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The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations at the regional and local scales

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In natural and semi-natural vegetation there is a spectrum of cases from those in which episodes of recruitment are tightly coupled with disturbance-events to those in which they are completely uncoupled. The dichotomy between these extremes leads to the recognition of two basically different types of seed bank. Nine means of persistence at the regional scale are spelt out, and aspects of temporal change in spatial distribution at the local scale are discussed. Finally emphasis is placed on the importance of recognizing the dichotomy between coupled and uncoupled recruitment when pursuing a quantitative understanding of population control in plants.

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1. Introduction

Recent literature has tended to emphasize the impact of the disturbance regime on temporal changes in the density of plant populations. This view-point is reflected, for example, by the many papers in the recent volume entitled 'The Ecology of Natural Disturbance and Patch Dynamics' and edited by Pickett & White (1985). It is also implicit in the continuing emphasis in textbooks, e.g. that of Begon et al. (1986), on so-called *r*- and *K*-strategists (in fact, better called early and late successional plants, Grubb 1987). Disturbance has been defined very variously, but the definition accepted here is that of Grime (1979): 'mechanisms which limit plant biomass by causing its total or partial destruction.' The central thesis of the present article is that a balanced view of vegetation involves a spectrum of cases from those where disturbance-events and recruitment are tightly coupled to those where they are completely uncoupled. An example of the first case is where a short-lived herb becomes established from the long-term seed bank in the soil in a primary forest only after tree fall. The opposite situation is exemplified by an annual which becomes established each autumn from the short-term seed bank in a shallow layer of soil on a rock outcrop, where no perennials can become established.

Section 2 of this paper deals with examples at various points along this spectrum from coupled to uncoupled recruitment. Section 3 spells out the need to recognize two basically different types of seed bank related to coupled and uncoupled recruitment respectively. In section 4 a summary of the known means of persistence of plant populations at the regional scale is presented. Section 5 deals with aspects of local persistence that do not arise explicitly when considering the regional scale. Finally the importance of the dichotomy between coupled and uncoupled recruitment for understanding the determination of plant population size is emphasized.

There is no uniquely satisfying definition of 'local' and 'regional' scales. The essential feature of the local scale is that it should take in several to many units of localized disturbance in the community in question. It might be of the order of 10^2 m^2 in a grassland subject to mound-building by gophers or moles, 10^3–10^4 m^2 in a semi-desert where scattered shrubs are killed by prolonged drought, or 10^8–10^{10} m^2 where forests suffer sheet destruction through fire or strong winds. The essential feature of the regional scale is that it should include all the habitats in which a given species lives, and between which there is a reasonable chance of dispersal in the short term. The areal extent and disturbance regime may be quite different for the various habitats in which a given species is found, e.g. recent glacial moraine, river gravel and rock outcrop for an alpine plant, or washes and upland slopes for a semi-desert plant.

'Persistence' is considered through periods when the mean climatic conditions are relatively constant, and the variance about the mean is relatively constant. Thus, in this article persistence is not considered with respect to 'Ice Ages' or the corresponding arid and pluvial periods away from the poles. It is accepted that the climate is never constant, but always changing to some degree and on various time scales (Davis 1986). However, relative to the modal life-length of established plants of most species ($10^{-1} - 10^2$ yr), or the modal return time of most disturbance-events ($10^0 - 10^2$ yr) it is reasonable to think in terms of climatic conditions as relatively constant. The short-term deviations from the mean can, of course, be immensely important for recruitment when the medium-term mean is relatively constant.

The review is confined to vascular plants. It is concerned with 'genets' sensu Harper (1977) and not 'ramets'.

2. The degree of coupling of disturbance events and recruitment

The tightest coupling is seen in plants which live at sites where there is a relatively dense vegetative cover most of the time, and which always become established immediately after the creation of some sort of gap. In forests well-known examples are plants, both woody and herbaceous, which emerge from the soil seed bank when a sufficiently large gap is created by wind-throw of a tree or trees. Other examples are the herbs, shrubs and trees that come from some kind of seed bank (in the soil or in woody fruits in the canopy) after fire. If these plants do not germinate almost immediately after the disturbance-event they have a very slight chance of establishment. The reasons may be various. They may be too light-demanding or too sensitive to below-ground competition (cf. Fenner 1978), or they may succumb completely to predators or disease organisms which build up quickly after the disturbance, especially if this is fire (Ashton & Willis 1982). There may be in one community several to many species which become established immediately after disturbance. Their persistence in mixture can be explained because (a) the conditions before successive disturbance-events are bound to differ, and the relative production of viable seed by different species is bound to differ, (b) the conditions following successive disturbance events also differ, and the conditions after any one will vary spatially, and thus different species will be favoured at different times and places (Horton & Kraebel 1955, Grubb 1977) and (c) some species will grow faster and live for a shorter time than others which can withstand some suppression in early years (Hanes 1971). The point of importance for this article is that all must become established almost immediately or not at all.

A group of plants only a little less tightly coupled to disturbance-events is that which invades within a few years of gap-formation, while the shading and perhaps use of below-ground resources is only moderate. For example, in a forest, the chance of invasion of a gap by a certain species may be maximal up to the second year, and considerable but declining over the next few years. The contrast between such a case and one where invasion has to take place in the first year is illustrated in Table 1, based on the work of Brokaw (1987). It is likely that the plants which become established in the 2nd–5th years reach the gap as freshly dispersed seed rather than from the seed bank, but there is little precise information on this point. In terms of persistence the species passes the time between one act of recruitment and the next as above-ground plants with well-illuminated canopies. It appears that the degree of coupling of the disturbance-event and recruitment does not need to be as tight as in the first group because the plants of the species concerned can tolerate a wider range of conditions as juveniles. There is certainly evidence that the chance of invasion in gaps formed in a given year does not decline steadily (cf. *Miconia argentata* in gaps formed in 1976, Table 1). The variation about the declining mean chance arises, just like the variation between years and sites in the first group considered, because of variations in the production of viable seed and variation in conditions during germination and establishment.

Recruitment is much less tightly coupled to disturbance-events in the remaining types of forest species considered here. We take first tolerant trees. For them recruitment is confined to the gap, pioneer, mature and degenerate phases of the regeneration cycle in the system of Watt (1947), and excluded only from the building phase, during which the degree of shade and/or below-ground competition is too great.

Table 1. Recruitment and survival of juveniles of two gap-demanding tree species in 30 tree-fall gaps in a tropical rain forest on Barro Colorado Island, Panama: numbers of plants recruited to the height class ≥ 1 m, and surviving for different lengths of time (from Brokaw 1987).

	Gaps formed 1975						Gaps formed 1976				
	Years of recruitment	Numbers recruited	Numbers surviving to year				Years of recruitment	Numbers recruited	Numbers surviving to year		
			77	78	81	84			78	81	84
Trema micrantha	75–76	12	11	10	4	4	76–77	47	35	17	12
	76–77	1		0	0	0	77–78	4		1	0
	77–78	0			0	0	79–81	0			0
	79–81	0				0	82–84	0			
	82–84	0									
Miconia argentea	75–76	16	13	11	8	8	76–77	9	8	6	3
	76–77	39		34	24	12	77–78	13		10	4
	77–78	24			18	6	79–81	35			14
	79–81	14				10	82–84	3			
	82–84	1									

Otherwise recruitment is dependent on the seed crop and/or weather conditions and abundance of predators and disease organisms at the time of germination and early establishment. We know that in some trees there are immense year-to-year fluctuations in seedling density, dependent on the seed crop, as in *Fagus sylvatica* (Ellenberg 1988) or *Picea abies* (Leikola et al. 1982). Next we may consider herbs that are effectively shade-demanding, like *Oxalis acetosella*; they are constrained by the disturbance cycle in that they are suppressed in not only the building phase but also the gap phase of Watt (1947). They may be recruited during a large proportion of the regeneration cycle, but many of them form extensive clones and the extent of change in genet density through time is unknown (cf. Rabotnov 1985). However, in some northern temperate deciduous forests there are shade-tolerant annuals which are recruited each spring, and at least one of these (*Floerkea proserpinacoides* of the Limnanthaceae in North America) is effectively shade-demanding. It dies out in large gaps, does not have a long-term seed-bank, and after a gap has been filled reinvades by isolated colonists each able to form a dense patch which enlarges slowly (Smith 1983). So there is a real constraint imposed by the disturbance cycle but within the limits set by that cycle there are successive recruitment events triggered by the spring weather. A final group of forest plants which is effectively similar in this respect is composed of the epiphytes and crown parasites which build up on large old trees in tropical and warm temperature rain forests (Richards 1952, Grubb et al. 1963), and which die when the tree falls and is covered by rapidly growing saplings in the gap. Recruitment is limited to the time when a tree is large enough to develop the appropriate micro-habitats but that time must span a large part of the regeneration cycle, perhaps a third to a half.

Plants of semi-desert show varying degrees of coupling between recruitment and the disturbance cycle, but in general the coupling is loose. The major agents of disturbance are prolonged drought (Hastings & Turner 1965, Beatley 1979/80) and, at least in some areas, destruction by plagues of insects (West 1983) or lightning-induced fires after years of unusually high production by the interstitial ephemerals (Lay 1976). Recruitment events, in contrast, are coupled to specific rainfall conditions (Jordan & Nobel 1979, Noble & Crisp 1979/80). However, the disturbance cycle may constrain effective recruitment to a degree that is analagous with that outlined in the preceding paragraph for various tolerant forest plants. Thus many succulents in the semi-deserts western North America need nurse plants, and may take part in a cyclic succession with a non-succulent shrub which is able to establish on bare gound, and in which the succulent has to establish. Such a cycle between an *Opuntia* and the shrub *Larrea* was worked out by

Yeaton (1978). More subtly a dependent species may become established only in degenerate bushes of the nurse species; such a case does not seem to have been documented rigorously, but it seemed to me that the small tree *Myoporum platycarpum* invading *Atriplex* at the site in South Australia described by Hall et al. (1964) provided an example. Other species, e.g. *Cassia sturtii* at that site, become established on bare ground between the crowns of established shrubs. For such species in the natural state weather events are all-important in governing when recruitment will occur (see also Roughton 1972 and Zedler 1981), and there is minimal coupling with the disturbance cycle. In some parts of the world today recruitment may be governed less by weather than by introduced livestock or pest-animals, as in the case of rabbits in Australia (Crisp & Lange 1976).

Therophytes in semi-desert are well-known to show huge year-to-year fluctuations in abundance (Bykov 1974, Loria & Noy-Meir 1979/80, Noble & Crisp 1979/80, Shmida & Ellner 1984), dependent on the weather and not the disturbance cycle. And yet some constraint is imposed at the scale of the area occupied by one shrub, because it is well established that some species are favoured in shrub crowns and others in the gaps between crowns (Shmida & Whittaker 1981). More deaths of shrubs by prolonged drought or fire will favour some species, and disfavour others. Species of therophyte able to become established in crowns and inter-crown spaces with an approximately equal chance, illustrated perhaps by *Filago depressa* in the Mojave Desert (Shmida & Whittaker 1981), must be among the plants which show the minimum possible coupling of recruitment and disturbance in natural vegetation.

The extent of coupling in perennial grasslands is probably very variable, and is certainly not well established. In arid grasslands, as in semi-desert, the effective forms of disturbance are prolonged drought and fire (Williams & Roe 1975, Loucks et al. 1985) and may be separated by years from episodes of recruitment coupled to particular rainfall events (Williams & Roe 1975). In tall moist-climate grasslands it has been supposed that recruitment is tightly coupled to the mound-building and trampling activity of animals (Curtis 1959, Watt 1974) but more critical work is needed. Where moist-climate grasslands are grazed by domestic stock or mown, recruitment almost certainly goes on in the turf irrespective of localized disturbances; this is strongly suggested by the 'age-state' spectra for many species in various grasslands in the U.S.S.R. summarized in the volume edited by White (1985). For closely grazed chalk grassland in Britain the potential of several species to invade tiny gaps (of the order of 1 cm^2) or even a 'continuous' canopy of other species has been shown in a field experiment by Mitchley & Grubb (1986). The short-lived plants in such a system do include a few which are certainly dependent on localized disturbance and emergence from the seed bank, e.g. *Arenaria serpyllifolia* ('turf-incompatible', Gay et al. 1982), but all the commoner species regenerate routinely in the continuous sward ('turf-compatible'). Examples of the latter are the hemi-parasites *Euphrasia officinalis* and *Rhinanthus minor*, the strict biennials *Gentianella amarella* and *Linum catharticum*, and the pauciennials *Carlina vulgaris* and *Picris hieracioides*. The numbers of flowering plants of these species can vary enormously from year to year, and are controlled by rainfall events, predators and turf height rather than localized disturbances such as hoof marks or mole heaps (Kelly 1982, Grubb 1984, 1986). Examples are shown in Fig. 1. Similar year-to-year variation, largely un-

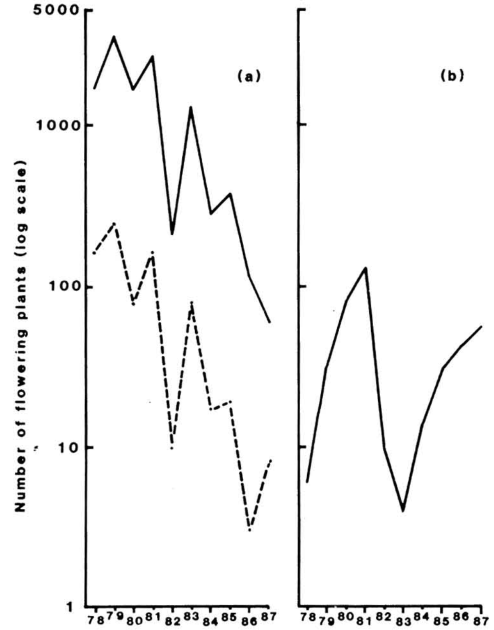

Fig. 1. The numbers of flowering plants of two hemi-parasitic summer annuals on a transect of 50 × 0.5 m in chalk grassland at a site in southern England described by Grubb et al. (1982): (a) *Rhinanthus minor*, (b) *Euphrasia officinalis* (data of P. J. Grubb & D. Kelly, unpublished). Over 92% of the *Euphrasia* plants occurred in a 3-m stretch of the transect, and the numbers of *Rhinanthus* plants in that stretch are shown by the pecked line.

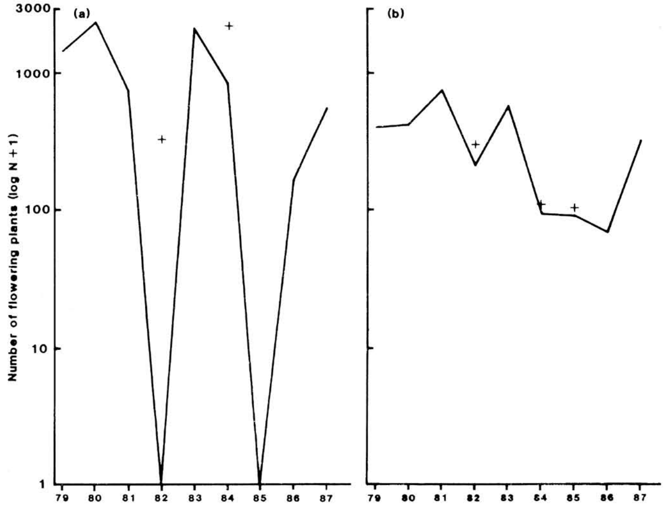

Fig. 2. The numbers of flowering plants of two winter annuals in five quadrats of 2 × 0.5 m on a grazed fixed dune system at a site on the eastern coast of England (described by Grubb et al. 1982, their site Y): (a) *Cerastium semidecandrum*, (b) *Erophila verna* (data of P. J. Grubb & D. Kelly, unpublished). The values for *Cerastium* include a few plants of *C. atrovirens*. Because the *Cerastium* failed completely in two years with very dry spring weather, log *N* + 1 is plotted rather than log *N*. The crosses indicate the totals including dead, non-flowering plants at the time of census in May.

related to disturbance-events, is known in the annuals of fixed dune systems, and examples are shown in Fig. 2; the total failure of one species in two years with very dry spring weather is especially notable, and it is certain that the recovery in the following years was from the seed bank. In the case of dune plants the substratum is much less fixed than in chalk grassland, and the dominant effects of weather do seem to interact with the disturbance-events of moderate sand-blow (Grubb et al. 1982). For a few turf-compatible species in chalk grassland I suspect that a subtle form of disturbance (moderate trampling), acting in concert with appropriate weather conditions, is important in eliciting maximum recruitment from the seed bank, as in the case of the tiny-seeded *Blackstonia perfoliata* and *Centaurum erythraea*.

The turf-compatible short-lived plants of chalk grassland can persist only if the turf is kept to a moderate height by grazing, and to that extent recruitment is dependent on disturbance but the relevant disturbance is continual rather than periodic, and 'all over' rather than localized, and the recruitment is not associated with the disturbance-events as such. Granted this caveat, we have here as complete an uncoupling of recruitment and disturbance-events as in the most convincing cases of therophytes in semi-desert or on rock outcrops.

Other cases of complete uncoupling are seen in the natural annual savanna grasses of northern Australia (Andrew & Mott 1983), the natural communities of annuals on shallow soil on rock outcrops such as the cedar glades of the eastern U.S.A. (Baskin & Baskin 1985), the analagous communities in vernal pools in California (Luckenbach 1973, Holland & Jain 1977). In the most productive annual grasslands found under the mediterranean type of climate only a few species are able to develop populations of adults each year where the accumulated mulch is not destroyed by burning, grazing, trampling or mound-building by animals. These few species with fully uncoupled recruitment have large seeds, grow tall and are perhaps more shade-tolerant as juveniles; in the studies in California reported by Heady (1958) *Bromus mollis* (= *B. hordaceus*) and *B. rigidus* were the outstanding examples. For most species in such grassland, especially those with smaller seeds, recruitment is increased by some kind of disturbance. Many of the species can persist for years as seeds at the soil surface or at some depth in the soil (Major & Pyott 1966). Thus, most species in annual grassland seem to have recruitment that is to some extent coupled with disturbance-events.

The annuals of drift-lines along coasts and big rivers occupy sites that are characteristically disturbed on an annual basis, but the episodes of recruitment are not coupled to the disturbance-events; recruitment occurs in the spring and the disturbance-events mainly in autumn and winter. In contrast, in the case of many arable weeds, it is indeed the turning over of the soil during ploughing and the exposure of the seed which leads directly to germination. Insofar as the arable weeds have been recruited from braided river systems, their germination was perhaps linked in the natural state to episodes of resorting of river gravels and silt.

Table 2. A spectrum of cases from those where episodes of recruitment and disturbance-events are tightly coupled to those where they are completedly uncoupled.

Degree of coupling	Examples
1. Recruitment is stimulated by the disturbance-event	Strongly intolerant plants of wind-fall gaps in forest, and hoof-marks in grassland; many plants in vegetation prone to fire
2. Recruitment must occur within a few years of the disturbance-event	Less stongly demanding plants of forest gaps
3. Recruitment is constrained to part of the regeneration cycle but that part occupies a large proportion of the whole cycle	Tolerant trees, shrubs and herbs in forest able to regenerate in all phases of the cycle except building; shade-demanding plants not able to regenerate in building or gap phases; epiphytes and crown parasites; semi-desert plants dependent on nurses
4. Recruitment is hardly affected by stage of regeneration cycle but maturation may be affected	Many semi-desert shrubs and ephemerals; possibly many herbs in grazed and mown perennial grassland
5. Recruitment depends only on continual overall disturbance and not localized disturbance-events	Some species of short-lived interstitial plants in grazed grassland, including chalk grassland and fixed-dune grassland
6. There are no perennials to suffer disturbance	Annuals on rock outcrops, in vernal pools, in natural and human-induced annual grasslands, and on drift-lines

The different degrees of coupling between recruitment and disturbance-events are summarized, with examples, in Table 2. It is clear that coupled recruitment predominates in vegetation-types which build up a large biomass, whereas uncoupled recruitment predominates in less productive vegetation-types. But the matter is not so simple. Tolerance of shade, below-ground competition, and the predators and disease-organisms associated with established vegetation are also important, and enables plants in tall, productive vegetation to have uncoupled recruitment. Tolerance of below-ground competition is vital in allowing uncoupled recruitment in many species of semi-desert, and in those short-lived plants which live in the interstices of perennial grassland on infertile soils. On the other hand coupled recruitment is important for the persistence of those species of unproductive annual grassland which flourish on localized disturbances.

3. The need to recognize two basically different types of seed bank

The analysis in Section 2 leads one to see that some plants need to produce a bank of seeds which are programmed to germinate after an appropriate disturbance-event, while others need a bank of seed which does not all germinate as soon as the conditions are appropriate because the whole generation may fail later on through predation or inclement weather. The *Cerastium* in Fig. 2 is a clear example of the latter case. It may be argued that the former group would also benefit from holding some seeds back, but there seems to be no evidence that the seeds are programmed to allow for this. In fact some seeds in a soil seed bank may fail to reach the surface after one disturbance-event, and remain to be exposed after another event, but that is a matter of chance.

The two types of persistent seed-bank are dependent upon two types of dormancy which we may call 'disturbance-broken' and 'risk-spreading'. Yet a third functional type of dormancy is discussed by Chesson (this issue) — that where the seeds await an appropriate environmental signal representing a particular type of weather and not a disturbance-event. This type seems to be especially common in semi-deserts; perhaps it may be called 'weather-dependent'.

In the case of coupled recruitment with 'disturbance-broken' dormancy the seeds are programmed to germinate when they 'sense' environmental changes typical of gap formation. For plants of vegetation not prone to fire the signals are increased amplitude of the daily temperature regime, increased light flux and change in the red/far red ratio, and in some cases increased nitrate concentration (Grime 1979). For fire-prone plants the release of seed from woody capsules may be as important as stimulation of germination by the high temperatures of a fire (Gill 1981). In the last few years it has been found that many fire-following herbs in California have their germination stimulated by extracts of charred wood (Keeley & Pizzorno 1986).

The plants with 'disturbance-broken' dormancy may have a dormancy mechanism of any of the three types recognized by Harper (1977). The 'innate' type is illustrated by those species which need a heat treatment to release the seed from some kind of woody fruit in the canopy, or to crack the coats of seeds in the soil. The 'induced' type is illustrated where, as a result of spending time on the soil surface beneath a leafy canopy before burial in the soil, seeds develop a need for bright light to stimulate germination (Fenner 1980). The 'enforced' type is illustrated by those species which need the chemical stimulus of extracts of charred wood, and also by those which need light for germination from the time of release (Cresswell & Grime 1981).

In the case of uncoupled recruitment the extent of the seed bank is extremely variable. For example, in many winter annuals on sand dunes it is negligible (Harper 1977), and persistence of a population through dry spring weather is dependent on very early flowering (as in *Erophila verna*) and/or tolerance of tissue-desiccation during the ripening of fruits (as in *Myosotis ramosissima* and *Valerianella locusta*). These three species were found by Kelly (1982) to have a negligible seed bank at our study site on the eastern English coast, while the *Cerastium semidecandrum* which fails utterly in very dry springs (Fig. 2) has an appreciable seed bank. In those cases, like the *Cerastium*, which do have a seed bank, we know almost nothing about the longevity of the seeds, the physiological control of dormancy and germination, the heritability of dormancy or any associated increase in defence of the seed against predators and disease organisms. Ernst (1981) found that in the sand dune winter annual *Phleum arenarium* the formation of a small seed bank did not depend on genetically distinct dormant seeds, but on the production of smaller seeds at the end of the growing season. A different type of case that has been investigated experimentally is that of the hemi-parasitic annual *Rhinanthus serotinus* (*R. angustifolius*); ter Borg (1972) kept seeds in moist conditions at 4°C in the laboratory for five years, and found that seed germinated at about 10-month intervals (Fig. 3). This strongly suggests an endogenous cycle that might be pushed onto a 12-month basis if the seed were exposed each year to summer temperatures.

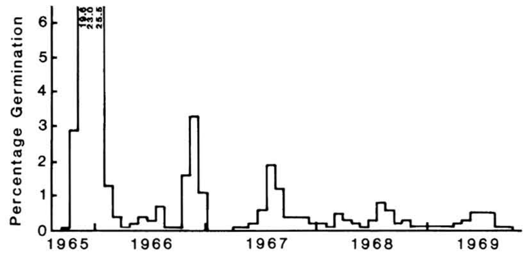

Fig. 3. Germination of seed of *Rhinanthus serotinus* (*R. angustifolius*) kept in the laboratory at 4°C for five years (from ter Borg 1972).

There are many woody plants with delayed germination, and in their case the mechanistic explanation is provided at least partly by the need for some kind of protective coat on the seed to rot. Most of the British trees and shrubs with bird-dispersed fleshy fruits show this effect (Beckett & Beckett 1979). A species which has been studied in detail is the North American black cherry, *Prunus serotina*; many of its seeds take three years to germinate, but few last longer than five years in the soil (Marquis 1975, Wendel 1977). This short-term storage can act as a buffer against annual fluctuation in fruit production and dispersal, as suggested by Canham & Marks (1985).

Most, and perhaps all, plants which have uncoupled recruitment and a seed bank can be said to display the 'innate' type of dormancy. At the time the seeds leave the parent plant they are 'prevented from germinating when exposed to warm, moist aerated conditions by some property of the embryo or the associated endosperm or maternal structures' (Harper 1977:65).

Cohen (1966) predicted on the basis of a model that the fraction of seed not germinating each year should be correlated with the probability of total or near-total failure to produce a seed crop (see Hanski this issue). Records of the type shown in Fig. 2, but preferably for a longer period, are needed to test Cohen's prediction. The issue is discussed in detail by Silvertown (1988). The kind of failure at the adult stage that I have exemplified in *Cerastium semidecandrum* may well be widespread, but it was not taken into account in the theoretical treatment by MacDonald & Watkinson (1981) of the ways in

Table 3. A suggested classification of the means of persistence at the regional scale.

Means of persistence	Examples
1. Long-term occupancy of the soil by a seed bank and transient occurrence in patches as plants above ground, following disturbance-events	Intolerant species of forest and grassland, usually herbs; also many species of fire-prone vegetation
2. Long-term occupancy of an appreciable part of the landscape as adults (often sparse) with recruitment of juveniles strictly localized in space or rare to occasional in time (no long-term seed bank in soil)	Some intolerant species of forest, usually trees or shrubs; some species of fire-prone vegetation (often with canopy seed bank); some perennials of semi-desert
3. Long-term occupancy of an appreciable part of the landscape as adults and juveniles	Tolerant species of forest and grassland; some perennials of semi-desert
4. Long-term occupancy of the soil by a seed bank plus occurrence above ground either every year or in some years, depending on weather rather than disturbance	Many ephemerals of semi-deserts and some annuals of rock out-crops, sand dunes and perennial grasslands
5. Seasonal occupancy of the soil by a seed bank plus appearance as plants above ground every year	Some annuals of rock outcrops and dunes, and some plants of annual grasslands and savannas
6. Long-term occurrence above ground as juveniles and immatures, plus seasonal occurrence as adults and seasonal or long-term occupancy of soil by a seed bank	Biennials and pauciennials of natural grasslands and rock outcrops; also in human-induced systems pauciennials that would naturally fall into type 1
7. Long-term occupancy of specialized habitats plus transient occurrence in temporarily available sites	Many early colonists in primary successions, as on glacial moraines, and in human-induced secondary successions, as in old-fields (in latter case usually with long-term seed bank in soil)
8. Occupancy of transient but not very short-lived sites, with newly available sites often immediately adjacent	Plants of mobile soils, as on young salt marshes and sand dunes; epiphytes and crown parasites
9. Long-term occupancy of one or more habitats by self-sustaining populations, plus long-term occupancy of others as a result of influx of seed	Plants of drift-line also found on dunes, plants of semi-desert washes also found on uplands; probably a very common situation

which seed banks might stabilize or destabilize populations of annuals, and it must complicate the argument of Klinkhamer et al. (1987) that one should expect a negative relationship between dispersibility and the degree of dormancy. Total failure at the adult stage is also important in relation to Westoby's (1981) argument that, in general, it is in the interest of the mother to have germination spread out through time, but in the interest of each embryo to germinate at the single opportunity which gives maximum chance of growing to maturity (and maximum fecundity). The individual embryo cannot possibly receive a signal indicating that failure will happen in some months' time, and therefore germination at the first opportunity is a gamble; certainly it will not always be the best proposition.

4. Means of persistence at the regional scale

Nine means of persistence are listed, with examples, in Table 3. Six of these follow directly from the discussion above on the degree of coupling between recruitment and disturbance-events, but types 7, 8 and 9 merit comment.

Most plants found in the early stages of primary succession have permanent homes in other habitats. For example, on glacial moraines many of the earliest colonizers, such as *Epilobium* species, have permanent homes on continually disturbed river gravels below the glaciers, while others such as species of *Dryas* and *Salix* have permanent homes in crevices on rocks where insufficient soil builds up for succession to forest, heath or grassland. Documentation for

Alaska is provided by Cooper (1923) and for the European Alps by Ellenberg (1988). Many of the plants found in the early stages of man-induced secondary successions similarly have alternative habitats with long-persistent populations. The issue was discussed critically by Marks (1983) for the case of old-field plants in north-eastern North America.

The major group of early-successional plants without alternative habitats and long-persistent populations, is associated with mobile soils, especially those of young sand dunes and young salt marshes. Such plants depend on a continual supply of newly available sites.

The last category in Table 3 concerns the many populations of plants which do not produce enough seed to perpetuate themselves, and which are maintained by a continual influx of seed from nearby populations which are more productive. The most elegant worked example is that of *Cakile edentula*, an annual studied at a site on the Canadian coast by Keddy (1981, 1982). The plant survives well, and makes abundant seed on the drift-line, but it consistently occurs as far inland as the inner side of the first dune ridge, where it grows slowly, suffers heavy mortality and produces few seeds. Watkinson (1985) has calculated that 50–80 % of the seed produced at the drift-line must have moved inland to sustain the landward populations recorded. We may thus think of 'source' and 'sink' populations in adjacent habitats. Shmida & Whittaker (1981) used the term 'mass effect' for this phenomenon, and Shmida & Ellner (1984) developed the idea in a model. Auerbach & Shmida (1987) have given evidence which strongly suggests that 'mass effects' are important for many species in arid vegetation in Israel.

5. Local persistence and temporal change in spatial distribution

For plants with recruitment that is coupled to localized disturbance-events, it is a trivial observation that there must be temporal change in the spatial distribution of peaks of abundance of each species, as the disturbance-events occur in different places at different times. What is much more interesting is to ask whether or not there is also temporal change in the spatial distribution of species with uncoupled recruitment.

Fowler (1988) emphasizes the fact that there are marked local differences in survival and fecundity of plants in apparently similar micro-sites within a single community or habitat, and these differences occur irrespective of the density of the plants in question. These subtle variations in population dynamics are likely to mean that there are source and sink subpopulations that we might not have expected at first sight. We then need to ask whether or not the sources and sinks move about through time. In fact, there is now unequivocal evidence that the peaks of abundance of certain annuals, biennials and pauciennials in chalk grassland in southern England do move appreciably (Grubb 1986). They show what I have called 'shifting clouds of abundance' (Grubb 1984). In a collection of nine species of short-lived plant at one site the degree of mobility was found to vary appreciably among species. For example, of the two species in Fig. 1 the *Rhinanthus* proved to be highly mobile at the scale of metres. If we consider the period before the steady drop in numbers (1978–83 as opposed to 1984–87), that is, the period when we might expect most year-to-year constancy in spatial distribution, then in three of the four years when the test can be made the number of flowering plants per 0.25 m^2 quadrat along the 50-m transect shows a strikingly short-lived correlation with previous years (Table 4). In contrast, the *Euphrasia* remained virtually confined to a 3-m length of the 50-m transect for 10 years. Within that small and even-looking patch of grassland, and within another similar sub-population, the clouds of abundance were found to move around. In addition quite new colonies of *Euphrasia* sprung up at intervals over the years, distant from previously known colonies, especially along a newly created cattle track. Differences in mobility between two biennials and among three pauciennials at the same site have been discussed earlier (Grubb 1986).

Table 4. The correlation coefficient between the number of flowering plants of *Rhinanthus minor* in a quadrat in one year (n) and previous years (n-1 to n-5). There were 100 quadrats of 0.25 m^2 along a transect of 50 m. Analysis by D. Kelly of data collected by Kelly and the author. *** $P<0.001$, ** $P<0.01$, * $P<0.05$.

Year *n*	*n*-1	*n*-2	*n*-3	*n*-4	*n*-5
1979	0.406***				
1980	0.274**	0.030			
1981	0.260*	–0.034	–0.156		
1982	–0.288**	–0.090	–0.148	–0.061	
1983	–0.141	0.284**	0.274**	0.018	0.025

The simplest explanation of the shifting clouds of abundance is that they arise because of random effects in seed dispersal and random changes in the position of clumped predators; there is evidence that the pattern of relative turf height along the transect has been constant over ten years (P. J. Grubb & D. Kelly, unpublished). A possibility is that in at least some species and some patches the seedling densities reach excessive levels and seed production per unit area is driven well below the maximum attainable, as happened in the populations of the annual *Erophila verna* studied by Symonides (1984), and modelled by Symonides et al. (1986), but we came upon clear evidence of such an effect only in one species in one year (*Rhinanthus minor* in 1979). Another possibility is that disease organisms and/or predators accumulate on dense patches and depress yield, as envisaged in the model of within-patch dynamics proposed by Thompson (1985), but we have no evidence that this is the case.

The phenomenon of shifting clouds of abundance may be superimposed on static patterns related to, say, soil depth or uneven cover by matrix-forming plants of the community. For example, in semi-desert where certain ephemerals are associated with shrub crowns, and others with the spaces between, it has been established that the clouds of abundance of a particular species of ephemeral in one cover-type can change position markedly between years (Nicolson 1985).

Local temporary extinctions are the extreme case in a system of shifting clouds of abundance. The most thorough study of local extinction in plants and reoccupation of sites by plants with recruitment not coupled to disturbance-events, has been that of van der Meijden (1979) and van der Meijden et al. (1985), who followed discrete 'populations' or 'interaction groups' of pauciennials on a Dutch dune system through a severe drought and the years of recovery afterward. The 'populations' were censused in 25-m^2 samples on numerous transects. The proportion said to become 'extinct' varied greatly among the nine species studied (0.09–0.88). However, it is probable that absolute local extinctions occurred only in those species with a negligible seed bank (*Arctium pubens, Carlina vulgaris* and *Cirsium vulgare*). For at least some species the risk of extinction above ground was much greater in some populations than others, with some sites acting as refuges and others being only transiently occupied. For example, in drought years the populations of *Senecio jacobaea* in the partial shade of shrubs were much safer than those in the open. Such cases merge with others of a 'source and sink' type considered above. It may be that for all the species studied by van der Meijden et al. the nexus of populations is stabilized by the presence of environmentally distinct refuges.

Even more intriguing, if it exists, is the case where the sites occupied by a species do not differ materially in their potential as refuges, so that extinction and reoccupation depend purely on the chances of dispersal and, say, aggregated predation (for a review of relevant models see Taylor this issue). An example might be provided by the prickly pear, *Opuntia stricta*, at some types of site in Australia, if Nicholson's 'hide and seek' model (as it was dubbed by Myers et al. 1981) does in fact apply. In this model it is supposed that the predator has a limited ability to find and destroy the plant, and that the predator dies out where it does succeed in finding the plant. Such sites are then open to recolonization by the plant dispersing from sites where (purely by chance) the predator failed to find it. It is now established that this model is not appropriate for populations in open woodland (Myers et al. 1981).

Granted that shifting clouds of abundance are indeed found in plants with recruitment not coupled to disturbance-events, it seems likely that they will be found to be superimposed on the patterns determined by disturbance-events in those species whose recruitment is more or less tightly coupled to those events. Some preliminary evidence that this is the case is certain mediterranean-climate systems is summarized by Grubb & Hopkins (1986). Insofar as chance factors are the determinants, this concept merges with the random walk model discussed by Hubbel (1979) and Hubbel & Foster (1986) for very species-rich tropical forests.

6. Concluding remarks

The dichotomy between coupled and uncoupled recruitment is basic to an understanding of the major patterns of temporal change in population size or density, and yet it does not receive explicit treatment in recent texts. It plays no part in the delineation of three basic 'demographic strategies' (saturation-, exploitation- and adversity-selected) set out in the textbook of Whittaker (1975) and in more detail in the paper of Whittaker & Goodman (1979). It is not exemplified in the array of common types of temporal change in population density given in Begon et al. (1986:550), based on the paper of Harper (1981). Similarly the issue receives no emphasis from Silvertown (1987). Yet the dichotomy must be recognized by anyone trying to achieve a quantitative understanding of population control. It is only in a few cases of uncoupled recruitment that a quantitative relationship between environmental factors and population size has been established for a plant, e.g. for the pauciennial *Senecio jacobaea* on sandy, drought-prone soils in relation to rainfall and herbivore load (Dempster & Lakhani 1979, van der Meijden et al. 1985). For plants with coupled recruitment a quantitative understanding must depend on measurement of the variables found in gap-replacement models of the type described by Shugart (1984). And for very many plants, with partially coupled recruitment, a hybrid approach will be necessary.

The fact that the contrast between coupled and uncoupled recruitment is not coped with in the much-discussed divide between *r*- and *K*-selection illustrates the need to bring out further dimensions in the analysis of vegetational dynamics, as Grime (1979) did in the case of 'stress'. Robert MacArthur himself toyed with selection in respect of several different dichotomies: generalists vs specialists, pursuers vs searchers, users of coarse-grained resources vs users of fine-grained resources (Cody & Diamond 1975: vii), youth vs old age, and predator escape vs feeding ability (MacArthur 1972:230). In respect of plant population dynamics, the dichotomy between coupled and uncoupled recruitment may be one of the more profitable to recognize in the pursuit of a balanced understanding.

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