O P I N I O N
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Resprouting of herbs in disturbed habitats: is it adequately described by Bellingham–Sparrow's model?

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Severe disturbances may result in a partial or complete removal of above-ground parts of plants. This is usually followed by establishment of new populations from seeds, either persisting in the seed bank or imported from the outside. Alternatively, vegetative resprouting from plant organs surviving the disturbance may ensure development of the plant cover. The later process has received relatively little attention so far. However, its role in re-establishment of severely disturbed vegetation has been recently considered by several authors (Noble and Slatyer 1980, Walker and Chapin 1987, Fahrig et al. 1994, Bond and Midgley 2001, Dietz et al. 2002). The dominant role of resprouting (= vegetative regeneration) in vegetation establishment on severely disturbed sites has been appreciated by authors dealing with a single life form (woody plants; Bell 2001, Del Tredici 2001) or studying response of vegetation to disturbance within a plant community (weeds on arable land, water plants communities; Wehsarg 1954, Barrat-Segretain et al. 1998, Combroux et al. 2001). A broader concept covering plant regeneration across several environments and plant groups is so far missing. A promising step forward was made by Bellingham and Sparrow (2000; referred to henceforth as B&S) who developed a graphic model showing frequency distribution of resprouting plants along gradients of disturbance frequency and severity. They found that this distribution is unimodal. According to their model species with a resprouting strategy (i.e. preferentially investing their resources into storage of assimilates and into a bud bank and resprouting after a disturbance) are more abundant at intermediate severity and frequency of disturbance than plants with a seeding strategy (i.e. preferentially investing into seed production). The latter are favoured when disturbance is moderate and rare (trees) or strong and frequent (annuals). B&S discussed in their paper only woody plants and virtually all examples given concerned trees and shrubs. This resulted in a misunderstanding of their model by Pausas (2001) who applied it to woody plants only. However, the model by B&S does not preclude herbaceous plants (see their Fig. 3).

The question is whether the B&S model is indeed sufficient to explain the population dynamics of herbaceous plants under disturbance. We will approach this question by concentrating on herbaceous plants growing in areas with a seasonal climate, with which we have experience from previous work. We exclude aquatic plants because their resprouting is discussed elsewhere (Barrat-Segretain et al. 1998, Combroux et al. 2001) and herbs growing in areas with a non-seasonal climate, such as in the wet tropics.

We will argue that sprouting from roots or plant fragments should be added to the responses of plants to disturbance severity and that time of disturbance in relation to season and plant ontogeny should be added to better understand the responses of plants to disturbance frequency. In contrast to the B&S model we do not expect a definite preponderance of seeding strategy in habitats subjected to frequent and severe disturbance. We will show that under these conditions resprouting perennials may represent a successful growth form as well. Some annuals and biennials persist and resprout in such habitats, too, and, eventually, transform into perennials.

Response of plant individuals

Disturbance severity

B&S distinguished four levels of severity of disturbance for trees: loss of leaves (axillary resprouting), branches (branch epicormic), crown (stem epicormic) and trunk (basal). Besides resprouting from above-ground structures (B&S: Fig 2), some species are able to resprout from below-ground organs, such as roots, rhizomes or lignotubers (Jeník 1994, B&S: p. 410). Therefore, these plants may not only survive disturbances removing all above-ground biomass but even disturbances affecting the upper layer of the soil, such as fires or small land-slides (Gill 1995, Del Tredici 2001). Furthermore, resprouting from fragments of woody plants is also known in some species, but this has been rarely mentioned in the literature (but see Karasovskaya 1950, Gartner 1989, Sagers 1993).

Thus the B&S model (B&S: Fig. 2) can be extended by including resprouting from below-ground organs and from plant fragments (Fig. 1). This extended model is valid for various life forms of vascular plants, ranging from annuals through perennial herbs to woody plants. The relative placement of the bud bank along the vertical axis of the plant is similar in different life forms (Fig. 1). However, there are great differences in the proportion of buds situated at different layers below and above the soil surface, in the persistence of the buds, in the size and placement of carbon storage and in the proportion of species capable of resprouting after an intense or repeated disturbance. Perennial herbs may develop their regeneration buds both below- and above-ground in the same way as woody plants do (Fig. 1). However, their above-ground organs are usually annual and the bud bank developed on them is damaged during winter. In most perennial herbs, regeneration buds and storage are concentrated close to the soil surface or in the upper layer of the soil. Thus, perennial herbs usually easily resprout after a complete removal of their above-ground biomass. For example, meadow plants can be harvested up to several times a year without detrimental effect, if enough nutrients are available (see also Iwasa and Kubo 1997, B&S). For woody plants, a disturbance causing moderate damage is a loss of branches, whereas a strong disturbance, in which not all species are able to survive, is loss of the trunk. In perennial herbs, a similarly strong disturbance is caused when over-wintering organs are damaged. These organs usually develop in the upper soil layer, rarely deeper than 10 cm (Klimeš et al. 1997). If a disturbance reaches deeper soil levels, such as in arable land and on river sediments, most perennials fail to resprout because they lose their bud bank and stored assimilates needed for re-establishment of their photosynthetic tissue. In temperate floras only a small proportion of herbaceous plants is able to resprout from roots situated in deeper soil layers. For example, only about 300 species, i.e. less than 10% of herbaceous plants of the central European flora, belong to this group (Klimešová and Klimeš, unpubl.). The proportion of root-sprouters seems to be higher among trees; Del Tredici (2001), for instance, estimated that 31% of North American tree species belong to root-sprouters.

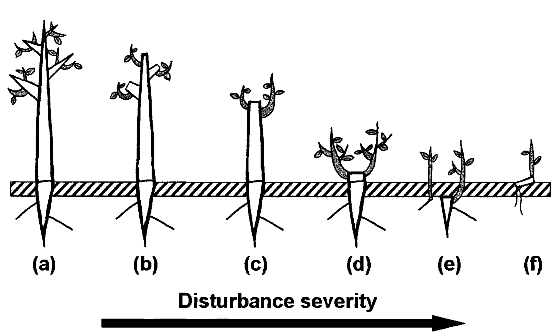

Fig. 1. A model of the effect of increasing disturbance severity on resprouting in vascular plants with modular structure growing in areas with a seasonal climate, applicable to all terrestrial life forms. (a) defoliation, (b) loss of branches, (c) decapitation (in trees loss of the crown, in herbs loss of the apical meristem), (d) complete loss of the above-ground stem, (e) loss of above-ground and part of below-ground organs, (f) fragmentation. Resprouted organs are shadowed. The upper soil layer where over-wintering organs of stem origin bearing buds are concentrated is hatched.

Due to root-sprouting some perennial herbs belong to the most noxious weeds common on arable land, such as *Cirsium arvense* and *Sonchus arvensis* (Kutschera 1960). Another successful strategy in habitats that are often disturbed below-ground is resprouting from fragments of the injured plant or from organs specialised for vegetative multiplication. Examples include weedy plants, such as *Cirsium arvense* which resprouts from small fragments of below-ground stems and roots (Hamdoun 1972), *Allium vineale* which multiplies by bulbils (Lazebny 1960) and *Cyperus esculentus* which produces a large number of tubers on its rhizomes (van Groenendael and Habekotte 1988, Habekotte and van Groenendael 1988).

A special life history strategy, not mentioned by B&S, is represented by monocarpic perennials in which vegetative growth, taking one to many years, is followed by a single event of generative reproduction, after which the plant dies. In some areas, such as central Europe, monocarpic perennials are well represented in early successional stages (Prach et al. 1997) and in habitats disturbed relatively frequently and severely. The relative vertical distribution of their bud bank is similar to that of trees. The probability of being disturbed at the vegetative stage is high in these plants because this stage represent a larger part of their life cycle. Therefore, disturbance is a factor affecting monocarpic perennials more strongly than annuals which remain vegetative for a relatively short part of their life cycle. Thus, it should not be surprising that, out of the relatively small number of perennial monocarpic plants, a high percentage are regular or occasional root-sprouters. For example, about 250 species are monocarpic perennials in central Europe (Krumbiegel 1999) and 14% of them are root-sprouters (Klimešová 2003). This is much more than the proportion of root-sprouters among annuals (see below).

Annuals, according to B&S, are typical representatives of plants with a seeding strategy, with regenerating buds distributed along the vertical axis of the plant similar to trees or perennial herbs (Fig. 1). However, they differ in the size and persistence of their vegetative organs. Annuals have a small bud bank and do not need to invest into storage of assimilates. In most annual species regenerating buds are not significantly concentrated at the soil surface (Krumbiegel 1998) and the proportion of annuals resprouting from roots is generally small (in Central Europe about 2%, for example; Klimešová 2003). In spite of that, there are annuals capable of resprouting even after a strong disturbance. In plant assemblages consisting of just annuals, we may distinguish species with seeding and resprouting tendencies in the same way as among perennials.

Disturbance frequency

According to B&S, the proportion of plants with seeding and resprouting strategies at a site are affected by productivity, competition, selection, gene flow and disturbance predictability. We suggest that timing of disturbance is another factor which should be considered. In a seasonal climate perennials build up carbon storage not only for resprouting after a disturbance, as simplified by Iwasa and Kubo (1997), but also for spring regrowth. Carbon storage and bud bank size therefore vary through a year, reaching their minimum in spring and maximum in autumn (Fonda and Bliss 1966, Masuzawa and Hogetsu 1977). Timing of disturbance may affect resprouting capacity of herbaceous plants because the initial stages of regeneration are largely dependent on the amount of the accumulated reserves (Leakey et al. 1977). An extreme example is pseudo-annuals which die in winter, except for an over-wintering tuber or rhizome fragment. After the storage organ is exhausted during the spring regrowth, the over-wintering organ dies. In autumn a new storage organ develops, which over-winters (Suzuki and Stuefer 1999). For example, *Trientalis europaea* produces storage tubers at the end of its long rhizomes. Rhizomes interconnecting tubers disintegrate in winter and new plants regrow in spring from apical buds. If an above-ground shoot is lost before new tubers develop, re-sprouting is not successful or regenerated plants are small and often fail to flower and set fruit (Piqueras 1999). Resprouting is affected by timing of disturbance in woody plants, too (Landhausser and Lieffers 2002, B&S and references therein).

B&S included only adult plants in their model. They did not consider younger individuals because immature plants lack generative structures. However, plants which behave as seeders and sprouters when adult may differ in their allocation to storage organs and in their ability to regenerate already when young. Examples have been reported from fire-prone ecosystems in south-western Australia (Bell 2001). In many temperate trees resprouting is more frequent in young plants than in adults and old plants belonging to the same species (Del Tredici 2001). Similarly, the capacity for pre-reproductive resprouting is higher than resprouting of flowering and fruiting plants in monocarpic perennials. Examples include *Brassica oleracea*, *Alliaria officinalis* (Dubard 1903), Oenothera biennis (Rauh 1937, Martínková et al. 2003) and *Barbarea vulgaris* (Kott 1963).

The difficulties with pre-reproductive plants in the B&S model are possibly partly caused by the definition of the seeding strategy. Even if the authors attempted to avoid a dichotomy between resprouting and seeding, seeding is considered the only alternative to resprouting. While resprouters can be defined as plants surviving a disturbance by a renewal of lost parts of their body from a bud bank utilising stored carbohydrates, the seeding strategy is delimited in the B&S model as an investment in the next generation. In fact, it follows from the B&S model that all plants which do not survive a disturbance are seeders. These are either species capable of persisting in a disturbed site due to seeds produced before the disturbance and stored in a seed bank, or species which are exterminated by the disturbance and lack a seed bank, but which re-colonise the site using diaspores produced in other populations. In our view, seeders should include all age categories of plants, including pre-reproductive individuals.

Implications for community response

In habitats with a highly predictable disturbance regime, such as on arable land, species using a single life-history schedule may prevail, such as winter annuals in winter wheat (Ellenberg 1986). This indicates that frequent disturbance is a strong selective factor. In frequently disturbed sites early flowering genotypes may be selected within a relatively short time (Mahn 1991). However, precipitous fruiting is favoured only if the timing of a disturbance is predictable. If the disturbance is delayed, in comparison with its usual timing, plants that postpone flowering and continue to grow acquire a competitive advantage (Law et al. 1977). In contrast, in irregularly disturbed sites, such as on river sediments, annuals and perennials often occur together (Ellenberg 1986). As these habitats are often disturbed early in the season before annuals form their generative organs, resprouting species are favoured. This concerns not only perennials, but also resprouting annuals and biennials which set fruit after resprouting and then die. In addition, a small group of plants with a plastic life cycle also colonises disturbed habitats. These plants behave as typical annuals or biennials using the seeding strategy when intact. However, after being damaged, they resprout and turn into polycarpic perennials (e.g. *Rorippa palustris*, *Barbarea vulgaris*; Rauh 1937, Kott 1963, Klimešová 2003).

Annuals usually prevail in disturbed habitats because their growth rate is higher than in perennials (Grime 2001). As they are often equipped for dispersal to longer distances (Crawley and May 1987), they can reach newly emerged sites created by disturbance faster than perennials. However, relative growth rate (RGR) values of seedlings may differ from RGR values of plants resprouting from a bud bank. This is an important difference that allows plant individuals of vegetative origin to play a significant role in disturbed sites. If disturbed patches are rather small, they can be reached by clonal plants with long stolons and rhizomes as fast as by plants spreading by seeds (Fahrig et al. 1994). They may also resproute from a bud bank already present at the time of the disturbance (Walker and Chapin 1987). We may therefore expect that Loehle's (2000) notion about sprouting trees ("such sprouts have tremendous advantage in growth rate over seedlings because of stored starch reserves and an existing root system.") is equally valid for herbaceous plants. The few studies dealing with this topic published so far seem to confirm this (Fahrig et al. 1994).

The idea that, in frequently and severely disturbed habitats, seeding strategy prevails over resprouting strategy implies that resprouting is negligible in herbaceous plants. Detailed information concerning root-sprouting in disturbed environments is readily available for a few species (Dietz et al. 2002 and references therein) but it has been largely overlooked. This means that, in studies focused on disturbed plant communities, only plant traits concerning generative regeneration are usually utilised (McIntyre et al. 1995, Lavorel et al. 1997, 1999, Schippers et al. 2001). A similar situation has been recently reported in research on woody plants by Bond and Midgley (2001). However, trees have several advantages for this type of research, such as a lower number of species (except for the tropics), better differentiated plant morphology and persistence of re-iterated structures over many years or decades after a disturbance. Therefore, resprouting of woody plants has attracted more attention than that of herbs.

A model of individual response to disturbance was developed by Noble and Slatyer already in 1980 and is still frequently cited. However, to test it a large set of input data is required, which is not easily obtainable for species-rich herbaceous communities. Thus, the model by Noble and Slatyer (1980) has rarely been explicitly tested in herbaceous vegetation. Further progress can be achieved if a bud bank concept is developed (similar to that of a seed bank) and comparative data on types of bud banks are obtained. For some groups of plants such surveys are already available, e.g. for weeds on arable land (Korsmo 1930, Wehsarg 1954) and for aquatic macrophytes (Willby et al. 2000), which show the importance of bud banks on roots and plant fragments, respectively. In the future more attention should be paid to plants in naturally disturbed terrestrial habitats, such as river beds, screes and land-slide prone areas, where resprouting plays a prominent role in numerous plant species. If we know more about resprouting of plants from roots and plant fragments, the two modes of resprouting which we added to the B&S model should improve our understanding of vegetation dynamics affected by severe disturbance.

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