Meta-population dynamics of biennial plants: how to exploit temporary habitats

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SUMMARY

Extinction of local populations of plants of many biennial plant species has been frequently reported. Survival of these species on the meta-population level implies a balance between extinction and regeneration, either through seed dispersal or from the seedbank. We distinguish between three types of biennials (transient, fugitive and persistent) and review the relation between dynamics of local populations and habitat characteristics, such as disturbance. Some species are safe-site limited whereas other species demonstrate a combination of safe-site and seed limitation. Meta-population dynamics are illustrated with two examples (*Senecio jacobaea* and *Cynoglossum officinale*). We distinguish between patch dynamics (loss and genesis of sites that are suitable for population development) and meta-population dynamics of biennials (population behaviour within and between sites, and dispersal). A hypothesis is developed on the regulation of patch dynamics. Finally we discuss the question: what makes biennials suited for exploiting temporary habitats?

Key-words: biennial plants, dispersal, disturbance, extinction, meta-population dynamics, patch dynamics.

INTRODUCTION

Biennial plants are typical examples of organisms that survive as meta-populations, i.e. as interacting groups of local populations. Local plant populations of many of these species frequently become extinct (at least the C-autotrophic stage) (Harper 1977; Gross & Werner 1978; Van der Meijden 1979, 1989; Schat 1982; Van Baalen 1982; Reinartz 1984; Van Leeuwen 1987; Klinkhamer 1988a). Harper (1977) gave an absolutely telling description of their behaviour (with special reference to *Digitalis purpurea*): 'It is a curious

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Because reproduction delayed to the third or a later year is the rule rather than the exception (Werner 1975; Baskin & Baskin 1979; Van der Meijden & Van der Waals-Kooi 1979; Van Baalen 1982; Kachi & Hirose 1983; Zedler *et al.* 1983; Reinartz 1984; Jong *et al.* 1986, 1989; Klinkhamer *et al.* 1987a, 1987c) the term biennial does not fully cover the behaviour of these plants. Terms have been coined such as pauciennials (Grubb 1986), monocarpic perennials (Gross 1981), perennial monocarpic or delayed 'biennial' species (Harper 1977), facultative biennials (Kelly 1985) or semelparous perennials (Silvertown 1984) as opposed to strict biennials that always flower in the second year. Although these terms may be more appropriate, in this paper we will use the term biennial because it is short, and moreover because under favourable circumstances for growth, all plants are able to reproduce within 2 years.

feature of the dynamics of these populations that when they are conspicuous enough to be chosen for study they are usually already in a condition of decline!'. That description is limited to the plant stage. Seedbanks of some biennials may be rather persistent.

The group of species that we call biennials (see footnote page 249) in fact shows a range of life-history strategies. Some species are strictly biennial; most species, however, may delay flowering for one or several years. Flowering is usually delayed if rosette size is below a certain threshold (Werner 1975; see Klinkhamer *et al.* 1987a, for a review). The common traits of biennial plants, a delay in flowering and a single, life-time reproductive effort (monocarpy), lead to a high reproductive output (big-bang reproduction, Harper 1977). As in annuals, biennials are dependent on continuous regeneration through seeds. Yearly seed production and/or seedling establishment show an enormous variation. As a consequence, the typical dynamics of biennials consist of large population increases following reproductive success and decreases and even extinction following reproductive failure.

Another important consequence of regeneration by seeds is the dependence on habitats that contain sites that are potentially suitable for germination and establishment ('safe sites'). In fact we are dealing with a sequence of factors. We will use the term safe site in a very restricted sense as the primary factor that enables a seed to grow into a mature plant under common conditions. Secondary (temporary) factors that limit survival, growth or seed production (such as drought- or nutrient-stress, herbivory and seed predation) are interpreted as seed-limiting agents. For biennials, the primary factor seems to be a small- to large-scale disturbance of the environment, providing an area of bare soil. Explosive population development, however, sometimes follows large-scale natural or man-made disturbances in several communities. On the one hand annual disturbances (as in crop production) and on the other hand absence of disturbance in late successional stages are fatal for plant development (Harper 1977). Therefore most habitats are only temporarily suitable for biennials; still these populations survive on the landscape level.

It is the combination of the genesis of new favourable growing sites and the capacity of the seeds of these plants to reach these new sites that enables them to survive. In certain species seeds can remain dormant for a number of years and for such species the probability of the original site becoming suitable again is important. Both seed dispersal and dormancy may prevent extinction as small numbers of individuals may initiate new population growth and thus act in a density-dependent mode. For instance, if a fixed percentage of the seeds produced in each population is dispersed and this leads to an even distribution of seeds over all sites, thereby adding a constant number to each potential growing site with either none, a few or many plants, then seed dispersal acts in a density-dependent way. Klinkhamer *et al.* (1987b) have shown that even very low levels of dispersal are very effective in increasing population growth rate at the meta-population level.

The effectiveness of dispersal will depend on the continuous genesis of new sites that are suitable for population development. Long-lasting survival of biennials on the meta-population level implies a balance between loss of old sites and the gain of suitable new sites. In this paper we will develop a hypothesis on the dependence of meta-population regulation on habitat dynamics.

Most studies on biennials are restricted to one or only a few local populations. Consequently, they do not provide an answer to the question of how these species fluctuate and survive over larger areas. This paper will focus on the meta-population dynamics of biennials. First we will review the available information on dynamics in local patches

and give a typology of biennials, next we give data on variation in dynamics between local patches. Finally we will discuss biennial behaviour in plants and ask the question: what makes biennials suited for exploiting temporary habits?

POPULATION DYNAMICS OF BIENNIALS IN LOCAL PATCHES

Population development

Development of local populations of biennials varies greatly between species and habitats. A spectrum of possibilities is realized. The types refer to local populations of plants (the C-autotrophic stage); additional information will be given on other characteristics such as dispersal power and seed dormancy:

(a) the 'transient' type with short-lived above-ground populations with bouts of abundant flowering during one or only a few generations, followed by disappearance of plants,

(b) the 'fugitive' type with short- to longer-lived fluctuating populations,

(c) the 'persistent' type with relatively stable long-lived populations with fluctuating abundances at sites within the local population.

This range of dynamics cannot be seen independently from the habitats to which these species are adapted that range from ephemeral to rather stable with respect to the presence of safe sites.

Table 1 provides an overview of biennials belonging to these types together with information on their habitat and several species characteristics. Some biennials are found to fit into two different groups. Some examples follow here to illustrate the spectrum.

The 'transient' type. Both well-known examples of this type stem from habitats in which secondary succession quickly leads to closing of the vegetation, woodland gaps and 'old fields'. An extreme case is reported by Gross (1980). In a 3-year 'old field' with a population of *Verbascum thapsus*, plots were experimentally disturbed and sown with 'natural' densities of seeds of *V. thapsus*. Only those plots in which the vegetation had been completely removed supported densities of flowering plants similar to the situation in the year before the experiment. Plants that survived to a third summer did not produce any seeds; germination became inhibited. So, in fact, population survival only lasted for one generation. That single generation, in the meantime, had built up a considerable seedbank (c. 180 000 seeds are produced per individual). *V. thapsus* seeds may have a longevity of more than 100 years (Kivilaan & Bandurski 1973). Clearly the decline in available safe sites limits population life time.

The population cycle of *Digitalis purpurea* is prolonged and more complicated (Van Baalen 1982). After a windfall, clearcut or burning, a population may become established from the seedbank. Van Baalen found an immediate response of only 1·5% recruitment from the seedbank. Nevertheless this led to abundant flowering and seed production in the second year after the disturbance. About half of these plants produced secondary rosettes that flowered in the third year. About a quarter of the seeds from the first flowering season germinated and produced a peak density of flowering plants 2 years later (the fourth season). Depending on vegetation cover, germination already became strongly inhibited in the fifth season. Flowering was then delayed and the probability of flowering was reduced followed by population decline. In the meantime a seedbank had accumulated more than 100 000 seeds m^{-2}. In that phase, populations of plants usually became extinct.

Table 1. A typology of biennials based on seed number, seed weight (g), and the presence of seedbank (sb, small[s] or large[l]), delayed flowering (df, yes or no) and a specific dispersal mechanism (di, yes or no). Habitat: w.g. (woodland gaps); o.f. (old fields); s.d. (sand dunes); l.q. (limestone quarries); c.g. (chalk grasslands)

	Habitat	Seed number	Seed weight	sb	df	di
Group 1						
Digitalis purpurea	w.g.	85551[1]	0·00009[1]	l[2]	y	n
Verbascum thapsus	o.f.	180000[3]	0·000067[3]	l[3]	y[3]	n
Group 2						
Arctium minus	o.f.	5000[4]	0·0075[1]		y	y
Carduus nutans		4082[1]	0·00326[1]		y	y
Carlina vulgaris	s.d.	233[5]	0·0018[5]		y[5]	y
Cirsium vulgare	s.d.	973[6]	0·0023[6]	s[6]	y[6]	y
Cirsium rhotophilum	s.d.	319[7]	0·00106[7]		y[7]	y
Cirsium palustre	s.d.	1587[6]	0·0011[6]	s[6]	y[6]	y
Cynoglossum officinale	s.d.	425[8]	0·020[8]	s[8]	y[9]	y
Dypsacus sylvestris		2960[1]	0·005[1]		y[10]	y
Echium vulgare	s.d.	5811[8]	0·00278	s[8]	y[8]	n
Heracleum sphondylium			0·012[1]		y	y
Inula conyza	s.d.	5168[11]	0·00021[11]		y[11]	y
Melilotus alba	l.q.	8010[13]			n[13]	
Pastinaca sativa	o.f.				y[14]	
Senecio jacobaea	s.d.	14955	0.00028	s[15]	y[15]	y
Group 3						
Carlina vulgaris	c.g.	33[12]	0·00129[12]		y	y
Daucus carota	c.g.	68[12]			y	
Gentiana amarella	c.g.	56[16]	0·00018[16]	s[16]	n[16]	
Gentianella germanica	c.g.	50[12]	0·00018[12]		n[12]	
Linum catharcticum	c.g.	13[16]	0·00017[16]	s[16]	n[12]	

[1]Salisbury 1942; [2]Van Baalen 1982; [3]Gross 1980; [4]Gross & Werner 1982; [5]De Heiden 1991; [6]Van Leeuwen 1987; [7]Zedler *et al.* 1983; [8]Van Breemen 1984; [9]Klinkhamer *et al.* 1987; [10]Werner 1975; [11]Van Sante & Volker 1978; [12]Schenkeveld & Verkaar 1984; [13]Klemow & Raynal 1985; [14]Baskin & Baskin 1979; [15]Van der Meijden & Van der Waals-Kooi 1979; [16]Kelly 1989a.

Later, during succession when a tree canopy has developed, especially when this is not entirely closed and when the understory vegetation has become very sparse, small *D. purpurea* populations may become more persistent. Also, in this second example, safe-site reduction limited plant-population survival.

The 'fugitive' type. Most examples of this type were studied in sand dune habitats (Table 1). Populations of *Cirsium vulgare* may survive for a longer period. Out of 96 local populations of this species that were selected for study in Dutch sand dunes in 1981 by De Jong & Klinkhamer (1988a), 64 were still present in 1984. A key-factor analysis applied to the population data showed that germination and seedling survival were key factors for differences in success between local populations. Population reduction due to low germination and survival of seedlings was most pronounced in exposed, open vegetation due to desiccation in 1982. Van der Meijden (1989) illustrated the fate of populations of this species in the same sand-dune from 1980 onwards. After 5 years 91% became extinct. One year later many of these populations recolonized. There is no indication

that population reduction in this species was caused by succession leading to loss of safe sites.

The 'persistent' type. Studied examples of this type are restricted to chalk grasslands. The chalk grassland biennials are different from the former species in that they are much smaller and yield only few seeds (Table 1). Kelly (1989b) monitored small quadrats of chalk grasslands. Although he observed strongly variable numbers of seedlings of *Linum catharcticum* and *Gentianella amarella* the local populations did not become extinct. Grubb (1986) called this behaviour 'shifting clouds of abundance'. He suspected either purely random effects of dispersal and slight differences in grazing of the vegetation or patchy effect of predators and pests led to the inconstancy in patch distribution.

Establishment of biennial plants

Disturbance and gaps. Although many plant species have been reported to require openings in the vegetation for establishment, the concept of the gap seems to apply particularly well to the habitat type to which biennials are adapted. There is probably not a single population study on this group of species that does not stress the importance of local disturbances or bare patches. Grubb (1977, 1986) drew attention to the importance of local gaps in the vegetation for understanding species richness and evolutionary divergence. Gaps, i.e. vegetation and/or soil disturbance may create a so-called safe site where an emerging seedling is freed from competition for light or nutrients with neighbouring plants. It may also bring light-requiring dormant seeds from a persisting seedbank to the soil surface.

An additional effect of disturbance is that a thin layer of substrate on top of seeds may greatly stimulate germination. Even with daily watering, 1 and 2 mm of sand cover increased germination by four times in *Senecio jacobaea* compared to seeds on the soil surface. Eight mm of covering sand completely stopped germination (Van der Meijden & Van der Waals-Kooi 1979). It is probably the moisture condition that leads to a lasting inhibition of the seed coat that stimulates germination.

Gaps may be created by the death of individual plants, but also by small disturbances like digging or scraping by animals, grazing or hoof prints, man-made disturbances, periodic drought conditions or flooding. The resulting, temporary bare patches may range from a few cm^2 in infertile chalk grasslands caused by grazing or digging by small rodents, to hundreds of m^2 in fertile woodland (windfalls or tree felling) and fertile 'old fields' left bare after cultivation.

So disturbance may have different effects on different biennials (production of competition-free space, or otherwise stimulated germination and release from the seedbank).

Safe site versus seed limitation. The chance that seeds and safe sites 'meet' determines the possibility for establishment. At one extreme where seeds are abundant, this will be determined by the density of safe sites. At the other extreme, the density of seeds will be most important. We know of only a few studies that attempt to discriminate between the two potentially limiting factors of seedling establishment.

An example of safe-site limitation was demonstrated by Gross (1980) in her study on *Verbascum thapsus*, a 'transient' biennial. This is an introduced species in north America. She removed different categories of vegetation from 'old field' plots with a population of

this species. In one series of plots, seeds were added so that the natural density was doubled. Another series served as contrrol. No significant differences in number of seedlings were found between the two series. However, germination in both groups was significantly and positively influenced by removal of the vegetation. This indicates that *V. thapsus* is indeed safe-site limited, at least under north American conditions. We expect that the conditions in European beech-wood windfalls or clear cuts on chalk, a typical habitat of *V. thapsus*, will lead to safe-site limitation as well.

An example of seed limitation was found in a similar experiment on *Cirsium vulgare* and *Cynoglossum officinale* ('fugitive' biennials). Klinkhamer & De Jong (1988) found that the number of established seedlings was increased 40-fold in *C. vulgare* and 5-fold in *C. officinale* by adding seeds. Disturbance of soil and vegetation alone had little effect on the number of seedlings establishing naturally, but slightly increased the number of seedlings in plots with seeds sown. The number of seedlings in *C. vulgare* or *C. officinale* sites where the species had recently become extinct (*C. vulgare*) or was declining (*C. officinale*) was only slightly lower than in flourishing populations, indicating that the habitat was still suitable and populations were mainly seed limited.

Most observations and experiments on disturbance and seed addition do not allow such a conclusion about factors that are limiting establishment and population growth. We will discuss some of these examples to illustrate the importance of disturbance for the population dynamics of the three types of biennials.

Transient biennials. All but two of the 24 populations of *Verbascum thapsus* studied by Reinartz (1984) were in recently cleared areas (burning, bulldozing). *Digitalis purpurea* may also become extremely abundant in windfalls and woodland clearings, but the plant also grows in late successional forests with a low percentage cover of the floor vegetation (Van Baalen 1982).

Fugitive biennials. Van Leeuwen (1987) found that in dense grass vegetation, relatively high numbers of seedlings of *Cirsium vulgare* and *C. palustre* could be observed on patches of bare soil (e.g. mole hills) in dune grasslands. Pons (1976) observed that in *Cirsium palustre* germination and establishment in ash coppice was stimulated after felling. In a disturbance experiment, raking the soil of coppice felled 7 years earlier resulted in 25-fold increase in germination from the seedbank (Pons 1984). Van der Meijden & Van der Waals-Kooi (1979) studied experimentally germination of *Senecio jacobaea* by sowing equal numbers of seed in pairs of plots with and without (i.e. removed) soil-covering vegetation, in woodlands and vegetations of grasses and herbs or mosses and herbs. Germination and establishment of plants were significantly higher in the disturbed plots.

Persistent biennials. Holt (1972) studied *Daucus carota* in young and old fallow fields and found, by adding seeds, that the percentage grass cover determines not only the level of germination and establishment, but also the probability of reproduction. Verkaar *et al.* (1983) found *Carlina vulgaris*, and *Linum catharcticum* more often in relatively open vegetation than in dense vegetation in chalk grasslands, although they were not limited to gaps on a micro-scale (During *et al.* 1985). In field experiments (seed addition) they found that germination and establishment of these species was reduced under shaded conditions. Unfortunately it is not possible to judge the effect of seed addition compared to natural seed densities from these data. The percentage germination in pairs of experimentally

clipped sites was much higher when wire netting was applied, indicating that seed predation was very important in reducing plant numbers. Kelly (1989a), who studied *Linum catharcticum* and *Gentianella amarella* in chalk grassland in England, emphasized the clear linkage to gaps. Germination was restricted to a narrow 'window' of germination sites where mean turf height was only 1–3 cm, indicating safe-site limitation as well. He also found that experimental seed addition resulted in much higher densities than in adjacent control squares, indicating seed limitation and gap limitation simultaneously in the natural sites.

Local extinction of plants

Transient biennials. Several factors have been suggested to be responsible for population decline. In species where populations are limited by safe-sites, closing of the vegetation is the most important factor leading to extinction (*Verbascum thapsus*: Gross [1980], *Digitalis purpurea*: Van Baalen [1982]).

Fugitive biennials. For populations with seed limitation, survival, growth and seed production will be most important. Greig-Smith & Sagar (1981) found that the low abundance of *Carlina vulgaris* in sand dunes was caused by seed predation. Seed predation (pre- as well as post-dispersal) caused a reduction in seed production of more than 70% in *Cirsium vulgare* (Klinkhamer *et al.* 1988). Levels of seed predation differed strongly between years as well as between populations. Thompson (1978) found a strong reduction in seed production in *Pastinaca sativa*. There was a strong positive relationship between plant size and level of attack.

Van der Meijden (1979) and Prins & Nell (1990) demonstrated that herbivory may lead to population reduction in *Senecio jacobaea* in sand dunes. The open and thus exposed growing sites in dunes and chalk grasslands make biennials of the 'fugitive' and 'persistent' type especially vulnerable to drought conditions during germination and seedling establishment, even when the biennial has vegetative rosettes or is a mature plant (Van der Meijden *et al.* 1985; De Jong & Klinkhamer 1988b; Kachi 1990a). This can lead to shifts in distribution from exposed habitat to more shaded sites in the immediate vicinity of shrubs and trees (Van der Meijden *et al.* 1985; De Jong & Klinkhamer 1988a).

Fugitive biennials may also be safe-site limited, not unexpectedly in nutrient-rich old fields with rapid closing of the vegetation and accumulation of litter (Gross & Werner 1982).

Persistent biennials. Biennials in chalk grassland have not been found to become locally extinct (Grubb 1986; Kelly 1989b). They show large fluctuations in number for which both safe-site limitation and seed limitations are responsible. Schenkeveld & Verkaar (1984) found that *Carlina vulgaris, Gentianella germanica, Daucus carota* and *Linum catharcticum* recruitment in chalk grassland was reduced by shade. In open habitat they found recruitment and survival to be limited by seed predation and drought. Similar results were obtained by Kelly (1989a) on *L. catharcticum*. In an experiment on the effects of a range of factors (clipping, watering, nutrient addition and herbivore exclusion), he found that excluding snails was the only manipulation that significantly increased survival and reproduction in *L. catharcticum*. Holt (1972) found vegetation density to be important in the decline of *Daucus carota* in old-field vegetation. Although *D. carota* is a typical representative of the 'persistent' type in chalk grasslands (Table 1), it is clearly not so persistent in nutrient-rich old fields.

Table 2. Fate of 91 populations of *Cynoglossum officinale* selected in 1981. Populations that were present in 2 successive years are called 'persisting'; sites without any plants in 2 successive years are called 'empty'; we then distinguish between populations that became extinct or were colonized. Observations were made in November of each year

Year	Persisting	Empty	Extinct	Invaded
81–82	88	0	3	0
82–83	85	1	3	2
83–84	85	2	2	2
84–85	85	2	2	2
85–86	82	1	5	3
86–87	78	4	7	2
87–88	62	9	18	2
88–89	60	18	4	9
89–90	63	19	6	3

Local extinction of plants in three sand-dune biennials

Extinction in three 'fugitive' biennials was studied in detail. De Jong & Klinkhamer (1988a) compared 96 sites in sand dunes where *Cirsium vulgare* became extinct (41%) or survived (59%) over a 3-year period. They found that three factors discriminated between the two groups: the initial density of flowering plants (=seed production), the water content of the top 10 cm of soil and the percentage seed predation. Density of flowering plants and water content were significantly higher and seed predation was significantly lower in surviving populations. Accumulation of litter or increase in perennial vegetation was apparently unimportant and seems to have no effect on a short time-scale. Out of 95 sites with *Cynoglossum officinale* (De Jong & Klinkhamer 1988) only seven populations became extinct in 3 years. This number increased considerably in later years (Table 2). They were all relatively exposed with a high cover percentage of bare sand and grasses, compared to the sites where the population survived. Van Lint (1982) did a similar analysis on sand-dune sites with *Senecio jacobaea* that had been monitored since 1973. He selected 29 sites in a reduction phase and five flourishing sites. The flourishing populations were found on sites with a significantly larger seedbank, a higher total-nitrogen concentration and a higher component of grasses and trees (indicating a more humid habitat).

POPULATION DYNAMICS OF BIENNIALS IN META-POPULATIONS

Two biennial species, *Senecio jacobaea* and *Cynoglossum officinale* have been studied in enough detail to make a comparison of the dynamics in separate local populations. Both species were monitored in 4 m^2 samples in *c.* 100 local populations in an area of about 4 km^2 in Dutch sand dunes (Van der Meijden 1979, 1989; Van der Meijden & Van der Waals-Kooi 1979; Van der Meijden *et al.* 1985; De Jong & Klinkhamer 1986, 1988a). Meta-population fluctuations of both species are illustrated in Figures 1 and 2. In both species local extinction and recolonization of sites was observed (Tables 2 and 3). Van der Meijden *et al.* (1985) demonstrated that some sites where *Senecio jacobaea* disappeared
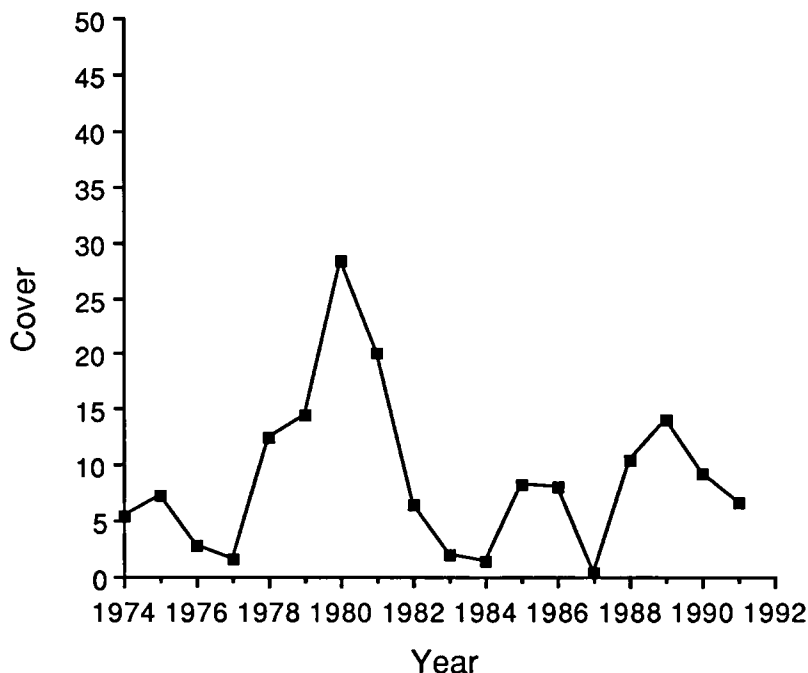
Fig. 1. Meta-population dynamics of 102 populations of *Senecio jacobaeae*. Cover in June is expressed as the mean number of dm² of *Senecio* per 4 m² sample.

were recolonized by dispersing seeds and others by germination from a (small) seedbank. Both processes were equally important with respect to the number of recolonized sites.

Extinction of local population does not necessarily imply large qualitative differences in dynamics between populations. Extinction might be caused by differences in amplitude of otherwise synchronous fluctuations.

Senecio jacobaea

In sand-dune populations in the Netherlands *S. jacobaea* fluctuates widely in biomass. Local populations may become extinct, but many sites are repopulated in later years (Table 3). Some populations survive for long periods, at least some decades! Apparently survival chance is different at different sites, some sites may act as refuges from which other sites may be repopulated through seed dispersal (Van der Meijden *et al.* 1985; Van der Meijden 1989).

Population change. To analyse differences between fluctuations in biomass in local populations, a cluster analysis (Biopat) (Hogeweg & Hesper 1972) was applied on the set of data. This analysis distinguishes groups of populations that show within-group fluctuations that are more or less similar by correlating population time series with each other. We used Spearman's Rank correlation because the data are not normally distributed. Five groups of populations were distinguished. These showed significant differences (Kruskal-Wallis test of the subsequent forks) in biomass in at least 8 of 18 years (Fig. 3). Data on biomass were collected at the end of May or the beginning of June each year (see Van der Meijden 1979). Total defoliation by *Tyria jacobaeae* in July and low
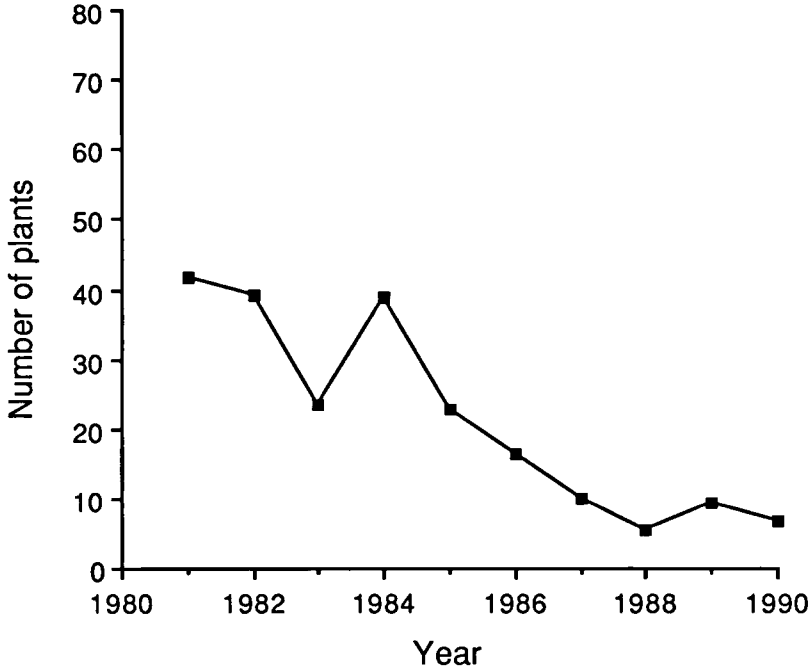
Fig. 2. Meta-population dynamics of 92 populations of *Cynoglossum officinale*. The mean number of plants in November per 4 m² is indicated.

precipitation in the summer period June, July and August are the most important factors limiting population size (Van der Meijden *et al.* 1985).

Type 1. Populations with a permanent reduction in biomass.
This type was represented by 17 populations, 16 of which were situated in woodland habitat where the cover of trees, shrubs and grasses increased from the beginning of the observations (1973) to 1991 from 71 to 100%. Light reduction as well as reduction of the number of immigrating seeds may have been responsible for the disappearance of *Senecio* from this habitat.

Type 2. Populations that permanently survived during the observation period.
This second type of fluctuation was found in only 10 populations. They were all situated in a relatively productive habitat with occasional trees, grasses and ground-covering mosses. The majority of these populations (eight) never became extinct.

Types 3, 4 and 5. Populations that became extinct temporarily but were recolonized.
By far the majority of these populations were found in low-productive open habitat, with large patches of bare sand and a vegetation of mosses/lichens, patches of grass and occasional shrubs or trees. It was in this habitat type that *S. jacobaea* plants were subject to the highest levels of defoliation by *Tyria jacobaeae* and to the highest levels of mortality by drought. In some years, peak biomass was reached in these populations (Fig. 3), although they were clearly not situated in the habitat in which *Senecio* is most persistent. There was a clear asynchrony in population fluctuations between these types.

Figure 4 illustrates the differences in habitat (in 1983) in which these types of fluctuations are observed (a more extensive study on the dynamics of these types will

Table 3. Fate of 102 populations of *Senecio jacobaea* selected in 1973. Populations that were present in 2 successive years are called 'persisting'; sites without any plants in 2 successive years are called 'empty'; we then distinguish between populations that became extinct or were colonized or were not monitored. Observations were made in June of each year

Year	Persisting	Empty	Extinct	Invaded	Missing
74–75	77	0	0	22	3
75–76	63	0	38	0	1
76–77	57	20	7	18	0
77–78	70	18	5	9	0
78–79	75	2	2	20	3
79–80	89	0	1	3	9
80–81	90	1	4	0	7
81–82	60	6	35	0	1
82–83	41	30	19	10	2
83–84	43	31	8	17	3
84–85	56	22	3	17	4
85–86	60	10	12	15	5
86–87	55	15	21	7	4
87–88	61	18	1	18	4
88–89	79	10	0	9	4
89–90	87	7	1	2	5
90–91	85	7	4	1	5

be published elsewhere). The combined percentage cover of trees, shrubs and grasses gradually diminishes from type 1 to type 5, indicating a decrease in productivity. The combined percentage cover of bare sand and mosses/lichens increases from type 1 to 5, indicating more exposed, drought-sensitive sites.

Life-time and extinction of local populations. Extinction risks of local populations of *S. jacobaea* differ greatly. Eighteen out of 102 populations survived between 1973 and 1991, 24 became extinct once, 32 twice, 19 three times and nine even more often. Populations in completely open habitat were more vulnerable than those in partly shaded areas with occasional trees and shrubs (indicated by occasional low percentages cover in Figs 3c, d and e). The total meta-population of *S. jacobaea* is reduced after dry years and defoliation by *Tyria jacobaeae* (Van der Meijden *et al.* 1985, 1991). Partly shaded areas form temporary refuges during meta-population reduction (Van der Meijden *et al.* 1985: Fig. 3).

Cynoglossum officinale

C. officinale has a much more restricted distribution than *S. jacobaea*. It may be locally common in sand dunes and other chalk-containing substrates in Europe. Recently it has become a local pest plant in Canada (Harris 1991). Few population studies have been made (De Jong & Klinkhamer 1988a). Unlike *S. jacobaea*, *C. officinale* has no important herbivores. Populations in sand dunes have a much lower extinction rate than *S. jacobaea* (Table 2). A spatial key-factor analysis by De Jong & Klinkhamer (1988a) on the dynamics of 100 populations indicated that germination and seedling survival are the differentiating processes for success or failure between local populations. Germination
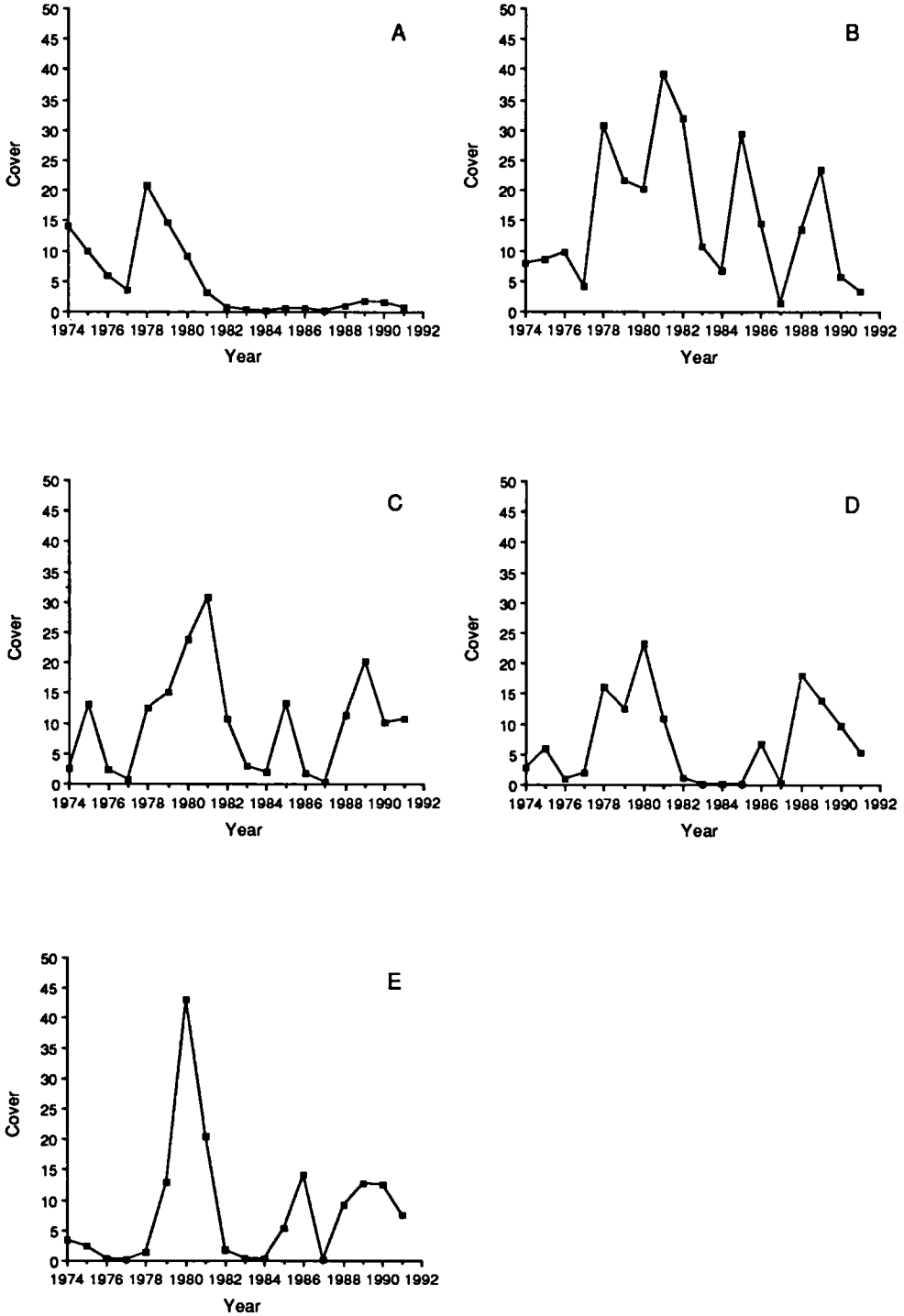
Fig. 3. Five types of local population dynamics of *Senecio jacobaea*. Cover is expressed as the mean number of dm² of *Senecio* per 4 m² sample.

Bare sand, mosses, lichen   Trees, shrubs, grasses
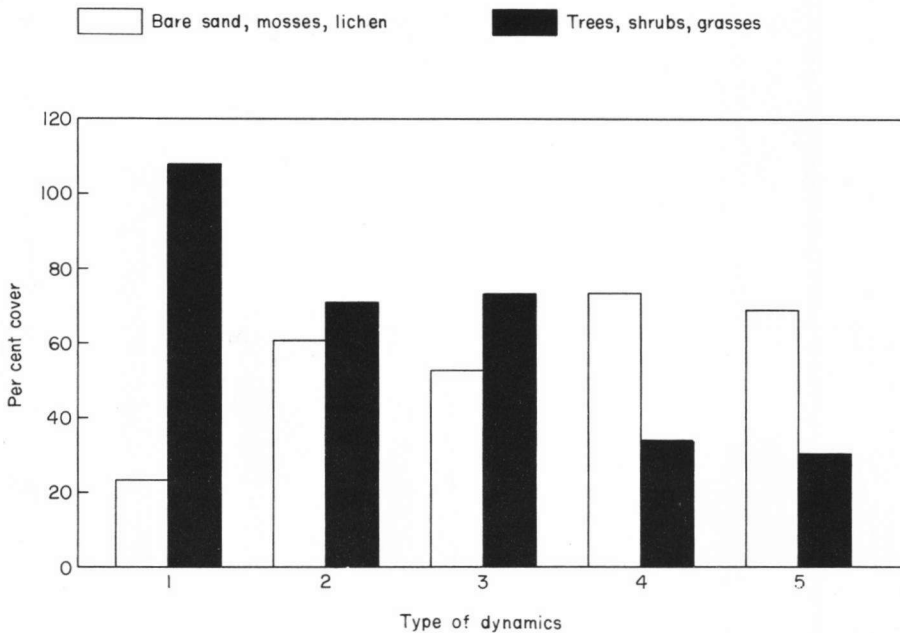

Fig. 4. Habitat characteristics of populations of *Senecio jacobaea* with different types of dynamics.

and survival were stimulated by environmental factors that reduced the effect of desiccation. As in *S. jacobaea* sites may become recolonized after extinction of plants. Both species have a small persisting seedbank. *C. officinale* can disperse its seeds a few metres (Van der Meijden *et al.* 1985), although occasionally seeds may be transported over much larger distances.

Population change. Data on plant numbers were collected early in November of each year (see De Jong & Klinkhamer 1988a). In the first 3 years of the study, *C. officinale* decreased and became confined to shaded areas. After 1984 *C. officinale* decreased steadily in both habitats. There is no indication that some areas act as refuges. The cluster analysis mentioned above showed that six groups of populations could be distinguished (Fig. 5). The meta-population dynamics (Fig. 2) indicate a continuous decrease in plant numbers during the period of observation.

Type 1 and 2. Populations with an initial strong increase followed by a long lasting decrease.
These two types, representing 32 populations, initially increased until the fourth year. Then they declined almost continuously. Only three populations became extinct. These populations had a relatively high soil moisture content. The majority (25) were situated in habitats with thickets and shrubs (Fig. 6).
Type 3 and 4. Populations with a slow, but steady decline in numbers.
These types represented 48 populations of which the majority (32) were found in open sandy habitat. Low summer rainfall in the first 3 years of the study led to a sharp decrease in plant numbers. Recovery in 1984 after a very wet season (De Jong *et al.* 1986) was followed by a continuous decline. About half of these populations (20)
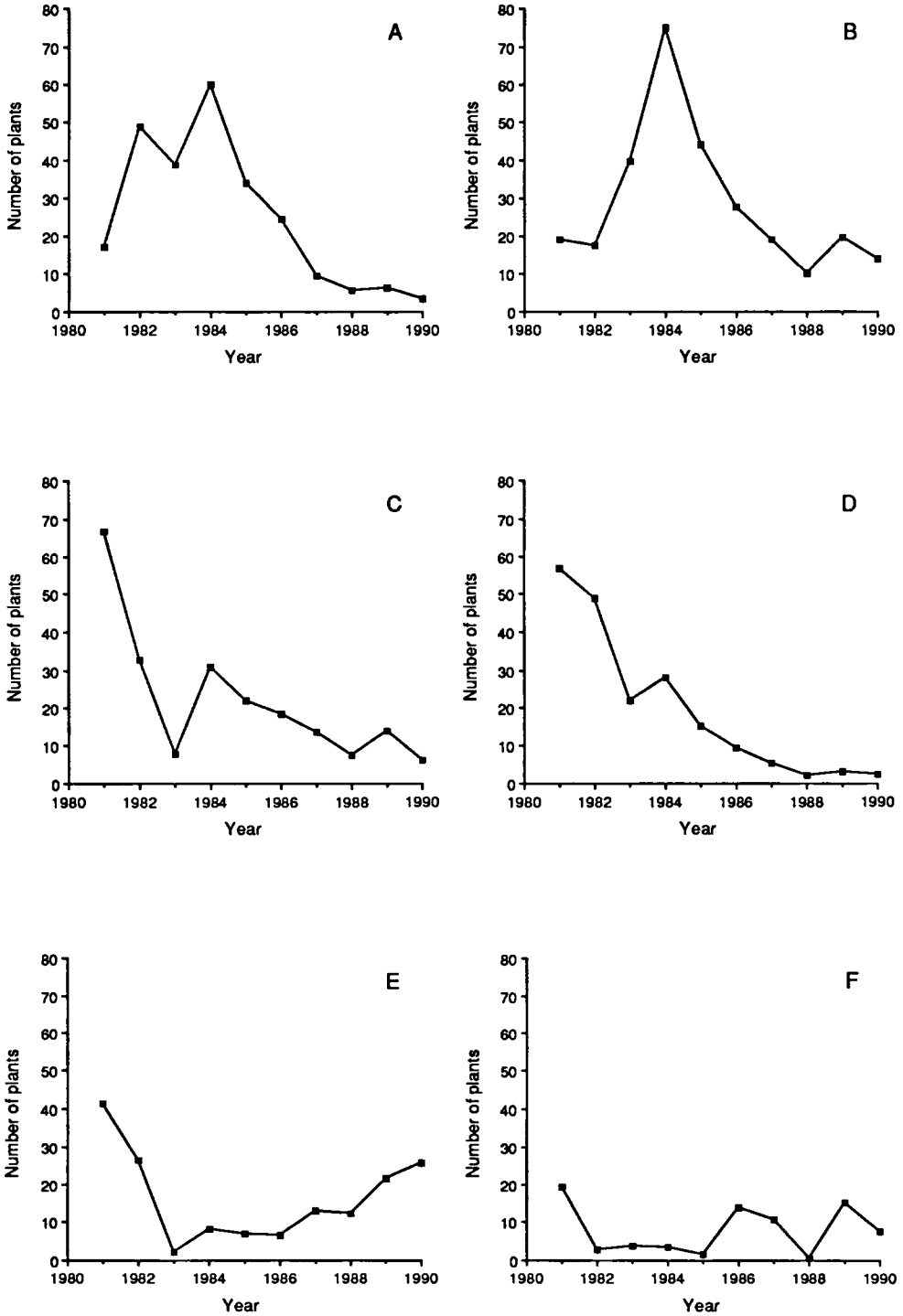
Fig. 5. Six types of local population dynamics of *Cynoglossum officinale*. The mean number of plants per 4 m^2 sample is indicated.
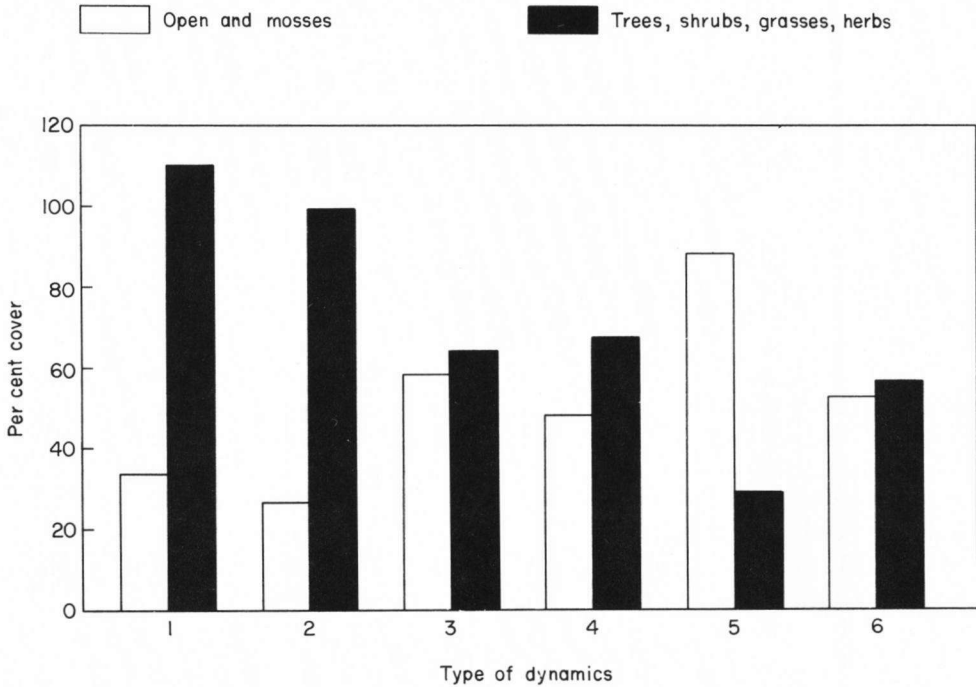
Fig. 6. Habitat characteristics of populations of *Cynoglossum officinale* with different types of dynamics.

became extinct, probably due to an increase in vegetation density and stabilization of the top layer of the sand which inhibited germination and establishment.

Type 5 and 6. Populations that decreased initially, but increased afterwards.

These groups combined 11 populations that showed an increase in plant numbers after an initial decrease. They were all situated in open habitat, partly covered with mosses, with a low percentage cover of higher plants. Two populations became extinct.

The asynchrony in the dynamics of *C. officinale* in different populations in the same dune habitat is one of the most obvious results of this study.

DISCUSSION

Most population studies on biennial plants have been limited to single or a few local populations over a small number of years. That approach limits the value of understanding the distribution and abundance of these species. They do not provide information on mechanisms that lead to establishment of new populations elsewhere and consequently on survival in larger areas (meta-populations). This is probably true for perennial species as well, but their populations usually survive much longer and we are only rarely confronted with local extinction within the time-scale of our observations. It is disappointing that despite Harper's message of 15 years ago, few people in this field have realized that to understand the dynamics of biennials one should focus on dynamics of patches and meta-populations instead of counting cohorts of plants on single sites.

The persistence of biennials on the meta-population level, combined with the observations on extinction of local populations, implies that there must be some balance

between rise and fall of sites that are suitable for population development. As chance processes would ultimately lead to a situation without any such site, there must be some form of regulation in the genesis of suitable sites. Moreover, the mechanisms of dispersal and/or dormancy should be adapted to the frequency in time of development of new sites and the distance between sites. Two separate processes have to be distinguished sharply: (a) patch or habitat dynamics that lead to the genesis of new sites suitable for population development and the loss of 'old' sites and (b) meta-population dynamics (the interaction between patch dynamics, dispersal and population dynamics within patches).

Patch dynamics

Transient biennials. The growing sites of these plants are windfalls and clear cuts in woodland; 'old fields' and other relatively large-scale disturbances of productive habitats. Natural forests (Northern conifer forests affected by fire and temperate and tropical forests affected primarily by the death of scattered individuals) are characterized by a fairly constant disturbance rate of *c.* 1% (ranging from 0·5 to 2% per year in large samples, Runkle 1985). So one can expect the number of gaps to be rather stable in time. Also the time-lapse between the successive genesis of gaps at a certain site is probably rather constant and should be approximately 50–200 years in this kind of forests. It is important to realize that immediately neighbouring gaps will arise at much shorter time intervals! If a tree is surrounded by six other trees, neighbouring gaps are expected with time intervals of only 17 years. Gaps will be separated by hundreds to thousands of metres.

This argument can probably be extended to man-made disturbances like the traditional fallow-cycle of agricultural land use, although they will have a much higher turnover rate and will be found at shorter distance from each other.

Present-day global-wide activities of man will increase rather than decrease the production of sites that are suitable for population development of this category.

Fugitive biennials. Many of these species are found in sand dune habitats and similar half-open habitats. Dunes are subject to herbivore grazing by rabbits or cattle. Excluding herbivores from these areas eventually leads to closing of the vegetation and loss of gaps (as was found during the myxomatosis epidemic among rabbits in western Europe in the early 1950s (Thomas 1960). North-facing slopes and moist slacks are usually too productive for herbivores to create long-lived gaps in the vegetation (Burggraaf-Van Nierop & Van der Meijden 1984) providing a mosaic of small-scale open, half-open and closed communities. Mammalian herbivores are usually food limited (Crawley 1983). We expect a feedback effect of the intensity of grazing of the vegetation (by wild herbivores as well as domestic cattle) on the amount of biomass, leading to the constant presence of a changing mosaic of abundant suitable sites for population development, i.e. collections of safe sites (from several to hundreds of metres from each other).

Persistent biennials. These species apparently have rather long-lived populations provided there is a reasonably constant management or grazing regime of the habitat (Grubb 1986). The habitat is much more homogeneous than that of the other groups. In that respect as well as in the fairly constant management regime they are different from the other groups of biennials. A feedback of the intensity of grazing by large herbivores (rodents or cattle, either naturally occurring or managed) on the amount of biomass (either by management or naturally) will result in a fairly constant number of safe sites, i.e. gaps, at close distance (decimetres to make metres) of each other in time.

Meta-population dynamics

Transient biennials. We have illustrated that these species have extremely short-lived populations and are mainly safe-site limited. They have a large and long-lasting seedbank. The high production of small seeds, that facilitate the build up of a seedbank, can be seen as an adaptation to regenerate in an environment that is only favourable during a short period, but has a high probability of becoming favourable again in the future after a new disturbance. The absence of a special long-distance dispersal mechanism can be explained easily. On the one hand disturbances at a particular moment are separated by large distances. It will be almost impossible to disperse seeds over such large distances, especially in woodland communities. The high probability, on the other hand, that closely neighbouring favourable sites will develop within a relatively short time-interval (see 'Patch dynamics') will select for a combination of short-distance dispersal (Gross & Werner 1982, mention passive dispersal in *V. thapsus* to 11 m) and seed dormancy.

Fugitive biennials. The systems where fugitive biennials are found consist of small, more or less isolated patches with safe sites. In dunes (and probably in other systems as well) grazing of the vegetation determines patch distribution and the number of safe sites and thus the upper population density limit. Due to the feedback effect of grazing on vegetation density (see 'Patch dynamics') systems may be long lived.

The number of safe sites filled and consequently local population dynamics and survival or extinction of populations in local patches, is dependent on seed production, seed survival and successful establishment.

Patches are not safe in all respects, especially in dry summers when complete cohorts of seedlings die. Drought is a major cause of mortality. The effect of drought increases with the lack of shelter against insulation, leading to survival differences in gaps of different sizes (Van Leeuwen 1987). This, together with additional mortality causes, e.g. herbivory and seed predation, results in frequent extinction of populations. Many of these sites are recolonized in later years, indicating that they have not become permanently unsuitable. Seed addition experiments (Klinkhamer & De Jong 1988b) in patches where *Cirsium vulgare* had become extinct produced normal densities of plants, indicating the importance of seed limitation.

Plants from the group of 'fugitive' biennials require a build up period after disturbance or extinction by seed immigration or germination from the few seeds in the seedbank.

Different species exhibit different types of meta-population dynamics (see Harrison 1991). Examples on *S. jacobaea* and *C. officinale* were given above. Both species show an asynchronous component in local population dynamics. *S. jacobaea* has refuge populations that may survive for a rather long period, together with populations that become extinct within short periods of time, representing the source–sink type. *C. officinale* meta-population dynamics are characterized by asynchrony without refuge populations, representing rather the 'classical' meta-population type of Levins (1969). In both species some population sites seem to have become permanently unsuitable.

These biennials usually have some hundreds or thousands of seeds, with special dispersion mechanism like pappus and a small seedbank. This seems to be a profitable set of characteristics in an environment with suitable sites at relatively short distance and a high probability that the original growing site remains favourable. The presence of a bank of rosettes (plants that delay flowering) which are less vulnerable to desiccation or to herbivory than seedlings, provides an additional mechanism which limits extinction frequency.

Occasional explosive population development which is normal in the transients can be found less frequently in the fugitive biennials with fewer but larger seeds. After the second world war when large zones of mines were removed from the Dutch dunes, *Echium vulgare* became so abundant that it coloured the dunes temporarily blue (G. J. de Bruijn and N. Croin Michielsen, pers comm.). Large-scale digging in the dunes for the construction of waterworks in the recent past led to dense flowering populations of *Senecio jacobaea* of several hectares which crashed immediately afterwards. Overgrazing of rangelands in Canada and the USA and of pastures on the northern islands of The Netherlands produces similar effects. As extinction of plants in this group is most often found after dry seasons in open habitat, we expect such explosions to be restricted to years with extremely favourable weather conditions.

Persistent biennials. Persistent biennials do not demonstrate meta-population dynamics in the time- and space-scale discussed here. In a sense the 'changing clouds' of abundance of these species represent meta-population dynamics. The only buffer mechanisms reported that may prevent local extinction of chalk grassland biennials when the number of safe sites remains constant, are seed dormancy and seed dispersal over extremely small distances. Large local fluctuations in the number of safe sites due to the lack of a feed-back effect of herbivore grazing with respect to vegetation growth are expected to increase extinction risks of these biennials.

What makes biennials suited for exploiting temporary habitats?

There has been much discussion about the adaptive value of the biennial life history, starting with Hart's (1977) paper 'Why are biennials so few?' that tried to explain the small number of biennial species (Van der Meijden & Van der Waals-Kooi 1979; Silvertown 1983, 1984, 1986; Thompson 1984; Kelly 1985, 1989a; De Jong *et al.* 1987; Kachi 1990b). Although the number of biennial plant species in floras is indeed considerably lower than that of annual and perennial species (usually less than 10%; Hart 1977; Silvertown 1983; Schat & Haeck 1984), biennials can be very abundant. Several biennials are known as common weeds or even as pests in agriculture (Harper & Wood 1957; Harris *et al.* 1978; Kok 1978; Harris 1991).

Often different species of biennials are found to grow together at the same sites (e.g. *Senecio jacobaea, Echium vulgare, Cirsium vulgare* and *Verbascum thapsus* in sand dunes) indicating that biennial behaviour is an adaptation to a special set of circumstances. These must be related to disturbances of the environment. Explosive population development follows large-scale natural or man-made disturbances in several communities.

Although it was realized in several of the studies mentioned earlier that the life-time of local populations may be short and that biennial behaviour should be seen in the context of meta-populations, we still do not have a satisfactory explanation for their success.

Three factors have not been incorporated in most models comparing fitness of annuals, biennials and perennials: longevity of the habitat, temporal and spatial heterogeneity of the habitat and the ability to disperse seeds out of local populations. In the habitats of transients only one or two generations are able to establish. In the paragraph on patch dynamics we reasoned that new suitable patches for transients will arise immediately beside windfalls within a relatively short period (*c.* 17 years). The mean time for the original patch to become suited again is *c.* 100 years. We therefore assume dispersal in transients to be extremely important. Let us assume that although a patch remains suitable for only a few years, on a larger scale the density of suitable patches remains more

or less constant. We may then equate fitness with the total number of seeds dispersed outside a patch during the life-time of that patch. This total number depends on the seed production in the patch and on the dispersal fraction. If a patch is only shortly suitable, for say 2 years, it can easily be shown that the optimal dispersion fraction for the annual is 0.5 and for the biennial and the perennial (that does not reproduce the first year) 1.0. These dispersal fractions are much higher than the actual dispersal fractions realized by short-lived herbs. Comparing the three life-histories, biennials have the important advantage of producing tall flowering stems that enable them to produce and disperse seeds in a closing vegetation. Furthermore it should be noted that as long as the relative growth rate of a plant is independent of its size, the total biomass increase of the progeny of a reproducing plant is always smaller than the increase in biomass of a non-reproducing plant. As long as plants are growing with a constant relative growth rate there is no penalty for having fewer generations (i.e. in being biennial compared to annual).

The habitats of fugitive species are characterized by intermediate longevity and large fluctuations in, e.g. seed predation and water availability. These fluctuations affect germination and establishment more than survival of established plants. In such habitats, the biennial life-history may form a compromise between exploiting suitable patches as long as possible (by reducing the extinction rate through a rosette bank) and a relatively high dispersal rate that better enables them to reach new suitable sites than either annuals or short-lived perennials. If the longevity of the habitat increases, longer-lived perennials take over.

The habitats of chalk grassland species are characterized by a more or less constant density of small-scale disturbances that form safe sites. A comparison of life-history strategies in such habitats has been modelled by Klinkhamer & De Jong (1989) and by De Jong *et al.* (1987) who showed that fitness is maximized by maximizing expected life-time seed production. Biennials must then produce at least four times the number of seeds of perennials and twice the number of seeds of annuals (if C_2 [survival of established plants] $= 0.5$; this is identical to Hart's 1977 conclusion except that it only depends on C_2 and not on C_1 [survival of seeds and seedlings]). Comparisons of seed productions show that these are well within the range of this condition.

It is clear that without disturbances biennials are losers compared to perennials. It is only during the first years following disturbance that biennials are successful. As perennials normally do not reproduce in their first year, the rate of increase for the first 2 years is similar to that of perennials ($\lambda = C_1 C_2 S$) in which S is seed production. During that short period we see two important differences with perennials: biennials start from a larger seedbank and have a higher reproductive allocation (Harper 1977), enabling them to build up a new seedbank or to reach new sites at a faster rate than perennials.

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REFERENCES

Baskin, J.M. & Baskin C.M. (1979): Studies on the autecology and population biology of the weedy monocarpic perennial, *Pastinaca sativa. J. Ecol.* **67**: 601–610.

Burggraaf-Van Nierop, Y.M. & Van der Meijden, E. (1984): The influence of rabbit scrapes on dune vegetation. *Biol. Cons.* **30**: 133–146.

Crawley, M.J. (1983): *Herbivory*. Blackwell Scientific Publications, Oxford.

De Heiden, J.H. (1991): Onderzoek naar *Carlina vulgaris* (Driedistel) in het duingebied van Meijendel. *Meijendel Mededelingen* **21**: 43–55.

De Jong, T.J. & Klinkhamer, P.G.L. (1986): *Population ecology of the biennials* Cirsium vulgare *and* Cynoglossum officinale: *An experimental and theoretical approach*. Thesis University of Leiden.

De Jong, T.J. & Klinkhamer, P.G.L. (1988a): Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a coastal sand dune area. *J. Ecol.* **76**: 366–382.

De Jong, T.J. & Klinkhamer, P.G.L. (1988b): Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand dune area: the importance of water for differential survival and growth. *J. Ecol.* **76**: 393–402.

De Jong, T.J., Klinkhamer, P.G.L., Geritz, S.A.H. & Van der Meijden, E. (1989): Why biennials delay flowering: an optimization model and field data on *Cirsium vulgare* and *Cynoglossum officinale*. *Acta Bot. Neerl.* **38**: 41–55.

De Jong, T.J., Klinkhamer, P.G.L. & Metz, J.A.J. (1987): Selection for biennial life histories in plants. *Vegetatio* **70**: 149–156.

De Jong, T.J., Klinkhamer, P.G.L. & Prins, A.H. (1986): Flowering behaviour of the monocarpic perennial *Cynoglossum officinale* L. *New Phytol.* **103**: 219–229.

During, H.J., Schenkeveld, A.J., Verhaar, H.J. & Willems, J.H. (1985): Demography of short lived forbs in chalk grassland in relation to vegetation structure. In: White, J. (ed.): *The Population Structure of Vegetation*. 341–369. Junk, Dordrecht.

Greig-Smith, J.T. & Sagar, R.G. (1981): Biological causes of rarity in *Carlina vulgaris*. In: Synge, H. (ed.): *The Biological Aspects of Rare Plant Conservation*. 389–400. Wiley & Sons, New York.

Gross, K.L. (1980): Colonization by *Verbascum thapsus* (Mullein) of an old-field in Michigan: experiments on the effects of vegetation. *J. Ecol.* **68**: 919–928.

Gross, K.L. (1981): Predictions of fate from rosette size in four 'biennial' plant species: *Verbascum thapsus, Oenothera biennis, Daucus carota*, and *Tragopogon dubius*. *Oecologia* (Berl.) **48**: 209–213.

Gross, K.L. & Werner, P.A. (1978): The biology of Canadian weeds. 28. *Verbascum thapsus* L. and *V. blattaria* L. *Can. J. Plant Sc.* **58**: 401–413.

Gross, K.L. & Werner, P.A. (1982): Colonizing abilities of 'biennial' plants species in relation to ground cover: implications for their distrubtion in a successional sere. *Ecology* **63**: 921–931.

Grubb, P.J. (1977): The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* **52**: 107–145.

Grubb, P.J. (1986): Problems posed by sparse and patchily distributed species in species-rich plant communities. In: Diamond, J. and Case, T.J. (eds): *Community Ecology*. 207–226, Harper & Row, New York.

Harper, J.L. (1977): *Population Biology of Plants*. Academic Press, London.

Harper, J.L. & Wood, W.A. (1957): Biological Flora of the British Isles: *Senecio jacobaea* L. *J. Ecol.* **45**: 617–637.

Harris, P. (1991): Classical biocontrol of weeds: its definition, selection of effective agents, and administrative–political problems. *Can. Ent.* **123**: 827–849.

Harris, P., Thompson, L.S., Wilkinson, A.T.S. & Neary, M.E. (1978): Reproductive biology of tansy ragwort. Climate and biological control by the cinnabar moth in Canada. In: Freeman, T.E. (ed.) *Proc. 4th Int. Symp. on Biological Control of Weeds*. 163–173. University of Florida, Gainesville.

Harrison, S. (1991): Local extinction in a meta-population context: an empirical evaluation. *Biological Journal of the Linnean Society* **42**: 73–88.

Hart, R. (1977): Why are biennials so few? *Am. Nat.* **111**: 792–799.

Hogeweg, P. & Hesper, B. (1972): Biopat, program system for biological pattern analysis. *Internal report Theor. Biol. Group*, University of Utrecht.

Holt, B.R. (1972): Effect of arrival time on recruitment, mortality and reproduction in successional plant populations. *Ecology* **53**: 668–673.

Kachi, N. (1990a): Optimal time of seedling emergence in a dune-population of *Oenothera glazioviana*. *Ecol. Res.* **5**: 143–152.

Kachi, N. (1990b): Evolution of size-dependent reproduction in biennial plants: a demographic approach. In: *Biological approaches and evolutionary trends in plants*. 367–385. Academic Press Ltd, London.

Kachi, N. & Hirose, T. (1983): Bolting induction in *Oenothera erythrosepala* Barbas in relation to rosette size, vernalization, and photoperiod. *Oecologia* (Berl.) **60**: 6–9.

Kelly, D. (1985): On strict and facultative biennials. *Oecologia* (Berl.) **67**: 292–294.

Kelly, D. (1989a): Demography of short-lived plants in chalk grassland. II. Control of mortality and fecundity. *J. Ecol.* **77**: 770–784.

Kelly, D. (1989b): Demography of short-lived plants in chalk grassland. III. Population stability. *J. Ecol.* **77**: 785–798.

Kivilaan, A. & Bandurski, R.S. (1973): The ninety-year period for Dr Beal's seed viability experiment. *Am. J. Bot.* **60**: 140–145.

Klemow, K.M. & Raynal, D.J. (1985): Demography of two facultative biennial plant species in an unproductive habitat. *J. Ecol.* **73**: 147–167.

Klinkhamer, P.G.L. & De Jong, T.J. (1987): Plant size and seed production in the monocarpic perennial *Cynoglossum officinale* L. *New Phytol.* **106**: 773–783.

Klinkhamer, P.G.L. & De Jong, T.J. (1988): The importance of small-scale disturbance for seedling establishment in *Cirsium vulgare* and *Cynoglossum officinale. J. Ecol.* **76**: 383–392.

Klinkhamer, P.G.L. & De Jong, T.J. (1989): A deterministic model to study the importance of density-dependence for regulation and the outcome of intra-specific competition in populations of sparse plants. *Acta Bot. Neerl.* **38**: 57–65.

Klinkhamer, P.G.L., De Jong, T.J. & Meelis, E. (1987a): Delay of flowering in the 'biennial' *Cirsium vulgare*: size effects and devernalization. *Oikos* **49**: 309–314.

Klinkhamer, P.G.L., De Jong, T.J., Metz, J.A.J. & Val, J. (1977b): Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theoretical population biology,* **32**: 127–156.

Klinkhamer, P.G.L., De Jong, P.G. & Meelis, E. (1987c): Life-history variation and the control of flowering in short-lived monocarps. *Oikos* **49**: 309–314.

Kok, L.T. (1978): Biological control of *Carduus* thistles in northeastern U.S.A.. In: Freeman, T.E. (ed.): *Proc. 4th Int. Symp. on Biological Control of Weeds.* 101–104. University of Florida, Gainesville.

Levins, R.A. (1969): Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Ent. Soc. America,* **15**: 237–240.

Pons, T.L. (1976): An ecophysiological study in the field layer of ash coppice. I. Field measurements. *Acta. Bot. Neerl.* **25**: 401–416.

Pons, T.L. (1984): Possible significance of changes in the light requirement of *Cirsium palustre* seeds after dispersal in ash coppice. *Plant, Cell and Environment* **7**: 263–268.

Prins, A.H. & Nell, H.W. (1990): The impact of herbivory on plant numbers the life stages of *Cynoglossum officinale* L. and *Senecio jacobaea* L. *Acta Bot. Neerl.,* **39**: 275–284.

Reinartz, J.A. (1984): Life history variation of common mullein (*Verbascum thapsus*). I. Latitudinal differences in population dynamics and timing of reproduction. *J. Ecol.* **72**: 897–912.

Runkle, J.R. (1985): Disturbance regimes in temperate forests. In: Pickett, S.T.A. and White, P.S. (eds): *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, London.

Salisbury, E.J. (1942): *The Reproductive Capacity of Plants.* Bell, London.

Schat, H. (1982): *On the Ecology of some Dutch Dune Slack Plants.* Thesis Free University of Amsterdam.

Schat, H. & Haeck, J. (1984): Hapaxanten in flora en vegetatie. *Vakblad voor biologen* **5**: 85–88.

Schenkeveld, A.J.M. Verkaar, H.J.P.A. (1984): *On the Ecology of Short-Lived Forbs in Chalk Grasslands.* Thesis University of Utrecht.

Silvertown, J. (1983): Why are biennials sometimes not so few? *Am. Nat.* **121**: 448–453.

Silvertown, J. (1984): Death of the elusive biennial. *Nature* **310**: 271.

Silvertown, J. (1986): Biennials: a reply to Kelly. *Am. Nat.* **127**: 721–724.

Thomas, A.S. (1960): Changes in the vegetation since the advent of myxomatosis. *J. Ecol.* **48**: 287–306.

Thompson, J.N. (1978): Within-patch structure and dynamics in *Pastinaca sativa* and resource availability to a specialized herbivore. *Ecology* **59**: 443–448.

Thompson, K. (1984): Why biennials are not so few as they ought to be. *Am. Nat.* **123**: 854–861.

Van Baalen, J. (1982): *Population Biology of Plants in Wood-Land Clearings.* Thesis Free University of Amsterdam.

Van Breemen, A.M.M. (1984): Comparative germination ecology of three short-lived monocarpic Boraginaceae. *Acta Bot. Neerl.* **33**: 283–305.

Van der Meijden, E. (1979): Herbivore exploitation of a fugitive plant species: local survival and extinction of the cinnabar moth and ragwort in a heterogeneous environment. *Oecologia* (Berl.) **42**: 307–323.

Van der Meijden, E. (1989): Mechanisms in plant population control. In: Grubb, P.J. and Whittaker, J.W. (eds): *Toward a more exact Ecology.* 382–393. Blackwell Scientific Publications Ltd, Oxford.

Van der Meijden, E., De Jong, T.J., Klinkhamer, P.G.L. & Kooi, R.E. (1985): Temporal and spatial dynamics in populations of biennial plants. In: Haeck, J. and Woldendorp, J.W. (eds): *Structure and Functioning of Plant Populations 2.* 91–103. North Holland, The Netherlands.

Van der Meijden, E. & Van der Waals-Kooi, R.E. (1979): Population ecology of *Senecio jacobaea* in a sand dune system. I. Reproductive strategy and the biennial habit. *J. Ecol.* **67**: 131–153.

Van der Meijden, E., Van Wijk, C.A.M. & Kooi, R.E. (1991): Population dynamics of the cinnabar moth (*Tyria jacobaeae*): oscillations due to food limitation and local extinction risks. *Neth. J. Zool.* **41**: 158–173.

Van Leeuwen, B.H. (1987): *An explorative and comparative study on the population biology of the thistles* Cirsium arvense, Cirsium palustre *and* Cirsium vulgare *in a coastal sand-dune area.* Thesis University of Leiden.

Van Lint, R. (1982): *Onderzoek naar de oorzaken van het optreden van de reduktiefase in de dichtheid van lokale populaties van* Senecio jacobaea L. MSc Thesis, University of Leiden.

Van Sante, B.M. & Volker, A.P. (1978): *Vergelijkende populatie-oecologie van* Inula conyza DC. *in vier verschillende populaties in de Wassenaarse duinen.* MSc Thesis, University of Leiden.

Verkaar, H.J., Schenkeveld, A.J. & Brand, J.M. (1983): On the ecology of short-lived forbs in chalk grasslands: micro-site tolerances in relation to vegetation structure. *Vegetatio* **52:** 91–102.

Werner, P. (1975): Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia* (Berl.) **20:** 343–359.

Zedler, P.H., Guehlstorff, K., Scheidlinger, C. & Gautier, C.R. (1983): The population ecology of a dune thistle, *Cirsium rhothophilum* (Asteraceae). *Amer. J. Bot.* **70:** 1516–1527.