

# The advantage of long-distance clonal spreading in highly disturbed habitats

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## Summary

Classical theory states that cover of annual plants should increase relative to perennials as disturbance frequency increases. However, it has been suggested that long-distance clonal spreading can allow some perennial plants to survive in highly disturbed areas by quickly spreading into disturbed patches. To evaluate these hypotheses, we analysed data of plant distributions in two different ecosystems, a barrier island and a short-grass steppe. The disturbances studied were sand deposition during storms (overwash) on the barrier island and grazing by cattle in the short-grass steppe. In each case the disturbance frequency varied over the ecosystem; we categorized different areas in terms of their disturbance frequencies. All plant species in each area were categorized as one of four plant life forms (1) annual or biennial, (2) herbaceous perennial without long-distance clonal spreading (3) herbaceous perennial with long-distance clonal spreading (i.e. guerilla form) and (4) woody plant. Percentage cover of each plant life form in each disturbance frequency category was calculated. In both ecosystems, (1) there was an increase in the relative cover of annuals as one moved from areas of low to moderate disturbance frequencies, but then a decrease in cover of annuals as one moved into the areas of highest disturbance frequency and (2) the guerilla forms showed the greatest relative increase in cover from moderately to highly disturbed areas. The combination of two factors can explain this pattern: (1) long-distance clonal spreading effectively reduces the time to colonization of recently disturbed sites and (2) effects of the disturbances in these two systems are probably more severe for seeds than for stems. We illustrate these effects using a spatially explicit simulation model of the population dynamics of plants in a disturbed landscape.

**Keywords:** disturbance; long-distance clonal spreading; life history; grazing; overwash; barrier island; short-grass steppe; spatial simulation model

## Introduction

Ecological disturbance is widely recognized as an important determinant of the occurrence and abundance of species (Grossman *et al.*, 1982; Sousa, 1984; Pickett and White, 1985; Smith, 1986). Life history attributes thought to allow species to persist despite frequent disturbances include early reproduction, short lifespan and high fecundity. A number of ecological theories rely on these ideas to varying degrees, including life history theory (Cole, 1954; Charnov and Schaffer, 1973; Iwasa and Cohen, 1989), *r-K* selection (MacArthur and Wilson, 1967), dynamic equilibrium (Horn and MacArthur, 1972; Huston, 1979), disturbance-mediated co-existence (Whittaker and Levin, 1977; Caswell, 1978), the disturbance/stress/competition triangular model of Grime (1979), the vital attributes model (Cattellino *et al.*, 1979) and the intermediate disturbance hypothesis (Connell, 1978). Evidence exists in support of relationships between disturbance and

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age at first reproduction, lifespan and fecundity (e.g. Platt, 1975; Grubb, 1976; McKee and Mackie, 1981; Resh *et al.*, 1988).

For plant populations, the suggestion is that species producing large numbers of seeds early in life will be best able to survive in highly disturbed areas. In the absence of disturbance, these species are often less competitive over the long term (e.g. Sohn and Policansky, 1977; Snow and Whigam, 1989). This leads to the prediction that annual plants should be associated with frequently disturbed areas and species with long lifespans and late reproduction (i.e. perennials, especially woody plants) should be found in undisturbed or rarely disturbed areas. Some field studies have confirmed this for individual species (Dyrness, 1973; Joenje, 1985; Watkinson and Davy, 1985; Collins, 1987; Halpern, 1988).

However, the ability of plants to produce stolons and rhizomes from which new stems are produced at some distance from other connected stems has also been suggested as a means of coping with high disturbance rates (Bertness and Ellison, 1987). Genetically, all such interconnected stems are part of the same individual. However, separate stems may experience quite different environments, including different disturbance regimes. Plants that produce new stems at long distances (e.g. greater than one plant height) from connected stems are termed 'guerilla' plants (Lovett Doust, 1981). We refer to production of such stems as 'long-distance clonal spreading'. It has been reported that perennial plants increase their rate of long-distance clonal spreading following a disturbance (Bazzaz, 1983; Halpern, 1988; Milchunas *et al.*, 1988; Gibson, 1989; Tappeiner *et al.*, 1991).

Long-distance clonal spreading can be an effective method for recolonization of disturbed areas principally because the plant can send 'offspring' into the recently disturbed patch without going through the seed stage. A new stem can be produced in the disturbed area in the same year as the disturbance occurred; if the plant were to rely on seed dispersal into the disturbed patch, the new stem would not be produced until the following year. Since there are very few annual plants that have long-distance clonal spreading, the potential advantage of long-distance spreading by perennials might counter the presumed advantages of the annual life form (high fecundity, short lifespan) in highly disturbed areas. However, the potential advantage of long-distance spreading would be countered by the fact that seed production of the guerilla plant would be reduced if the plant is putting energy into production of rhizomes and runners (Cook, 1985). Advantages of long-distance clonal spreading would need to outweigh advantages of short lifespan and high fecundity in order for the guerilla to be more successful than the annual in highly disturbed areas.

It is important to note that an event that operates as a disturbance to an individual or population by causing mortality or a reduction of biomass may not operate as a disturbance at the level of the community. For example, Milchunas *et al.* (1988, 1989) showed that grazing on the short-grass steppe is a disturbance at the individual level since it creates opportunities for establishment of new individuals or clonal shoots. However, community-level predictions from disturbance theory regarding species diversity are not upheld in this system if grazing is postulated as a disturbance at the community level. They suggest that this is because the short-grass steppe has a long evolutionary history of grazing with the result that grazing is the 'norm' for the community, while lack of grazing can be viewed as a disturbance (Milchunas *et al.*, 1990). The present study is a consideration of life history response to disturbance and does not address community-level disturbance hypotheses. We define a disturbance as any event that causes plant mortality or loss of biomass that creates an opportunity for seedling establishment or clonal spreading.

The goal of the present study was to examine the relationship between disturbance frequency and *relative* cover of plant life forms. The starting point of the study was the result of Fahrig *et al.*

(1993) on the distribution of plant life forms on a barrier island off the coast of Virginia, USA. They found that, contrary to expectation from life history theory, the relative number of annual species did not increase and the relative number of herbaceous perennials did not decrease, with increasing disturbance frequency. However, they did not divide the herbaceous perennial plants into those with and those without long-distance clonal spreading.

The present study is a combination of field data and general life history modelling. We examine two extensive data sets for the relative cover of plant life forms with increasing disturbance frequency. The data sets are a reanalysed version of the barrier island data set referred to above (Fahrig *et al.*, 1993) and a plant cover data set from a short-grass steppe in Colorado, USA. In both cases the plant life forms were categorized into four groups: (1) annuals or biennials (without long-distance clonal spreading), (2) perennial herbs without long-distance clonal spreading, (3) perennial herbs with long-distance clonal spreading (i.e. guerillas) and (4) woody plants. Both data sets indicated an increase in the relative cover of annuals as one moves from areas of low to moderate disturbance frequencies, but then a decrease in cover of annuals as one moves into the areas of highest disturbance frequency. In both cases the guerillas showed the greatest relative increase in cover from moderately to highly disturbed areas. Since this pattern is not anticipated by classical models of life history, we also explore a new model that focuses on the relative merits of plant life forms including long-distance clonal spreading, in highly disturbed areas.

## Data analyses

### *Plant life form distribution in relation to overwash disturbance on a barrier island*

The Virginia barrier islands are long thin islands running lengthwise along the Virginia coastline (east coast of the southern Delmarva Peninsula), several hundred metres to a few km from the coast. The surface material of the islands is sand. Geomorphically, the islands are extremely dynamic. Each year winter storms cause events of high wave activity on the seaward side of the islands (Dolan and Hayden, 1981), often resulting in overwash events in which waves wash over the low-lying islands, carrying with them sand from the beach face of the island, sometimes completely across the island. Extreme storms can change the shapes of islands, creating new inlets and new land areas. In terms of the plant ecology of the islands, an overwash disturbance can result in several cm (depth) of sand being deposited onto plants during a single storm. Effects of sand deposition include (1) burial of seeds to depths such that germination cannot occur, (2) complete or partial burial of individual plants causing mortality and (3) partial burial of individual plants causing reduction of biomass but not leading to plant mortality. In the latter case partial burial of a plant may include burial of a stem (or stems) of a clonal plant; the stem is buried but the remainder of the clone survives. Overwash can therefore be a large disturbance and it is well recognized as a factor influencing patterns of barrier island vegetation (Schroeder *et al.*, 1979; Zaremba and Leatherman, 1986; Roman and Nordstrom, 1988).

The relationships between overwash disturbance pattern and occurrence of each of the 95 species found on a particular Virginia barrier island, Hog Island (37° 27' N, 75° 50' W), are described in Fahrig *et al.* (1993). In that analysis, an index of overwash disturbance frequency at any point on Hog Island was calculated. Data used for this calculation were from analyses of aerial photographs by R. Dolan, B. Hayden and coworkers at the University of Virginia, in which the distance from the beach face to the edge of the sand deposit was estimated. Fahrig *et al.* (1993) analysed 7 years (1949, 1955, 1962, 1967, 1977 and 1988) of data to calculate an estimate of the probability that any 2m × 2m point on the island is found in a disturbed state, i.e. is recently overwashed and covered with sand, with insufficient time for recolonization by plants. The

Table 1. Mean index of disturbance probability for McCaffrey (1975) assemblages, given in increasing order and arranged into disturbance groups

Community name	Symbol	Disturbance index
<i>Group 1</i>		
Low thicket	LT	0.006
Open dunes – thicket	DUT	0.024
Upper low salt marsh	ULSM	0.046
Tall thicket	TT	0.053
Low salt marsh	LSM	0.057
<i>Group 2</i>		
Fresh marsh	FM	0.086
Brackish marsh	BM	0.104
Dense grass	DG	0.127
Sparse grass	SG	0.171
<i>Group 3</i>		
Salt flat	SF	0.307
Dunes – dense grass	DUDG	0.330
Wash flat	WF	0.395
<i>Group 4</i>		
Dunes – grass	DUG	0.631
Beach	B	0.909

analysis therefore did not provide an estimate of disturbance frequency *per se*, but rather an index of disturbance frequency.

Plant species distributions were determined from data collected by McCaffrey, 1975. She used a combination of aerial photography and ground-truthing to produce a vegetation map of Hog Island. The map consisted of 14 plant assemblages (see Fahrig *et al.*, 1993). Each assemblage was characterized by the percent cover of species. By overlaying the map of overwash disturbance index with the vegetation map, we calculated the mean disturbance index for each of the 14 assemblages. These fell into four disturbance index classes (Table 1).

For our present purpose, we categorized each species on Hog Island into (1) annual or biennial (A), (2) herbaceous perennial without long-distance clonal spreading (H), (3) herbaceous perennial with long-distance clonal spreading or guerilla (G) and (4) woody species (W). We then compared the four kinds of species (life forms) with the four levels of disturbance (disturbance groups). We calculated the percentage cover of each life form in each assemblage type using the percentage cover of each species in each assemblage type (Table 1). To calculate the percentage cover of each life form in each of the four disturbance categories (Fig. 1) we weighted the life form cover data from each assemblage by the percentage occurrence of that assemblage (by area) relative to the total of all assemblages in that disturbance category.

#### *Plant life form distribution in relation to grazing disturbance in a short-grass steppe*

Data for the short-grass steppe were collected from the Central Plains Experimental Range (CPER) which is administered by the United States Department of Agriculture-Agriculture Research Service located in north-central Colorado, approximately 60 km northeast of Fort Collins (40° 49' N, 104° 46' W). Long-term mean annual precipitation is 321 mm (SD = 98 mm)

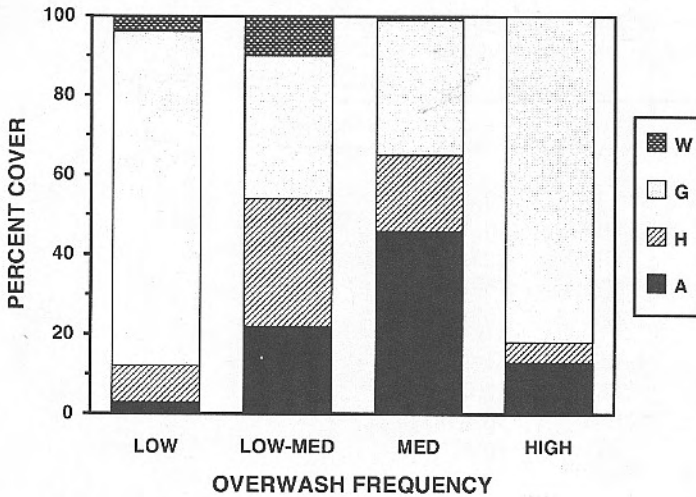


Figure 1. Relative cover of four life forms of plants within four overwash disturbance groups on Hog Island. The total area in each disturbance group is the total of the areas of the communities that comprise the group (Table 1). The four life forms are (1) annual or biennial (A), (2) herbaceous perennial without long-distance clonal spreading (H), (3) herbaceous perennial with long-distance clonal spreading or guerilla (G) and (4) woody species (W).

and mean monthly temperatures range from  $-5^{\circ}\text{C}$  in January to  $22^{\circ}\text{C}$  in July. The topography consists of level uplands and lowlands connected by gentle slopes. Vegetation is typical of the short-grass steppe and includes a number of perennial grasses, sedges, succulents, half-shrubs and forbs and annual grasses and forbs.

Disturbance regime was defined by cattle grazing intensity. Lightly (1.4 ha per yearling per month), moderately (1.1 ha per yearling per month) and heavily (0.7 ha per yearling per month) grazed pastures have been maintained at the CPER since 1939. These mean stocking rates represent a mean of 20, 40 and 60% removal, respectively, of the standing crop over a 6 month period during the growing season (Klippel and Costello, 1960). The disturbance effects of grazing include (1) consumption of flowering culms, seeds and inflorescences (Jameson, 1969; Rickard *et al.*, 1975) leading to reduced seed availability (Coffin and Lauenroth, 1992), (2) consumption of plant biomass leading to mortality, especially for annual plants (Milchunas *et al.*, 1989), (3) consumption of plant biomass not causing mortality but leading to changes in carbon allocation patterns among plant parts (Watt and Haggard, 1980; Brown, 1987) and (4) faecal pat deposition causing biomass reduction and mortality and creating sites for colonization (Coffin and Lauenroth, 1988).

Plant cover data in each grazing intensity pasture were determined from Gill (1985). Percentage canopy cover for each of the 62 species was estimated using 60 50-cm diameter quadrats at each of three topographic positions (upland, slope, lowland) in each pasture. Plants were grouped into the four life form categories (A, H, G and W) and values were then averaged across topographic positions to obtain percentage cover by life form for each disturbance regime (Fig. 2.).

#### Conclusions from data analyses

In some ways the results from both sites are in agreement with the expectations from classical theory described in the Introduction (Figs 1 and 2). First, woody plants, which in general have

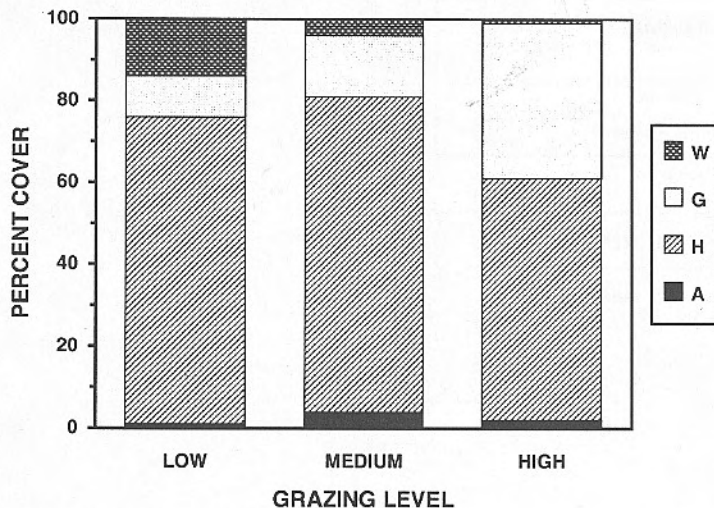


Figure 2. Relative cover of four life forms of plants within four grazing disturbance categories in the short-grass steppe. The four life forms are (1) annual or biennial (A), (2) herbaceous perennial without long-distance clonal spreading (H), (3) herbaceous perennial with long-distance clonal spreading or guerilla (G) and (4) woody species (W).

longer lifespans and later reproduction than other plant life forms, are scarce or non-existent in highly disturbed areas. Second, herbaceous plants without long-distance clonal spreading decline in representation from moderately to highly disturbed areas, but unlike the woody plants they are still well represented in the highest disturbance group. Finally, annual plants increase in relative abundance from low to intermediate disturbance categories.

Of particular interest, however, is the fact that in both ecosystems at the highest disturbance frequencies there is a decline in annuals and an increase in the cover of guerillas. A possible reason for this is that long-distance clonal spreading may be a quicker way to recolonize disturbed areas than seed dispersal, since seeds do not germinate until the following year. To examine the potential importance of this effect we used a generalized spatially explicit simulation model of the population dynamics of a single plant life form in the presence of disturbance. The purpose of the simulations was to see whether the advantage of long-distance clonal spreading in perennial herbs could outweigh the prolific seed production by annuals in highly disturbed areas.

## Simulation experiments

### *The model*

Our goal was not to model a particular species or situation (e.g. Cain *et al.*, 1991), but rather to develop a simple model in which the general aspects of life history – age at first reproduction, lifespan, fecundity, clonal spreading – could be varied to make general predictions about relationships between these aspects and species response to disturbance. The model is a single-species age-classified population model with dispersal occurring through seed production and/or long-distance clonal spreading (Fig. 3). Time and space are discrete but not restricted to particular spatial or temporal scales. Instead, time is divided into time ‘steps’; in the present application one time step represents 1 year. The landscape is divided into a grid of spatial ‘cells’; the population is subdivided into subpopulations that inhabit the cells and dispersal of seeds and/or clonal stems occurs between cells. The numbers of steps and cells are specified at the start of

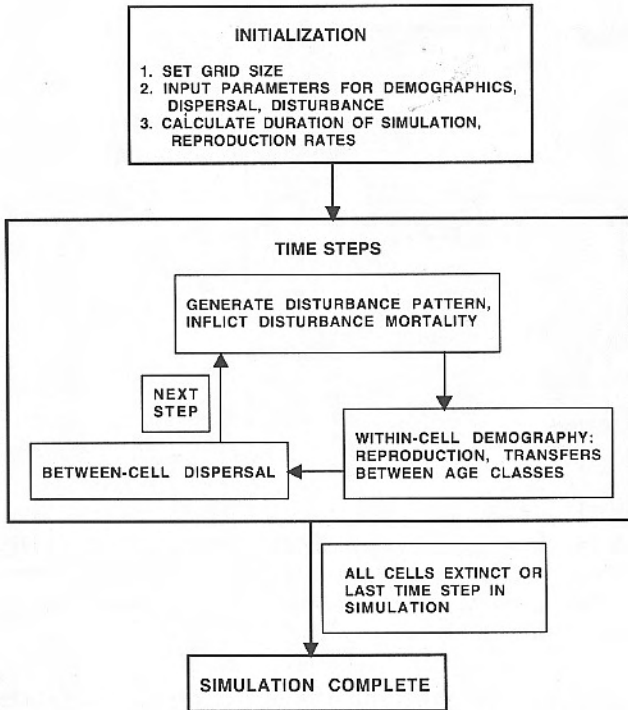


Figure 3. Summary of model structure. Parameters and parameter values are given in Table 2.

each simulation. For a review of simulation approaches to spatiotemporal dynamics of plant populations see Czárán and Bartha (1992).

We assumed disturbances of one cell in size. Disturbance frequency is the probability per time step that a cell will experience a disturbance. Disturbance intensity is the fraction of the population within a disturbed cell that is killed by the disturbance event. Spatial and temporal distributions of disturbances are random; each time step for each cell a random number between 0 and 1 is drawn from a uniform distribution and if the number is less than the disturbance frequency, the cell is disturbed.

The population in each grid cell is age-classified; the number of age classes is specified at the beginning of a simulation. For plants, 'birth' may be divided into seed production and production of clonal stems. From the point of view of recovery from disturbance, shoots produced by long-distance clonal spreading are considered to be equivalent to those arising from seeds, even though the clonal shoot does not represent a new genetic individual. Although there is no density-dependent adjustment of population growth within cells, there is a ceiling to the cell population (the carrying capacity), that applies to stems only (not to seeds).

Caswell (1985) applied graph theory to life histories of clonal organisms. His figure 6.5, redrawn here in Fig. 4, is a generalized version of the life history in each spatial cell of our model.  $N_i$  is the number of individuals (stems) in age class  $i$ , where  $i = 1$  is the seed age class and  $i = 2$  is the youngest plant age class (seedling or clonal shoot).  $F_i$  is the annual seed production rate of  $i$  and  $V_i$  is the annual clonal stem production rate of  $i$ .  $P_i$  is the survival rate from  $i$  to  $i + 1$ . We assumed that the annual survival rates were constant across age classes such that 1% of  $N_1$  survives to the final age class:  $P_i = 0.01^{1/(n-1)}$  and  $P_n = 0$ , where  $n$  is the number of age classes.

To compare the performance of different life history strategies (e.g. long-distance clonal

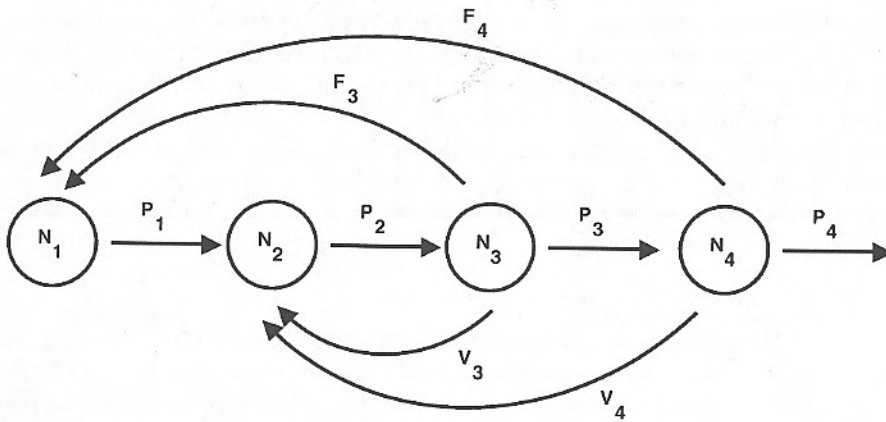


Figure 4. Demography of a plant population that can 'reproduce' both sexually and clonally; redrawn from Caswell (1985, Fig. 6.5):  $N_i$  = number of individuals (stems) in age class  $i$  ( $i = 1$  for seeds,  $i = 2$  for seedlings and/or new clonal shoots),  $P_i$  = annual survival rate from  $i$  to  $i + 1$ ,  $F_i$  = annual seed production rate of  $i$ ,  $V_i$  = annual clonal shoot production rate of  $i$ .

spreading vs no long-distance clonal spreading), the fecundity per age class was normalized so that the total lifetime reproductive output was the same for the cases being compared (Gordon, 1989). Therefore, variations in any of the other life history features (time to first reproduction, lifespan, clonal spreading) produce variations in the fecundity per age class. Fecundity *per se* is not varied independently in the simulation experiments. The normalization results in short-lived organisms having high annual fecundities (e.g. annuals) with respect to long-lived organisms, which spread their reproductive output over a larger time-span with resultant lower annual fecundities (e.g. woody plants).

If one were modelling only sexual reproduction, one would most likely normalize for the total lifetime reproduction in terms of seeds ( $N_1$  in Fig. 4). However, to include clonal spreading, we normalized in terms of the new shoot age class ( $N_2$  in Fig. 4); this includes both seedlings and new clonal shoots. If the number of age classes is  $n$ , the total lifetime net reproductive output per individual is  $B$  (expressed as number of individuals in age class 2) and the proportion of  $B$  attributable to seed production (i.e. seedlings vs clonal shoots) is  $S$  then,

$$BS = P_1(F_3P_2 + F_4P_2P_3 + \dots + F_nP_2P_3 \dots P_{n-1}) \quad (1)$$

for seedling production and

$$B(1 - S) = V_3P_2 + V_4P_2P_3 + \dots + V_nP_2P_3 \dots P_{n-1} \quad (2)$$

for clonal shoot production. Notice that the seedling production Equation 1 is multiplied by the seed survival rate ( $P_1$ ). If we simplify by assuming that yearly *per capita* survival rate ( $P$ ), seed production rate after the age of first sexual reproduction ( $F$ ) and clonal stem production rate after the age of first clonal stem production ( $V$ ) are all independent of age, then

$$F = \frac{BS}{P^2 + P^3 + \dots + P^{n-1}} \quad (3)$$

and

$$V = \frac{B(1 - S)}{P + P^2 + \dots + P^{n-2}} \quad (4)$$



Equations 3 and 4 are used to calculate  $F$  and  $V$  for different values of  $n$  (lifespan). In this way the reproductive rates are normalized to maintain a constant total lifetime reproductive output ( $B$ ), irrespective of lifespan. In conducting the simulation experiments, it was then necessary to run the simulations for some multiple of the lifespan.

The shape of the dispersal curve (for both seed dispersal and clonal spreading) away from a point of dispersal (cell  $a$ ) follows a negative exponential function as in DeAngelis *et al.* (1985). The number of dispersers reaching the distance  $r$  from  $a$  (i.e. landing on the circle with radius  $r$  from  $a$ ) is

$$D_a(r) = 2\pi r D_{a,0} e^{-kr} \quad (5)$$

where  $k$  is a parameter that determines the rate of decay of the negative exponential curve and thereby determines the mean dispersal distance. To find the number dispersing to a 'doughnut' around  $a$  (delineated by distances  $r_1$  and  $r_2$ ), we take the difference of the integral of Equation 5 from  $a$  to  $r_1$  and  $a$  to  $r_2$ . The number dispersing to a single cell ( $b$ ) in this doughnut is proportional to the size of the cell relative to the size of the doughnut. The immigration rate is:

$$D_{a,b} = \frac{2D_{a,0} [e^{-kr_2}(-r_2 - (1/k)) + e^{-kr_1}(r_1 + (1/k))]}{k(r_1 + r_2)} \quad (6)$$

If we know (or can assume) the total number of dispersers leaving  $a$  (i.e.  $D_{a,all}$ ) we can substitute  $D_{a,0}$  in Equation 6 with  $D_{a,all}k^2/(2\pi)$  obtained by integrating Equation 5 over  $r$  from 0 to  $\infty$ .

The negative exponential dispersal curve appears to be appropriate for many plants (McEvoy, 1984; Farah *et al.*, 1988; Okubo and Levin, 1989). Alternatively, dispersal can be modelled as a diffusion process (Kareiva and Shigasada, 1983; Lande, 1987; Fleischer *et al.*, 1988). This assumes the distribution of dispersers follows a Gaussian distribution centred at the starting point of the dispersal. This is qualitatively similar to the negative exponential and conclusions drawn from our simulation experiments should apply to these cases as well. Again, dispersal in the model can occur through both seed dispersal and long-distance clonal spreading through rhizomes and stolons.

#### *Simulation experiment I: reduced time to colonization*

Long-distance clonal spreading as a means of reducing the time to colonization of disturbed sites should be advantageous in a habitat in which disturbances are frequent. However, this advantage would have to outweigh the advantages of short lifespan and high fecundity of annuals for clonally spreading perennials to do better than annuals in highly disturbed areas. The first simulation experiment was designed to study the importance of this reduction in time to colonization for the clonally spreading perennial.

The simulation experiment consisted of four separate sets of simulations, each corresponding to one of four types or 'life forms' of plants. The four life forms were (1) short-lived, early reproducing, reproducing by seeds only, (2) intermediate-lived, early reproducing, reproducing by seeds only, (3) intermediate-lived, early reproducing, reproducing both by seeds and by long-distance clonal spreading and (4) long-lived, late reproducing, reproducing by seeds only. These categories roughly correspond respectively to the four plant life forms used in the analyses of the data from the barrier island and the short-grass steppe: (1) annual or biennial (A), (2) perennial herb without long-distance clonal spreading (H), (3) perennial herb with long-distance clonal spreading (G) and (4) woody plant (W). Note that for the clonally spreading plant, the lifespan here is the lifespan of an individual stem, not a genetic individual.

The correspondence is rough in that other possible differences among these four plant types (e.g. differences in seed dormancy or in the shapes of the curves for survival vs age) were not

Table 2. Parameter values used in the simulations

a. Parameter values constant among all simulations				
Grid size	15 cells × 15 cells			
Starting cell population size	500 plants			
Maximum cell population size	500 plants			
Net lifetime reproductive rate	10 seedlings or clonal shoots per individual			
Dispersal rate	10% leaving parent cell			
<i>k</i> in dispersal curve	2.0			
Disturbance size	one cell			
Disturbance duration	one time step (i.e. 1 year)			
Disturbance intensity	85% killed			
b. Parameter values differing among life forms				
	Annual (A)	Non-clonal herb (H)	Guerilla (G)	Woody (W)
Lifespan	2	10	10	30
Age at first seed production	2	2	2	6
Proportion of reproductive output as seeds	1.0	1.0	0.5	1.0

accounted for. Indeed, to make the results of the four groups directly comparable, all aspects of the model were consistent among simulations except for parameters determining lifespan, age at first reproduction and clonal spreading. Reproductive rates (sexual and clonal) and survival rates were normalized (see above), so that total lifetime net reproduction in the absence of disturbance did not vary among life forms, but annual reproductive output per individual decreased with increasing lifespan. The number of time steps for each simulation was five times the lifespan of the life form. Only the final three-fifths of each simulation was used in the collation of the results. Most of the parameter values in the model were constant among the simulations of the life forms (Table 2a). The values of these parameters are largely arbitrary since they are not important in the interpretation of the simulation results. A small number of parameters were used to distinguish among life forms; these were varied among simulations (Table 2b).

For each of the four sets of life form parameters, three replicate simulations were conducted at each of nine disturbance frequency values (0.1, 0.2, . . . , 0.9). Replication was included to account for effects of the random disturbance process. However, results among replicates were very similar.

The results of the simulation experiment indicate relative abilities of the four life forms to survive under increasing disturbance frequencies (Fig. 5). Since the simulations for each life form were conducted separately, with no interspecies competition, the population size under conditions of no disturbance is the same, namely the maximum possible (500 per cell). The expectation that increased lifespan reduces the ability of a population to recover from disturbance is demonstrated by comparison of the curves for the annual (A) with the non-clonal herbaceous perennial (H) (Fig. 5); the annual population is better able to survive in the face of high disturbance frequencies. The very long lifespan of the woody plant combined with its later onset of reproduction makes it even less able to cope with high disturbance frequencies than the non-clonal herbaceous perennial. These results corroborate the expectation that short-lived species with early reproductive onset are better able to survive in highly disturbed areas than long-lived species with delayed reproductive onset. With regard to clonal spreading, it appears

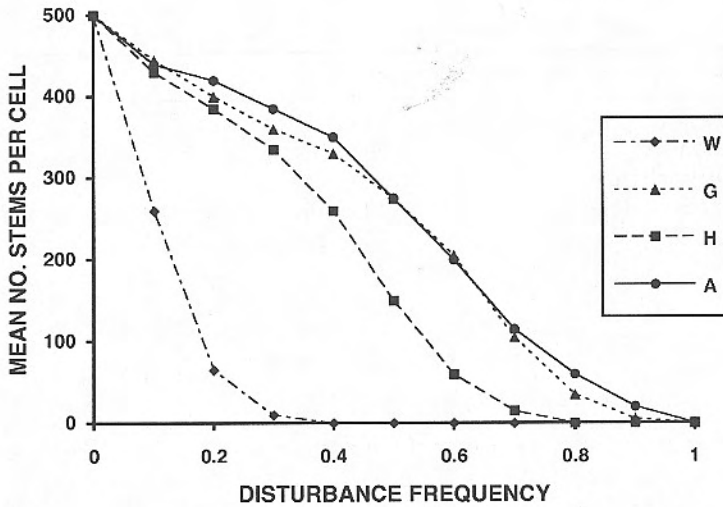


Figure 5. Results of simulations of population dynamics for four life forms of plants, defined by different parameter values given in Table 2b, for different disturbance frequencies.

there is a significant advantage of bypassing the seed stage and directly producing new stems clonally thus shortening the time to colonization (Fig. 5, H vs G). This makes the guerilla similar to the annual plant in its ability to cope with high disturbance frequencies, even though the annual reproductive rate of the guerilla is much lower than that of the annual because of its longer lifespan.

#### *Simulation experiment II: mortality of stems vs seeds*

Although the simulation experiment above shows there may be an advantage to clonal spreading, it does not indicate this advantage is likely to outweigh the advantages of the annual life form. However, survival of a guerilla form may be further improved if mortality due to disturbance has a more severe effect on seeds than on stems. This seems likely for both the overwash disturbance on the barrier island and the grazing disturbance in the steppe.

The main effect of overwash disturbance on Hog Island is to deposit a layer of sand over the vegetation; the depth of sand deposited varies from 1 or 2 to over 15 cm. The probability of mortality of a stem (whether a seedling or a clonal stem) is lower than that of a seed, when covered with the same depth of sand and seed banks in dune soils are small to non-existent (Ehrenfeld, 1990). The recovery of a stem or a seed depends on the stem or seed having enough stored energy to send a shoot up through the sand to the surface. Stems in general have more stored energy than seeds and they may be only partially covered with sand and therefore able to recover (Zaremba and Leatherman, 1986). Therefore, in the case of overwash disturbance, the disturbance intensity is probably higher for seeds than for stems.

Likewise, when plants are grazed on the short-grass steppe, portions of stems, crowns and roots may be left and new shoots can be sent up. However, if the plant is an annual and the seed-bearing portion of the plant is eaten by a grazing animal toward the end of the growing season, the plant may not be able to produce more seeds before the end of the season. It will therefore not produce any progeny in the following year.

The second simulation experiment illustrates how this difference in disturbance intensity on seeds and stems could make guerillas better able to survive high disturbance rates than annual plants, as was observed in the data. Design of the simulation experiment was identical to the first

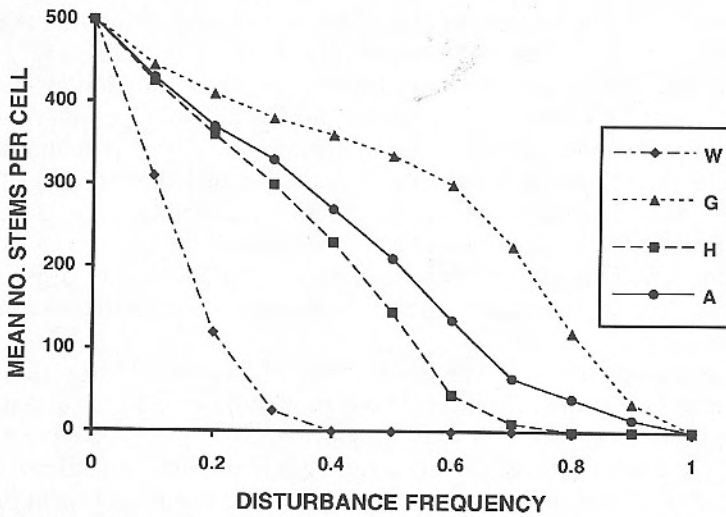


Figure 6. Results of simulations of population dynamics for four life forms of plants, as in Fig. 5, but with disturbance intensity = 0.75 for plants and 0.95 for seeds.

simulation experiment with one exception: the disturbance intensity for seeds was 0.95 and for stems was 0.75 (i.e. disturbances killed 75% of stems and 95% of seeds).

In this set of simulations, trends were similar for woody plants and non-clonal herbaceous perennials as those in the first simulation experiment (Fig. 6). However, instead of annuals and guerillas having similar responses to disturbance, now the guerillas recovered more easily from high disturbance frequencies than did annual plants. This is because the guerillas have less of their reproductive output invested in seeds and more in clonal stems. Since these clonal stems are not hit as hard by disturbance as the seeds are, the population of guerillas recovers from disturbances more quickly than does the population of annuals.

## Discussion

Classical life history theory predicts that species with early maturation, short lifespans and high annual fecundities should be best adapted to life in highly disturbed habitats. This leads to the prediction for plants that the cover of annuals relative to perennials should increase with increasing disturbance frequency. Contrary to this prediction, we found for two very different ecosystems that as one moves to the most frequently disturbed areas, relative cover of annuals decreases and relative cover of perennial plants with long-distance clonal spreading (guerillas) increases. We suggest the relative advantage of guerillas is due to the combination of two factors. First, long-distance clonal spreading allows such plants to recolonize a disturbed area within the same year as the disturbance, thus shortening the time to colonization. From a demographic point of view this is equivalent to shortening the time to maturation. Second, in both systems studied the effect of disturbance is more severe on seeds than on stems. Guerilla plants therefore have a higher probability of recovery and recover more quickly from disturbances than annuals.

Other spatial models have been proposed for comparison of life forms in the presence of disturbance, although not for comparison of annual and guerilla forms. In a spatial simulation model of competition in the presence of disturbance, Inghe (1989) compared the relative survival rates of clonal plants with and without long-distance spreading (i.e. guerilla vs phalanx types). When disturbance rate was low the phalanx form dominated whereas when disturbance rate was

high the guerilla form dominated. The former result was due to the assumption that the phalanx form won in local competitions with the guerilla. The latter result was due to the longer dispersal distance (i.e. spreading distance) of the guerilla form. Inghe's (1989) formulation for the guerilla type was similar to Crawley and May's (1987) formulation for the annual type in a similar plant competition model, where the competition was between annuals and clonal perennials. In both cases the two features assumed for the disturbance-adapted type (whether the guerilla or the annual) were longer dispersal distance and inferior competitive ability. The difference in dispersal distance was most extreme in Crawley and May (1987) in which annuals were assumed to disperse evenly over the whole spatial grid whereas perennials could only disperse to the nearest grid cells; this assumption gives annuals a great advantage when disturbance frequency is high.

Unlike these competition models, the differences we obtained among life forms in our model did not depend on differences in dispersal distances; in our simulations the dispersal distances for all life forms were assumed to be the same. There is some evidence that the assumption of equal dispersal distance for seeds and long-distance clonal spreading is reasonable, at least for plants on barrier islands (Ehrendfeld, 1990). The differences among life forms in our model occur because of differences in age at maturity and because of the trade-off between annual fecundity and lifespan. In simulation experiment I the abilities of annuals and guerillas to survive under highly disturbed conditions were similar because the reduction in time to 'maturation' (by reduction in time to colonization) for the guerilla balanced the higher annual fecundity of the annual; both were able to take advantage of openings by dispersal.

At first glance our finding might seem counter to the extensive literature on disturbance-adapted annuals. However, our goal was not to examine whether particular species are disturbance-adapted, but to ask the more general question: is the annual life form better adapted than other life forms (particularly the guerilla form) to very highly disturbed habitats? This question must be addressed by examining changes in relative covers of the different life forms, including all species present in the ecosystem, as one moves from areas of lower to areas of higher disturbance frequency. To our knowledge, the present study is the first to do this. For two very different ecosystems we conclude that the long-distance clonally spreading perennial (guerilla) life form is better adapted than the annual life form for survival in highly disturbed habitats.

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