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Early successional changes after land abandonment: the need for research

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SUMMARY - Land abandonment implies a process of ecological succession, in which vegetation reoccupies former farm land. Research in southern Britain gives examples of areas requiring special attention if we are to design effective methods to manage biotic change on abandoned land to desired end points. The sources of species for colonization are of key importance. Reseach has suggested that dispersal is a random process from neighboring patches. These processes result in a high species diversity relatively early in succession but the specific level is a function of many factors internal and external to the field. Much more research is required before we can predict these patterns. Relatively little is known about animal-plant interactions in succession. While animal diversity may be correlated with plant diversity, hervibory by specific animal groups may shift the relative importance of the plant species in vegetation. Much more research is required on these processes.

Key words: sucession, Britain, plant diversity, patches, hervibory, colonization.

RESUME - "Changements précoces dans la succession après l'abandon des terres: le besoin d'une plus grande recherche". L'abandon des terres implique un processus de succession écologique, au cours duquel la végétation revient occuper ce qui était auparavant une terre agricole. La recherche qui s'est développée dans les régions du Sud de la Grande-Bretagne nous montre des zones à étudier attentivement afin de mettre au point une méthode efficace pour que les modifications biotiques débouchent sur le résultat souhaité dans les terres abandonnées. La provenance des espèces destinées à la recolonisation est de la plus grande importance. Selon les recherches effectuées, la dispersion serait un processus aléatoire dont les points de départ seraient les petits terrains environnants. Ces processus débouchent sur une grande diversité des espèces assez tôt dans l'ordre de succession, mais leur distribution individuelle est fonction de plusieurs facteurs extérieurs ou inhérents à cet endroit. Avant d'être en mesure de prévoir ces processus, il faudra effectuer encore de nombreuses recherches. Nous ne connaissons pas profondément les interactions animal-plante lors de cette succession. Bien que la diversité des espèces animales puisse être corrélée à la diversité des plantes, des groupes spécifiques d'animaux herbivores peuvent faire varier l'importance relative des espèces de plantes dans la végétation. Nous devons donc continuer la recherche sur ces aspects.

Mots-clés: Succession, Grande-Bretagne, diversité végétale, taches de végétation, herbivore, colonisation.

Introduction

Succession is such a conspicuous and commonly documented ecological process, that it is tempting to think our knowledge of the subject is adequate. Even when Clements seminal work was published in 1916, he was able to cite over 1000 references, mainly in the form of descriptions of the sequence of plant species in primary or secondary successions in various geographical regions. Since then, there has been an ever-growing literature on the subject and the introduction of a more mechanistic approach. However, the majority of detailed studies have been based on old field successions in the eastern United States (e.g. Bard, 1952) and, consequently, focus on successions in established swards. What is noticeably lacking is an understanding of the patterns and processes involved in early succession (but see Brown and Southwood, 1987). This gap is both surprising and significant, since the initial stages of colonisation of land are often crucial to the pattern of succession (e.g. Egler, 1954) and the 'fine-tuning' of these, by appropriate management, can greatly modify the direction and rate of successional change (Gibson and Brown, in press a). It is therefore particularly pertinent to the ecology of abandoned land.

A management strategy for abandoned land must include appreciation of plant-soil, plant-plant and plant-animal interactions. While the two former interactions have been the subject of extensive work by agronomists and plant ecologists (e.g. Lloyd and Pigott, 1967; Grace and Tillman, 1990), especially in mature communities, the characteristic features of the latter have seldom been considered. If the opportunities presented by land abandonment, in terms of the creation of new landscapes and conservation, are to be fully realised, there is a vital need for more emphasis and more research on early succession. While current knowledge may be sufficient for ecologists to predict general trends, it is unlikely to enable them to maximise species diversity or to enhance such habitats for rare species.

The aim of this paper is to highlight areas which deserve special consideration and where research effort is particularly needed. The paper will draw heavily on examples from work currently being undertaken in southern Britain, since this was especially designed to investigate early successional changes in plants and animals after abandonment from agriculture. These examples are intended only as pointers to the type of research needed and to the nature of the results which may be expected. Ultimately, the aim is to establish generalisations about early succession, based on a sound scientific framework, which can then be disseminated to those involved in the management of abandoned land. In this paper, four ecological research goals will be addressed:

1. Sources for colonisation
2. Patterns of early successional vegetation
3. Implications for the fauna
4. Effects of invertebrate herbivory

Experimental field sites

The two experimental sites are on ex-arable land. One is on acidic, sandy soil at Silwood Park, Berkshire, which had previously been under a rotation of winter wheat, field beans and Brussels sprouts. Here, the experiments began on vegetation establishing on bare ground (see Southwood *et al.,* 1979; Brown and Gange, 1989a). Each year since 1977, a new experimental succession has been established to provide estimates of temporal variation. The other experimental site at Wytham, Oxfordshire, is on shallow soil overlying Jurassic corallian limestone which had been under cereal cultivation since 1960. The site was regularly cultivated until 1981 when a crop of winter wheat was sown, but not harvested. The succession was in its fourth year when the experiment began in 1985. This experiment incorporates different sheep grazing regimes to demonstrate how early succession can be modified or manipulated by management.

Thus, the emphasis of this work is on land abandonment following arable cultivation rather than the abandonment of permanent pasture. The research initiatives outlined in this paper will therefore be mainly pertinent to this type of change in land use.

The research goals

1. Sources for colonisation

It is generally accepted that land which has been under agriculture for some years has an impoverished seed bank (Chancellor, 1986). Moreover, seeds present are likely to be those of ruderal annual species, often agricultural weeds. The more desirable perennial forb (non-graminaceous) species are notably lacking because they tend to form less persistent seed banks (Graham and Hutchings, 1988). The depletion in the size of the seed bank with time and the preponderance of annual forbs can be demonstrated by germination trials comparing soil from agricultural land, ploughed each year following crop growth, and soil from permanent pasture. In two adjacent field sites at Silwood Park, Stinson (1983) recorded 579 seedlings of which 61% were annual forbs and 16% perennial forbs from 785 cm of arable soil, whereas only 254 were recorded from the same volume of pasture soil, with similar proportions of annuals and perennials. The greater potential for the colonisation by annual species, including pernicious weeds, after soil disturbance is a major problem in habitat restoration programmes (Graham and Hutchings, 1988; Gibson and Brown, in press b).

In view of the poor seed bank of perennial forbs commonly associated with abandoned land, the immigration of 'new' species is dependent on source pools of established vegetation to provide propagules. The process of immigration tends to be slow and stochastic (Gibson and Brown, in press a, b). In the Wytham experiment, seven years after abandonment, 246 plant species had colonised the experimental field, including 77 species characteristic of ancient grassland. Of these, only one (*Sanguisorba minor*) was from the resident seed bank (Woodell and Steel, 1990). Of the more widely occurring calcicolous species, 24 arrived from the seed bank together with 73 other species. However, even after eight years colonisation, one hundred species from the potential species pool had not appeared in the experimental field. Generally, it was the stress tolerators (*sensu* Grime *et al.,* 1988) which were absent (Graham and Hutchings, 1988; Gibson and Brown, in press a). From this work, it was concluded that species dispersing into the field were the result of a random draw of species from adjacent patches of ancient grassland and were not related to specific life-history traits (see Grime *et al.,* 1988), dispersule form or weight or habitat association. Their dispersal and establishment is probably governed by heterogeneity within the species pool and by abiotic and biotic conditions in the site (see later).

Species diversity is, *inter alia,* the result of the species turnover rate (i.e. the balance between immigration and extinction). Species turnover can be greatly modified by management. For example in the Wytham study, sheep grazing increased both establishment and extinction rates (Gibson and Brown, in press a). This operated mainly through gap formation (by the creation of microsites for seed germination (Watt and Gibson, 1988). The effect was maintained far longer by more extensive grazing, but excessive grazing eventually lowered diversity (Gibson and Brown, in press a, b).

The relative importance of the two sources of potential immigrants into newly-abandoned areas is therefore of key importance and there is much scope for qualitative observations, but particularly for field experiments. The implications of management on these two processes also need to be assessed.

2. Patterns of early successional vegetation

Generally, early succession is characterised by a flush of ruderal, annual species (mainly forbs), followed by other annuals and short-lived perennials. The establishment of perennial forbs and grasses usually coincides with the extinction of the ruderals (e.g. Brown and Southwood, 1987). Such a trend commonly leads to maximum diversity early in succession, at a time when some annual species persist but perennials are establishing (Tramer, 1975). The timing of these changes varies from succession to succession (e.g. Hendrix *et al.*, 1988), although the general pattern is consistent.

Climate, soil type and previous land history all impact considerably on the patterns of colonisation. The influence of land history on the seed bank has already been stressed. In addition, the former use of the land may result in high variability in organic and nutrient content. For example, the nutrient content of ex-arable land is generally high (Gough and Marrs, 1990) and this will greatly affect the species composition. For example, when early colonisation took place on unfertilised soil at Silwood Park, corn spurrey, *Spergula arvensis,* was the dominant species with a cover abundance of 60%. The addition of a single application of fertiliser (NPK) completely changed the species composition and scentless may weed, *Tripleurospermum inodorum*, became dominant with a cover abundance of over 60%. Generally, the lower the nutrient levels, the more forb rich the species composition, since high nutrient levels promote the growth of the vigorous grasses which out-compete the forbs (Bakker, 1987). Restoration programmes therefore often recommend the use of cereal crops to lower soil fertility (Marrs and Gough, 1989).

Recently, the role and significance of mycorrhizas in early succession have been highlighted (e.g. Miller, 1987). It has generally been considered that early successional plant species are either mycorrhizal or facultatively mycorrhizal (Janos, 1980). However, examination of the ruderal plant community at Silwood Park has shown several common species are highly mycorrhizal. Indeed, if mycorrhizal infection is reduced by the application of fungicide, the plant community has a lower species richness and vegetation cover (Gange *et al.*, 1990). The importance of mycorrhizas in the nutrient uptake and water relations of plants is suggestive of their significance in early succession. This is an area where more work is needed.

The timing of abandonment during the season modifies the pattern of early succession. This was illustrated at Silwood Park, when successions on bare soil were begun in March and July. The species richness, composition, vegetation cover and grass: forb index were very different in the two successions. Indeed, certain species only occurred in one of the successions. For example, redshank, *Polygonum persicaria,* and pale persicaria, *P. lapathifolium,* were very common in the succession begun in March, but were absent in the later succession. Obviously, the seed germination biology is a key factor (Grime *et al.,* 1981).

Even greater variation can result from year to year variation. This is simply demonstrated by the dramatic difference found between successions created in 1977 and 1978 at Silwood Park on adjacent plots of land (with similar land history and seed bank). In the former, by 1990, there were trees (*Betula pendula, Quercus robur, Pinus sylvestris*) up to 4 m high. In the site created just one year later, there were no trees. The likely explanation for this rests with the drought of 1976, which decreased the seed bank and also the invertebrate herbivores (mainly molluscs). Thus, tree seeds which germinated became established seedlings without the usual severe competition from herbaceous species or extensive damage by invertebrate herbivores. Once above the herb canopy, the growth of the woody species was unchecked. The summer of 1977 was far wetter and these limiting factors did not apply.

There is, therefore, considerable plasticity in the species composition of early successional vegetation as a result of previous land use, seasonal and annual fluctuations. Ample scope exists for research in this area and highlights the need for field experiments well replicated in both space and time.

3. Implications for the fauna

During early succession, Southwood *et al.,* (1979) demonstrated that the diversity of the invertebrate fauna closely tracked that of the plants. Thus, ways of maximising plant species diversity will have significant implications for the associated fauna. More especially forb species often have specialist species (mainly insects) associated with them. Many of these, such as the Lepidoptera, are of high conservation value. In this context, the importance of appropriate management is paramount. The effects of reducing sward height by defoliation or cutting can have dramatic effects on the species richness and composition of the fauna (Morris, 1971), even in early succession (Brown *et al.*, 1990). Many insect groups are affected by vegetation structure and/or composition. For example, the parasitic dipteran family, Tachinidae, are attracted to the wide range of flowering annuals of early succession (R. Belshaw, pers. comm.). Leaf miner species are influenced by plant species composition, host-plant structure, phenology and leaf size. All of these change markedly during the early years of succession and are much affected by management (Brown *et al.*, 1990).

The same general principles apply to many vertebrates. Churchfield and Brown (1987) have shown that small mammal populations can be extensive even in the very early stages of colonisation. Furthermore, small mammals interact with their habitat in a complex manner, both as primary consumers of vegetation and as secondary consumers of invertebrates. Likewise, some bird species are dependent on the high availability of seeds among the annual forbs (Middleton and Chitty, 1937; Murton *et al.*, 1964; Newton, 1967; Southwood *et al.*, 1986).

It is amongst the higher trophic levels that research is particularly needed. Not only do early successional habitats provide a vital (and sometimes unique) resource for certain species, these organisms can often cause unexpected, and sometimes undesirable, effects on the developing plant community. The next section provides an example.

4. Effects of invertebrate herbivory

The effects of vertebrate herbivory on abandoned land are easily demonstrated by fences or exclosures. Furthermore, the effects on the plant community often occur very rapidly and can be dramatic even when grazing is at low intensity (see Gibson and Brown, in press a). In the context of abandoned land, the effects of invertebrate herbivory have hitherto been ignored or considered insignificant. However recent work, mainly at Silwood Park, has demonstrated that insect herbivory, so clearly seen in the crop situation, can be an important determinant in the dynamics of developing plant communities (see Brown, 1985; Brown and Gange, 1989a, Brown, 1990). This work has centred on the use of long-term manipulative field experiments. These experiments have involved the judicious use of insecticides, to reduce natural levels of above- and below-ground herbivores, and the comparison of characteristics of the plant community with and without the effects of insect herbivores. Whereas a reduction in foliar herbivory enhanced the growth of perennial grasses, that of below-ground herbivory produced a high forb species richness and maintained a balance between the forbs and the grasses (Brown, 1989; Brown and Gange, 1989b). These findings have important implications for the management of abandoned land. Firstly, the promotion of perennial, vigorous-growing grasses such as common twitch, *Agropyron repens*, when foliar insecticide is applied highlights the potential danger of the use of such compounds, either directly or by drift, when a perennial forb rich vegetation is required. Secondly, the application of a soil insecticide at an early stage in colonisation enhances forb species richness at the expense of the perennial grasses. This is desirable for its visual effect and also for the large number of specialist insect species which rely on specific plant species as a source of food.

Conclusions

Current changes in land use have highlighted the need for greater understanding of the patterns and processes underlying colonisation and early succession. Despite a wealth of literature on succession, there are a surprisingly large number of questions still to be addressed. Many of these involve the complex interactions between plants and soil or plants and other organisms. Thus, an interdisciplinary approach is essential. The way forward should be: firstly, a synthesis of existing knowledge in the light of constraints imposed by abandoned land and its management and secondly, the targeting of specific research goals. In this paper, I have briefly considered only four such goals, all of which involve basic ecological research of an interdisciplinary nature. Research in these and similar areas should be based on field experiments, sometimes of a manipulative nature, well replicated in time and space. The extent of current land use change in Europe gives an unrivalled opportunity for collaborative research. Research projects in different habitat types and different geographical regions will lead to ecological generalisations. Such generalisations are essential if ecologists are to give advice on the selection of land to be abandoned and the management of such land to policy makers, planners, land managers and farmers.

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