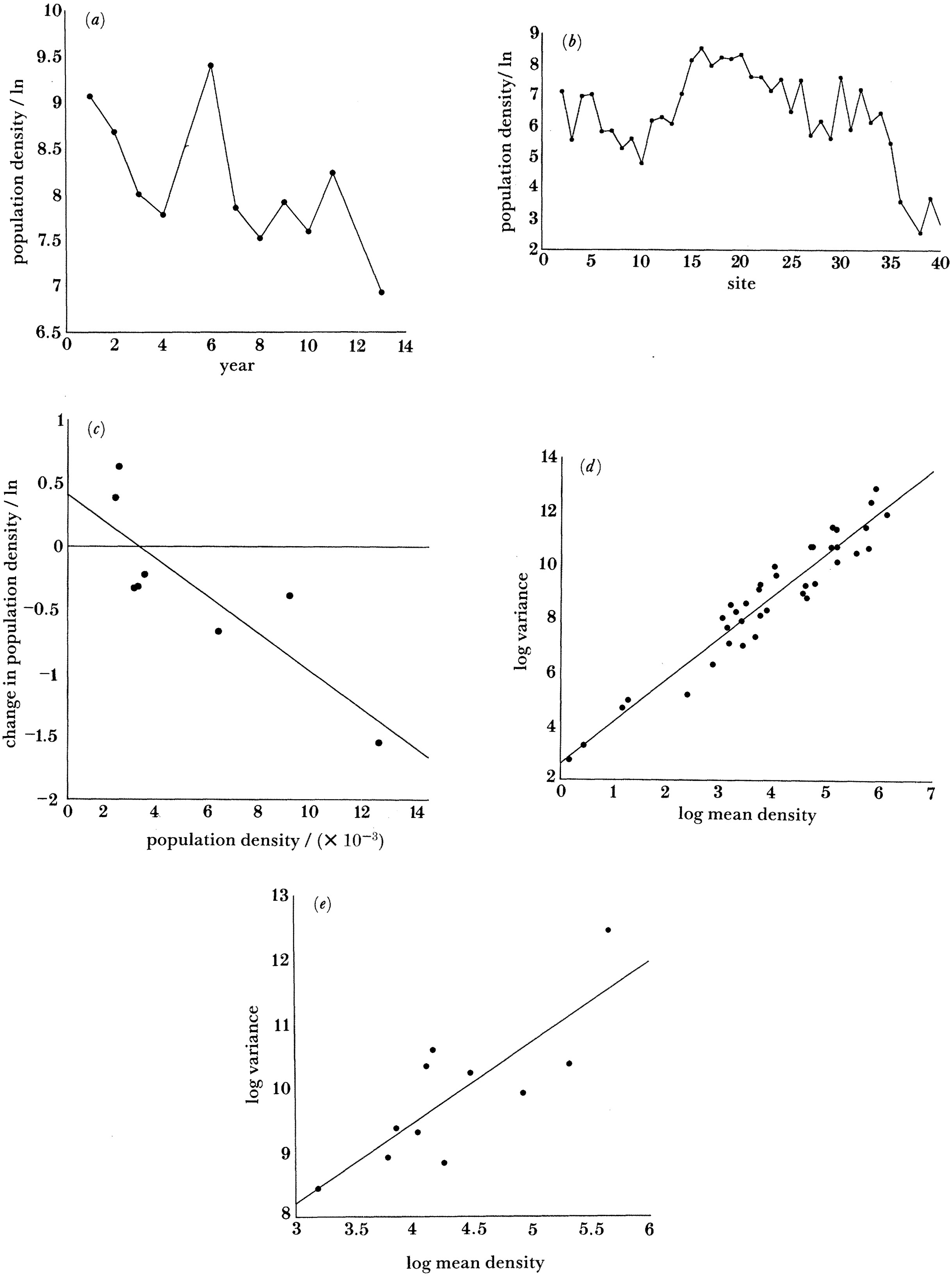

Figure 5. Population dynamics of *Salicornia brachystachys* in Holland. (*a*) Time series. (*b*) Spatial distribution. (*c*) Population regulation. (*d*) Temporal power law. (*e*) Spatial power law. For details see text.

(*c*) *Overview*

Drawing together the data for *Salicornia* and *Glaux* with the classic long-term studies of Epling *et al.* (1960) on desert annual *Limnanthes parryae* and Symonides (1984) on the dune annual *Erophila verna* with our own studies on ragwort *Senecio jacobaea* (Crawley & Gillman 1990) we can begin to compare the relative magnitude of temporal and spatial variation (table 2). In all cases but one, spatial variation exceeded temporal variation by a factor of between 1.7 and 4.4.

Even in the case of *Limnanthes*, however, the spatial

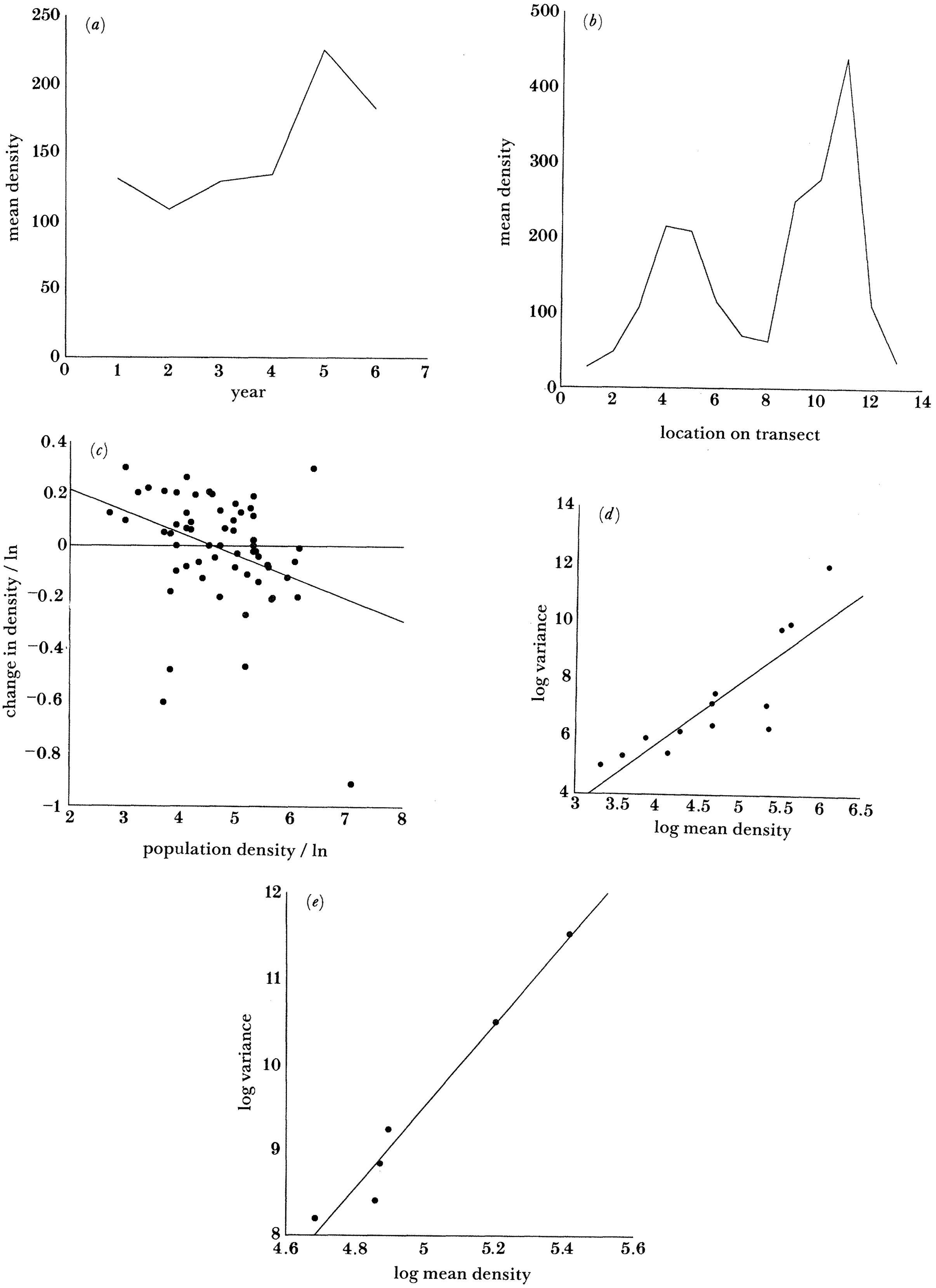

Figure 6. Population dynamics of *Glaux maritima* in Sweden. (*a*) Time series. (*b*) Spatial distribution. (*c*) Population regulation. (*d*) Temporal power law. (*e*) Spatial power law. For details see text.

dynamics were pronounced and consistent. Epling *et al.* (1960) write 'Within any year their dispersion is not uniform but follows a very local pattern of greater or less concentration. This pattern has persisted over the period of study'.

6. DISCUSSION

Our understanding of general patterns in plant population dynamics has been hampered by shortcomings in all the important scientific aspects of plant

Table 2. *The relative magnitude of spatial and temporal variation in population density for five plant species, measured as the standard deviation in log population size. In four cases the spatial variation is substantially greater than the variation from year to year. The exception* (*Limnanthes*) *is a widespread desert plant where recruitment is limited by widespread, unpredictable rain storms. For sources, see text*

species	time	space	multiple
Salicornia	0.717	1.48	2.07
Erophila	0.157	0.688	4.39
Limnanthes	0.754	0.313	0.41
Glaux	0.270	0.853	3.16
Senecio	0.793	1.340	1.69

ecology: in its theoretical development, in an unwillingness to carry out simple experiments, and in the short-sighted protocols of observational studies.

Plant populations dynamics theory has relied too heavily on models borrowed from animal ecology. Thus many of the essential attributes of plants have been played down (their longevity, tremendous size plasticity, the importance of neighbours, the constancy of yield per unit area), and the models have adopted the animal ecologists' relish for assumptions of equilibrium, predictable recruitment, and constant rather than successional environments.

The reluctance to carry out simple manipulative field experiments on recruitment has meant that the relative importance of seed, microsites, competition and herbivory remains unknown even in systems that have been studied over many years. The practice of sowing extra seeds and following their fate and the fate of any seedlings they may produce should be a routine element of any field study in plant dynamics. Seeds should be sown into a range of microhabitats, apparently unsuitable as well as apparently suitable, so that we increase our understanding of why plants do not occur in certain places.

Observational studies of plant populations are typically set up around existing mature plants and empty quadrats are ignored. This has two undesirable consequences: (i) most observed populations drift inexorably to extinction, and (ii) because recruitment may occur in empty rather than occupied quadrats, such studies lead to serious underestimates of the population's actual rate of increase. Observational studies must include empty quadrats, and quadrats should be sited at random within the chosen habitat, unless persuasive arguments to the contrary can be presented. Bias in siting the quadrats is one of the most pernicious problems in field ecology.

Incorporating spatial dynamics into the mainstream of plant population dynamics studies is important because spatial variation is as great or greater than temporal variation in most studies for which suitable data are available. Spatial variation in density should not be regarded as a nuisance, but rather as something that is interesting and important to study in its own right. The 'empty' quadrats are important: are they habitable or not; are they really empty, or do they contain dormant seeds; are they empty because they have not received propagules or because they have undergone successional change rendering them uninhabitable until the next major disturbance?

Spatial heterogeneity also exists in the kind of dynamics exhibited by a given species. For example, there may be within-species differences in life histories that have both genetic and environmental causes. Thus *Plantago lanceolata* sets more seed on dry soils than on wet; there is variation in the production of side shoots, the size of seed bank; the mass of individual seeds and seedling competitiveness; mature plant size and longevity also vary from site to site (van Groenendael & Slim 1988). Adding the complexity associated with overlaying spatial heterogeneity in genotypic composition on spatial heterogeneity in environmental conditions represents a major challenge to theoreticians and experimentalists alike.

Plant population dynamics are relatively tame compared to animal dynamics, and we have few convincingly documented examples of cyclical plant populations and none of chaotic dynamics among plants (exceptions include certain annuals (Symonides 1984), vines (Mueller-Dombois 1981), some shrubs (Watt 1964) and trees exhibiting 'wave dynamics' (Sprugel 1976), but in most cases these are age-structure effects, rather than generation-to-generation delayed density dependence effects). There are at least three reasons for this. The first is morphological. Because of their iterated, modular construction, plants are immensely plastic in their growth form. There is typically a linear relation between size and fecundity and there is rarely any threshold size below which reproduction is impossible (Rees & Crawley 1989). This means that the tendency for over-compensating density dependence in fecundity is reduced (but see the special case of *Erophila verna*, above). The second reason is that the nature of plant competition is essentially asymmetric. Plants contest rather than scramble for light, so that there are winners and losers. The relatively large plants prosper, no matter what the details of the size distributions among the smaller plants. The smallest plants are almost always the most likely to die. This combination of a linear size-fecundity schedule followed by contest competition among the recruits is sufficient to guarantee extremely stable dynamics in a constant environment, and rapid recovery from catastrophe in a fluctuating environment. Thirdly, recruitment is often not seed limited. Thus population fluctuations tend to be due mainly to exogenous controls on recruitment, rather than to the kind of over-compensating density dependence that can cause cycles or chaotic dynamics in model systems.

It is possible to develop mathematical models of plant dynamics that exhibit 'interesting dynamics' like cycles or chaos (Pacala & Silander 1985), but the consensus is that these models are more animal-like than plant-like in their behaviour (Watkinson 1985). More realistic plant models, incorporating linear size–fecundity relation, constant final yield and contest competition, tend to exhibit much more stable dynamics (Crawley & May 1987).

The role of herbivores in plant dynamics has been the subject of controversy (Crawley 1983; Hairston

1989). As so often, the protagonists are arguing about different sides of the same coin. Herbivores as a group appear to have relatively little impact on system level properties of the plant community like total biomass (the world is green despite herbivory). This does not mean, however, that herbivores have no impact on the abundance of individual plant species. Small changes in herbivory can change the identity of the dominant plant species (Crawley & Pacala 1991). The importance of herbivory is implicit in the recognition of certain plant species as increasers or decreasers under grazing. It is important to bear in mind, however, that the classification of a given plant is seldom unequivocal, and there is considerable inconsistency in the behaviour of increasers and decreasers. For example, a plant that might increase under moderate grazing intensities, might decrease rapidly under more intense grazing pressure (Crawley 1983).

There are a number of important plants traits that make plant dynamics (or more strictly the dynamics of sessile modular organisms) fundamentally different from those of animals (and other mobile, unitary organisms). (i) They exhibit extraordinary phenotypic plasticity in size, so that the fecundity of an individual genotype can vary by four orders of magnitude depending upon the conditions it experiences during development. (ii) Plants are sedentary, and so neighbour relations are extremely important (performance is well predicted by the number of neighbours larger than a given individual; smaller neighbours are typically of little consequence). (iii) The importance of competition in animal population dynamics is a matter of debate; in plant population dynamics it is quite clearly of over-riding significance in the majority of cases. (iv) Stock recruitment curves are often useless in understanding plant population dynamics, because of seed banks, immigration, repeated reproduction and the existence of strong age classes (in this, plants are like fish). (v) Plant populations have more stabilizing refugia than most animal populations, in the form of long-lived seed banks, very long life, ungrazeable perennating organs, repeated reproduction and wide seed dispersal.

The directions for future research in plant populations dynamics are reasonably clear. (i) We need to carry out simple experiments on seed, microsite and herbivore limitations on recruitment. These experiments should be carried out on a variety of plant growth forms in a range of different habitats. (ii) Observational studies should place their quadrats at random within suitable habitat, instead of around selected mature individuals. If we want to understand recruitment, we need to observe empty quadrats. (iii) We should develop theoretical models specifically for plants, incorporating the key aspects of plant biology outlined above, and attempting to make these models spatially explicit.

7. SUMMARY

(i) Plant populations are regulated by density dependent processes. This may involve competition between seeds for access to limited microsites, or strongly asymmetrical competition between seedlings and established adult plants. Herbivory can regulate plant density below the level that would be set by plant competition (but note that when it does so, unpalatable plants often increase in density to take up the available space).

(ii) In terms of their overall relative importance in plant population dynamics, this review suggests that the various processes be ranked as follows: interspecific competition > herbivory > intraspecific competition for microsites > seed limitation.

(iii) Plant competition is fundamentally asymmetric. Plants contest rather than scramble for resources and this has a major stabilizing effect on plant population dynamics.

(iv) Plant population dynamics are relatively tame. We have very little evidence for cyclic dynamics caused by over-compensating density dependence, and no evidence for chaotic dynamics.

(v) Spatial dynamics of plants are very important, and plants conform to Taylor's Power Law in their patterns of both spatial and temporal variation. In four studies out of five where it was possible to contrast the relative variation of temporal and spatial dynamics, the spatial component of variation was greater by a factor of between 1.7 and 4.4.

(vi) Protocols for theoretical, experimental and observational studies of plant population dynamics are proposed.

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Discussion

G. J. S. Ross (*Rothamsted Experimental Station, Harpenden, Herts. U.K.*). In Dr Crawley's historical survey of plant population changes he mentions the Rothamsted Park Grass experiment. The relative abundance of different species on each plot has been estimated for several occasions from 1862 onwards, and the divergence from the original composition at the start of the experiment is well recorded.

Unfortunately the difficulty and expense of maintaining this tradition has meant that there are no comparable recent estimates. I hope that the interest of those at Silwood Park and elsewhere will be fruitful.