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On the ecology and evolution of annual plants in disturbed environments

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Abstract

This paper is concerned with the effect of disturbance on some crucial characteristics of annual plants. The theoretically optimal life-history traits that maximize individual fitness in disturbed environments are described and critically evaluated. It seems that none of them holds for all annual species.

Self-pollination and especially seed polymorphism are considered important adaptations to life in unpredictable environments. The thesis is put forward that amphicarpic annuals, which exhibit both self-pollination and extreme seed polymorphism, are best adapted to life in hazardous habitats. The hypothetical course of the evolution of amphicarpy is demonstrated on the grounds of the comparison of contemporary annual species producing chasmogamous and cleistogamous flowers on a single individual.

Nomenclature: follows Flora Europaea (Tutin *et al.* 1964–1980), except for non-European species where the nomenclature used in the papers cited has been followed.

Introduction

Disturbance has been defined as mechanisms which limit the plant biomass by causing its partial or total destruction (Grime 1979), as relatively discrete events in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or physical environment (Pickett & White 1985), or even wider as unusual events relative to a normal situation (Begon *et al.* 1986). Disturbance can differ in type, frequency, extent and intensity; nevertheless, it is a crucial aspect of ecological reality for most organisms regardless of their life-history patterns (see e.g. Bazzaz 1983; Grubb 1985).

From recent papers it may be inferred that the search for correlations between life-history traits and features of disturbed environments is especially interesting in the case of annual plants. On the one hand, due to their life cycle restricted to only a few months or weeks, even short disturbance in their environment may considerably affect a plant's chance of survival and reproduction. On the other hand, the short life cycle of many contemporary annual species has been probably formed in response to disturbance, and favoured by natural selection. It is well proved by the fact that even amongst semelparous (monocarpic) species with undetermined life length the fraction of individuals terminating their life cycle in one year is clearly higher in disturbed than in undisturbed environments, as in *Poa annua* (Fig. 1). Moreover, in populations of typical winter annuals like *Erophila verna* and *Galium aparine* new ecotypes originating due to disturbance have been observed to terminate their cycle within spring and summer (Symonides 1983a, b; Groll & Mahn 1986). It is also worth noting that periodically and continu-

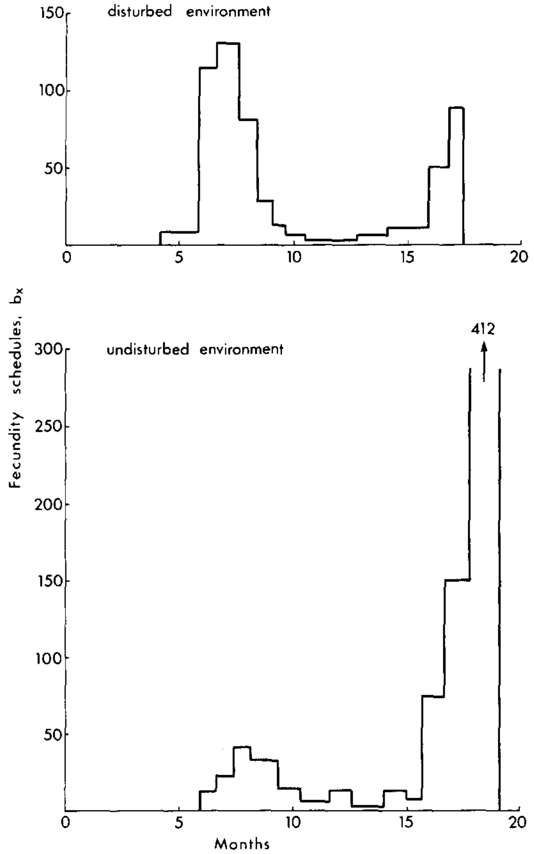

Fig. 1. Fecundity schedules for two populations of *Poa annua* derived from contrasting environments (From Law *et al.* 1977).

ally disturbed environments are usually colonized, and often dominated in late successional stages, by annual plants.

This paper will only survey the crucial traits of annual plants in environments that are disturbed in time and space, mainly physiological and behavioural properties that enable them to minimize loss of energy for reproduction and (or) minimize offspring mortality.

Optimal life history: models and reality

Theoretically, high fecundity will be typical of annual plants. Optimal life-history models make some important predictions about the life-history traits that might be expected to maximize individual fitness in short-lived organisms. These include: (a) a rapid switch from vegetative to reproductive growth late in the life cycle (Vincent & Pulliam 1980; Kermit 1983); (b) translocation of nutrients from vegetative to reproductive organs (Chapin 1980); (c) a high reproductive effort (King & Roughgarden 1982); (d) maximization of seed number within available resources, resulting in low individual seed weight (Baker 1974); (e) a long-term seed dormancy and the presence of a seed bank as bet-hedging tactics in an unpredictable environment (Cohen 1966; Leon 1985), or alternatively a strong tendency to disperse in space (Venable & Lawlor 1980). Finally, semelparity should also be associated with high survival of juvenile individuals (Silvertown 1987).

A question arises whether the actual strategy of annual plants, especially those from disturbed environments, corresponds to that which is theoretically optimal. The recent papers show that this is only partly true, and only for some species.

Against theoretical predictions a rapid switch from vegetative to reproductive growth in reality is rather rare. Maybe it is true only for species with genetically determined timing of flowering, e.g. for *Plantago erecta* (King & Roughgarden 1983), *Echinocystis lobata* (Silvertown 1985), and *Aira caryophyllea* (Rozijn & van der Werf 1986). Some annuals may shorten their life cycle and fairly rapidly start flowering in response to various perturbance agents like excessive increase in the CO_2 concentration, as in the case of *Layia platyglossa* and *Clarkia rubicunda* (Omer & Horvath 1983), essential increase in water temperature, as in *Ludwigia leptocarpa* growing in a reactor sewage (Christy & Sharitz 1980), or strong oscillations in water level, as in the case of *Limnanthes floccosa* (Ritland & Jain 1984). However, species that continue vegetative growth during the reproductive phase, and hence early allocate a part of their resources for the production of generative organs, are much more numerous. Doubtless, such resource partitioning increases the fitness of an organism in periodically disturbed environments. It is typical of, e.g. many *Veronica* species (Harper 1977), *Polygonum minimum* (Jackson & Bliss 1984), *Soliva pterosperma* (Maxwell *et al.* 1986), *Aira praecox* (Rozijn & van der Werf 1986), *Urtica urens* (Boot *et al.* 1986), *Lesquerella gordonii* (Delph 1986), and other species both from natural and man-made ecosystems. Most annuals of this group produce seeds gradually over an extended period or in a number of discrete flushes. In a sense they are uniseasonally iteroparous (polycarpic) species (Kirkendall & Stenseth 1985). Amphicarpic species i.e. plants producing two kinds of fruits on a single individual, are classical iteroparous annual.

It also seems that translocation of nutrients from vegetative to reproductive organs is not a rule amongst annuals, although it occurs in some species from disturbed, unstable habitats e.g. in *Bromus mollis* (Woodmansee & Duncan 1980), *Aristida oligantha* (Adams & Wallace 1985), as well as *Phleum arenarium* and *Erodium glutinosum* (Ernst 1983). However it has not been observed in *Cassia fasciculata* (Kelly 1986), and may also be true for other annuals of disturbed environments if their generative organs are capable of photosynthesis (as in *Cassia*), or if generative and vegetative phases overlap.

Reproductive effort is also extremely variable amongst annuals (Table 1). It may vary significantly among local populations of a single species and in successive generations (e.g. Symonides 1974; Kawano 1975). Morphs diversified, e.g. in respect of resources provided for reproduction may occur within one generation (van Andel *et al.* 1986). Sometimes even within one cohort, that represents one form, individuals exhibit a highly different reproductive effort; in populations of *Erophila verna, Veronica triphyllos* and *Arabidopsis thaliana* from arable fields the reproductive effort between neighbours may differ by more than 30% (Fig. 2). In some species, e.g. *Polygonum cascadense* and *Trifolium hirsutum,* an increase in the reproductive effort occurs with disturbance (Hickman 1975; Jain 1983). In others the opposite phenomenon takes place which seems to be correlated with an increased level of ploidy, like in some closely related *Setaria* species (Kawano & Miyake 1983). It should be noted, however, that a reproductive effort as discussed above has been evaluated on the grounds of biomass or energy

Table 1. The range of reproductive effort (RE) in annual species.

Species	RE (%)	References
Chenopodium album	≥ 60	Maillette 1985
Spergula arvensis		Maillette 1985
Polygonum cascadense	50 – 60	Hickman 1975
Plantago insularis		Bell *et al.* 1979
Spergula vernalis		Symonides 1974
Chaenactis carphoclinia	41 – 50	Bell *et al.* 1979
Plantago indica		Symonides 1979
Phleum arenarium		Ernst 1981
Astragalus sabulanum	31 – 40	Bell *et al.* 1979
Schismus arabicus		Bell *et al.* 1979
Leavenworthia stylosa		Solbrig & Rollins 1977
Oenothera deltoides	21 – 30	Bell *et al.* 1979
Amaranthus powelli		Weaver *et al.* 1982
Leavenworthia crassa		Solbrig & Rollins 1977
Androsace septentrionalis	11 – 20	Symonides 1979
Polygonum minimum		Hickman 1977
Cerastium semidecandrum		Symonides unpubl.
Medicago laciniata	≤ 10	Friedman & Elberse 1976
Abutilon theophrasti		Abrahamson 1979
Erodium cicutarium		Jaksic & Montenegro 1979

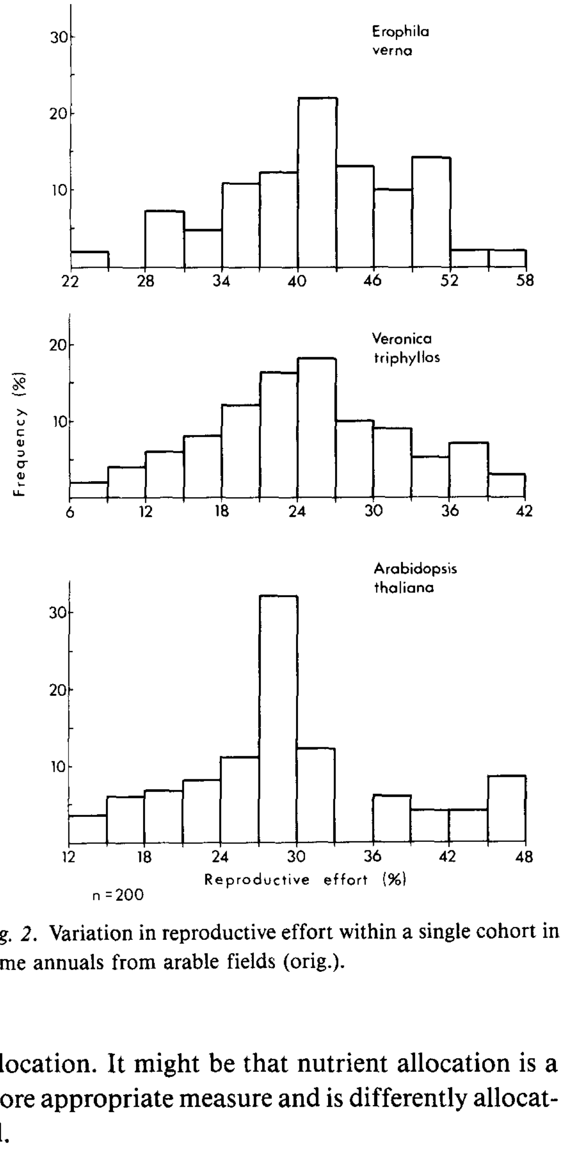

Fig. 2. Variation in reproductive effort within a single cohort in some annuals from arable fields (orig.).

allocation. It might be that nutrient allocation is a more appropriate measure and is differently allocated.

The total seed number per individual plant may also vary, ranging from 1-3 diaspores in *Vulpia fasciculata* (Watkinson & Harper 1978) to hundreds of thousands of seeds in *Chenopodium album* (Maillette 1985). In addition, many species both in stable and unpredictable environments have evolved towards an increase in the weight of seeds, not in their number. The cases of *Capsella bursa-pastoris, Arabidopsis thaliana* and *Sesbania vesicaria* indicate that annual plants may respond to current disturbance (e.g. herbivore pressure) by an increase in the seed weight and a decrease in the seed number (Hurka & Benneweg 1979; Marshall *et al.* 1985). Also plasticity in partitioning of resources between seeds and fruits is a common phenomenon in species that experience the stress of biotic and abiotic perturbance. From a theoretical viewpoint it is surprising that annuals from unstable habitats often maintain high numbers of fruits, while the seed number per fruit decreases (see e.g. Delph 1986). This may lessen the resource pool potentially allocated to increase seed production. However, such plasticity raises the fitness of an organism in an unpredictable environment. In summary, it seems that the total seed number, the weight of a single seed, as well as the partitioning of resources between fruits and seeds vary with variable environmental conditions. One may presume that the theoretically assumed tendency to produce the highest seed number within the available resource pool does not occur in nature. Such a strategy would inevitably lead to a reduction of seed weight, which amongst many annuals is already fairly low. However it may characterize some species under highly unfavourable conditions when a decrease in seed weight associated with an increase in seed number, in spite of all, raises the chance of reproductive success (cf. Watkinson 1981; Kelly 1984).

Again, following the cited authors, we may conclude that annuals are highly diversified in respect of both longevity and dispersability of seeds regardless of the environment in which they grow and disturbance types which have been selectional agents in the course of their evolution. This problem has been discussed by Symonides (1988). It is also worth noting that the thesis of Venable & Lawlor on negative correlation between dispersal in space and that in time is highly disputable. The correlation appears to hold for species producing two dispersal morphs on a single plant, but as might be expected, does not always hold when comparisons are made between species. For example, the dispersing seeds of *Spergula vernalis* form a persistent bank, whilst non-dispersing seeds of its neighbour *Erophila verna* are short-lived (Symonides 1974, 1984).

Finally, from the data published to date it may be concluded that both winter and summer annuals show great variety of survivorship patterns between germination and seed set ranging from Deevey type I to extreme Deevey type III. It also appears that there is a lack of correlation between the number of seeds produced per plant and the shape of survivorship curve, as well as between survivorship pattern and the environment of individual species (cf. Symonides 1988, and references therein). For example, in a single community of psammophilous annuals in the Toruń Basin an extreme variety of survivorship curves of plant populations have been found although they experience similar environmental conditions (Fig. 3). Again the survivorship curve cannot be considered as characteristic of a given species. It may vary markedly depending upon the habitat conditions and population density (Symonides 1974, 1983; Klemow & Raynal 1983; Beeftink 1985).

Self-pollination and seed polymorphism as important adaptations

Self-pollination

Stebbins (1970) suggested that the transition from predominant outcrossing to predominant selfing is more common in the angiosperms than any other evolutionary change. The change in the pollination mode and ability to produce offspring 'single-handed' is crucial for short-lived semelparous organisms, especially those living in hazardous environments. No wonder this is a widespread phenomenon among both wind- and insect-pollinated annual plants, although only some species are as well self-fertile. Self-pollination has been observed among many annual species of *Arenaria, Gilia, Setaria, Erophila, Veronica, Bromus, Ipomoea, Vicia, Limnanthes* etc.

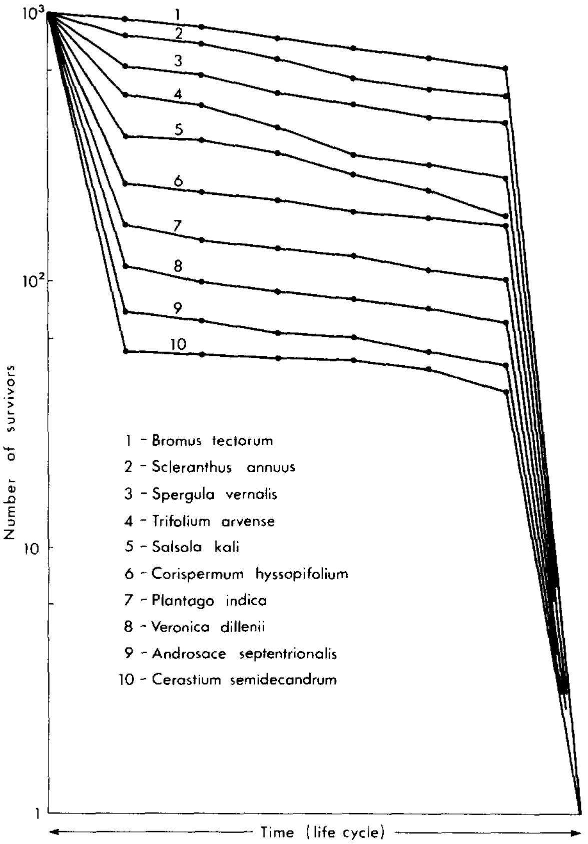

Fig. 3. Survivorship curves in ten annual species in a disturbed grassland, Toruń Basin (orig.).

So far the results of the studies have not answered satisfactorily the question when, how and why self-pollination evolved. But the relation between disturbance in the environment and transition from outcrossing to selfing seems undoubted. According to Cruden (1977) the evolutionary shift from xenogamy to obligate autogamy and cleistogamy is associated with a significant decrease in the mean pollen-ovule ratio, which is low in disturbed ecosystems and high at late successional stages. Most authors suggest that the evolution of self-pollination in different species has resulted from strong selection to ensure seed production under the conditions that make outcrossing difficult or impossible due to the effect of unfavourable, abiotic and biotic agents (e.g. Solbrig 1972; Arroyo 1975; Solbrig & Rollins 1977; Lloyd 1979; Schoen 1982a, 1982b; Gouyon *et al.* 1983). For example, competition for pollinators may lead to the evolution of self-pollination, as in *Ipomoea hederacea* (Stucky 1984) and *Arenaria uniflora* (Wyatt 1986).

Lack of data makes it impossible to evaluate the ecological consequences of the change in pollination mode in annuals. Its effect is only known to be either negative or positive. For example, in *Leavenworthia crassa* and *L. alabamica* self-fertilization is associated with lower seed production and lower seed quality (Lloyd 1965). This, however, is not common amongst annuals (cf. Solbrig 1980, and references therein). The individuals of self-pollinated populations of *Arenaria uniflora,* although they are smaller and produce smaller numbers of flowers which are also devoid of nectar, have a higher reproductive effort than those in cross-pollinated populations (Wyatt 1984). In *Gilia achilleifolia* selfed progeny from a normally cross-pollinated population shows unexpectedly high fitnesses relative to outcrossed progeny, suggesting that if such a mutant should arise it would increase in frequency (Schoen 1983). It has also been shown that self-pollinated populations are highly polymorphic and usually consist of a large number of specialized genotypes (Jain 1983; Zangerl & Bazzaz 1984a, 1984b). Hybridization is also a common phenomenon amongst annuals of disturbed environments. Due to self-pollination these new lines may be fixed in just a few generations (Zohary & Plitmann 1979).

Seed polymorphism

Seed polymorphism is a crucial characteristic amongst annuals that have evolved in variable, disturbed environments, although to a different extent in various species. In the simplest case, morphologically identical seeds have diversified dormancy, as in *Lactuca serriola* (Marks & Prince 1981), *Erucastrum gallicum* (Klemow & Raynal 1983) and *Papaver dubium* (Arthur *et al.* 1973). Thus, from one seed pool two or more cohorts appear having different size, mortality and seed production, as a result of the different growth conditions experienced by the individuals in different cohorts.

More often somatic polymorphism of seeds, originating in a single fruit, is associated with different seed weight, like in *Ludwigia leptocarpa* (Dolan & Sharitz 1984) or *Raphanus raphanistrum* (Stanton 1984), and in some species with different seed structure, as in *Hypochoeris glabra, Heterotheca latifolia* and some other composites (Baker & O'Dowd 1982; Venable & Levin 1985a, b, c). Sometimes somatic polymorphism of seeds is associated with their physiological polymorphism. The phenomenon has been analysed in a few annual halophytes: *Salicornia europaea, S. patula, Atriplex triangularis* (Ungar 1987). For example, in *Salicornia patula* large seeds may germinate at high soil salinity and over a wide range of temperature and light conditions, whilst small seeds are less tolerant to unfavourable environmental conditions (Berger 1985).

In all annuals with polymorphic seeds only small and light seeds are capable of germinating for a number of years. It has already been stated that long-term seed dormancy can be seen in terms of bet-hedging of an individual plant in disturbed environment with a high probability of seedling failure in any given year (Cohen 1966). However the presence of a large reservoir of seeds in the soil also has the consequence of stabilizing population fluctuations from year to year and preventing rapid directional selection (Epling *et al.* 1960).

From the above examples it may be concluded that many annual species adopt a mixed strategy by equiping some seeds for long-distance dispersal and others for staying near the mother plant, as well as for synchronous and long-term germination. The question of how many large and how many small seeds will be produced is a problem of Evolutionary Stable Strategy, since the production of large numbers of non-dispersing seeds would lead to sib competition.

Hypothetical evolution of amphicarpy and its ecological consequences

Amphicarpic annual plants seem to be best adapted to life in disturbed unpredictable environments. They also exhibit both self-pollination and extreme seed polymorphism. They have evolved not only towards dual resource allocation but also towards a dual reproductive strategy. The latter consists in the production of potentially cross-pollinated chasmogamous, aerial flowers and self-pollinated cleistogamous, subterranean flowers. The phenomenon is fairly rare, although it has evolved independently in seven different families (Cheplick 1987).

From the comparison of contemporary plants with both cleistogamous and chasmogamous flowers on a single individual one may guess about a possible evolution of amphicarpy (Fig. 4). Cleistogamous flowers have probably derived from chasmogamous ones, which is well illustrated by *Collomia grandiflora:* within a single inflorescence flowers exhibit a gradient from large, open, potentially cross-pollinated to small, closed, self-pollinated. The second evolutionary stage is characterized by the lack of transient flowers. A single plant produces only chasmogamous-, only

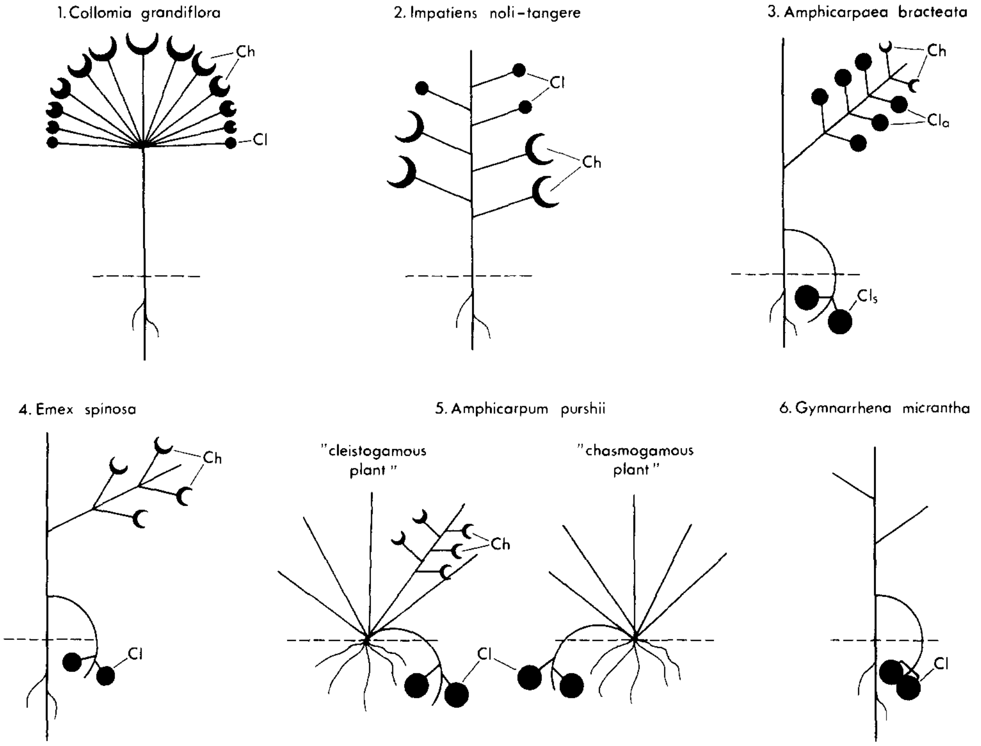

Fig. 4. The hypothetical stages in the evolution of amphicarpy. Ch – chasmogamous flowers, Cl_a – cleistogamous, aerial flowers, Cl_s – cleistogamous, subterranean flowers.

cleistogamous-, or both types of flowers. The process depends upon environmental conditions: the more unfavourable they are the higher is the fraction of cleistogamous flowers (Schemske 1978; Falencka 1983). It should be noted that, like in *Collomia,* both types of flowers develop here only on aerial shoots. The next step is the production of three types of flowers: chasmogamous, aerial cleistogamous and subterranean cleistogamous. Subterranean flowers have required remodelling of the system of reproductive organs, especially the change in the geotropism of a pedicel from negative to positive. *Amphicarpaea bracteata* is a classical example (Schnee & Waller 1986). At the further stage plants produce cleistogamous flowers and fruits only below the ground, like in *Emex spinosa* (Weiss 1980) and *Cardamine chenopodifolia* (Cheplick 1983). At last, an intriguing form of amphicarpy has evolved, called pessimistic by Zeide (1978). Its classical form occurs in *Amphicarpum purshii,* a grass from disturbed habitats. Its populations are usually dominated by the individuals of cleistogamous origin which allocate about 40% of their biomass to reproduction: 37% to early, heavy, subterranean diaspores and only 3% to a few light aerial seeds which develop one month later. Whilst the reproductive effort of the plants of chasmogamous origin is only 22%, they produce solely subterranean seeds and fruits, which arise two weeks later than in their cleistogamous neighbours (Cheplick & Quinn 1982).

An extreme form of pessimistic reproductive strategy that consists in almost total extinction of dual resource allocation is the last stage in the hypothetical scheme of evolution of amphicarpy. It has been found in the small desert plant *Gymnarrhena micrantha.* From the beginning of their growth each plant allocates most resources to the production of 1-3 very heavy, subterranean diaspores, and only under exceptionally favourable conditions it takes the risk of chasmogamous reproduction (Koller & Roth 1964).

Cheplick (1987) discusses some disturbance agents which probably have been responsible for the evolution of amphicarpy (drought, fire, herbivore pressure), and some selective advantages of this strategy. In fact, there are some arguments that the life history of amphicarpic annuals is optimal in disturbed environments: (a) minimum energy loss resource allocation that enables plants to carry over the biomass stored in subterranean seeds; (b) the chance of undisturbed reproduction below the ground in spite of possible disturbance above, followed by the ultimate reproductive success; (c) germination of subterranean 'stay-at-home' seeds and growth of seedlings in a safe site already experienced by a parent plant; (d) large size of seedlings growing from heavy, subterranean seeds, and in consequence having high tolerance to unfavourable abiotic conditions and to the competition stress; (e) the chance to increase both offspring number and its genetic variability under favourable conditions due to chasmogamous reproduction.

Conclusions

From these data it may be concluded that there are many patterns of life history of annual species that enable them to exist in disturbed environments, although bet-hedging, risk-avoiding tactics are common in their evolution. The tolerance to unfavourable habitat conditions on the one hand, and low competitive ability of short-living plants on the other, cause that most annuals colonize hazardous and pioneer environments, which are permanently or periodically disturbed both by natural and anthropogenic factors. Some authors emphasise that the species which are capable of living without mycorrhiza are especially well adapted to colonize disturbed environments, in spite of their weaker growth and lower competitive ability in comparison with mycorrhizal species (Allard 1965; Moorman & Reeves 1979; but see also Medre 1984).

The life-history traits of annuals, described in this paper, explain often their dominance in communities subjected to natural and anthropogenic disturbance (Joenje 1985; Lee & Ignaciuk 1985; Nakagoshi 1985; Watkinson & Davy 1985; Hatton & West 1987). Such plant communities are characterized by rapid, often irregular fluctuations both in species composition and dominance structure (e.g. Symonides 1979; Pineda *et al.* 1987). Partly they result from a specific response of single species to various disturbance agents (see Mahn 1984; Davy & Smith 1985). In this case the presence of some species in a community, as well as the sizes of their populations may play the role of indicators of a form and intensity of disturbance (Hobbs & Hobbs 1987). However, some studies show that fluctuations in species composition and quantitative relations between populations may result from non-interactive structure of an annual community, which is variable in time and depends on the intensity of disturbance (Hobbs & Hobbs 1987; Pineda *et al.* 1987).

One may currently observe rapid changes in the life-history traits of plants due to man-made disturbance. New biotypes originate which are resistant to herbicides, air pollutants or heavy metals. Short life-cycle and self-pollination may cause new lines to be fixed over a few generations (see e.g. Zohary & Plitmann 1979). Moreover, new forms may differ in traits that on the surface are unrelated to their tolerance to disturbance like a lower reproductive effort, delayed flowering or lower competitive ability, observed for biotypes of *Amaranthus retroflexus* resistant to atrozine (Conard & Radosevick 1979; Weaver *et al.* 1982). Probably, further studies will show whether such response occurs in other species and due to other disturbance agents.

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