The Circumstances and Characteristics of Spoil Colonization within a Local Flora [and Discussion]

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The circumstances and characteristics of spoil colonization within a local flora

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Information from a vegetation survey comprising all the major habitats of the Sheffield region in northern England has been examined to identify the plant species that have most effectively colonized spoil habitats. The most frequent components of spoil vegetation are perennial herbaceous species, many of which are grasses of widespread occurrence in the region as a whole. A distinctive group of colonists within the spoil flora consists of species that exploit substrates, such as cinders and lead-mine spoil, which are inhospitable to the majority of plants and of scattered occurrence in the landscape. These specialist colonizers are mainly uncommon dicotyledons; many are ephemerals and most depend upon efficient distribution by wind or by man's activities.

Published sources and data from laboratory screening experiments have been used in an attempt to recognize general characteristics of spoil colonizers. A high proportion are perennial plants of base-rich soils. The majority display the potential, as seedlings, for moderate to rapid rates of dry matter production and have 2*C* nuclear DNA amounts concentrated in the range 2.0–10.0 pg. Plants colonizing spoil tend to exhibit an extended flowering period and include many species with relatively small seeds, but they are widely divergent with respect to flowering season, breeding system, capacity for wind dispersal, dormancy of freshly collected seeds, seed bank characteristics and germination responses to temperature and irradiance.

It is concluded that the characteristics of spoil colonization in the Sheffield region are broadly consistent with the 'infection pressure' theory of Salisbury (1953, in *The changing flora of Britain* (ed. J. E. Lousley), pp. 130–139) and are but one symptom of massive changes occurring throughout the landscape under the impacts of disruptive land-use and eutrophication. These changes are predictable by reference to the C–S–R theory of primary plant strategies and to recent evidence relating strategy theory to patterns of ecological specialization and evolutionary advancement within the angiosperms.

INTRODUCTION

The journal *Watsonia* and the *Atlas of the British Flora* (Perring & Walters 1962) bear witness to an unrivalled British tradition of expert field botany and detailed description of plant distributions. As the following quotations from *The changing flora of Britain* (Lousley 1953) make clear, these long-established activities made it inevitable that plant taxonomists and ecologists working in Britain would recognize the widespread occurrence of species expansions and would be among the first to attempt to explain such phenomena in general terms.

> 'The British flora is not an event but a process, that is continuing both with respect to accretions and diminutions.' (Salisbury 1953)
>
> 'Quantitative changes in our flora are always going on, though of course, at varying rates; in trees they are slowest and in annuals most rapid.' (Tutin 1953)

> 'The two most important natural factors producing changes in our flora are evolution and altering climate, both very powerful and far-reaching but both slow-acting.' (Tutin 1953)
>
> '...changes in the plant population of open habitats has been in no small degree an accompaniment of man's activities which have created sanctuaries of reduced competitive pressure in areas where such might naturally be non-existent or rare.' (Salisbury 1953)
>
> '...it would appear that there has been a broad correspondence between the extent of communication between areas and the frequency of plant introductions from them, such that human agency may have been a prime factor in determining the time of arrival.' (Salisbury 1953)
>
> 'Perhaps the most interesting feature of the changes in our weed population has been the diverse manner in which these various species have spread.' (Salisbury 1953)
>
> '...all exhibited a slow rate of spread followed by a rapid one which I suggest is a phenomenon analogous to the "infection pressure' of epidemic disease. In each instance, the rapid spread followed upon local increase due to the artificial provision of suitable habitats.' (Salisbury 1953)

It is no accident that five of these quotations are from E. J. Salisbury. His work remains the outstanding contribution to the study of colonizing plants and two of his books, *The reproductive capacity of plants* (1942) and *Weeds and aliens* (1964) show a breadth of perspective and depth of penetration into mechanism which belie their deceptively homespun style and appearance.

Most studies of expanding plant ranges in the British flora have been autecological and have involved analysis of changing geographical distributions, either by direct observation over the long lifetime of the observer (Salisbury 1953, 1964) or by compiling historical records (see, for example, Salisbury 1932; Kent 1956, 1960, 1964*a*, *b*; Bangerter & Kent 1957, 1962; Davey 1961; Conolly 1977; Simpson 1984). The objective in this paper will be to complement the insights gained from such broad geographical studies by reference to a more quantitative and comparative study of plant colonization in one type of habitat within a regional flora in Northern England.

Attention will be confined to spoil habitats. This is not to suggest that colonization is restricted to this habitat; rapid expansions in plant ranges are also taking place in other parts of the landscape, particularly those subjects to disruptive patterns of land use (e.g. arable, paths, road verges, 'improved' pastures and plantations). Spoil habitats have been selected here in order to ensure that the vegetation studied is entirely the result of relatively recent processes of natural colonization of initially bare substrates.

SOURCES OF DATA

(*a*) *Vegetation survey*

The field data used in this paper are drawn from a vegetation survey conducted over the period 1968–74 (Grime *et al.* 1986) describing 2748 samples of herbaceous vegetation, distributed throughout an area of 2400 km^2 (figure 1). All major habitats, including those recently created by agriculture, industry and urban development, were sampled in each part of the survey area. In each vegetation sample the frequency of each vascular plant species was recorded within an area of one square metre and additional information relating to the site and its management was collected. The intensity of sampling was sufficient to allow a diagram to be drawn for each species describing its frequency of occurrence in each type of habitat (figure 2). The potential of such data to provide a basis for comparisons of colonizing ability is

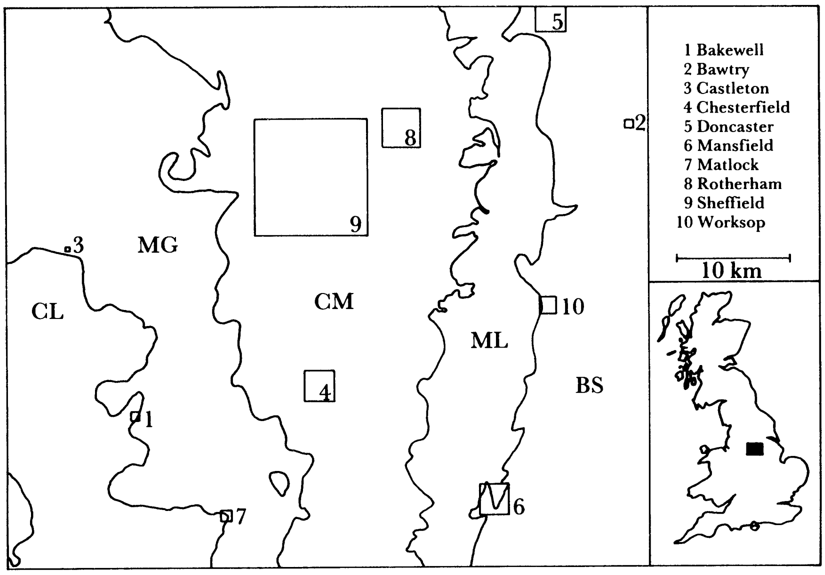
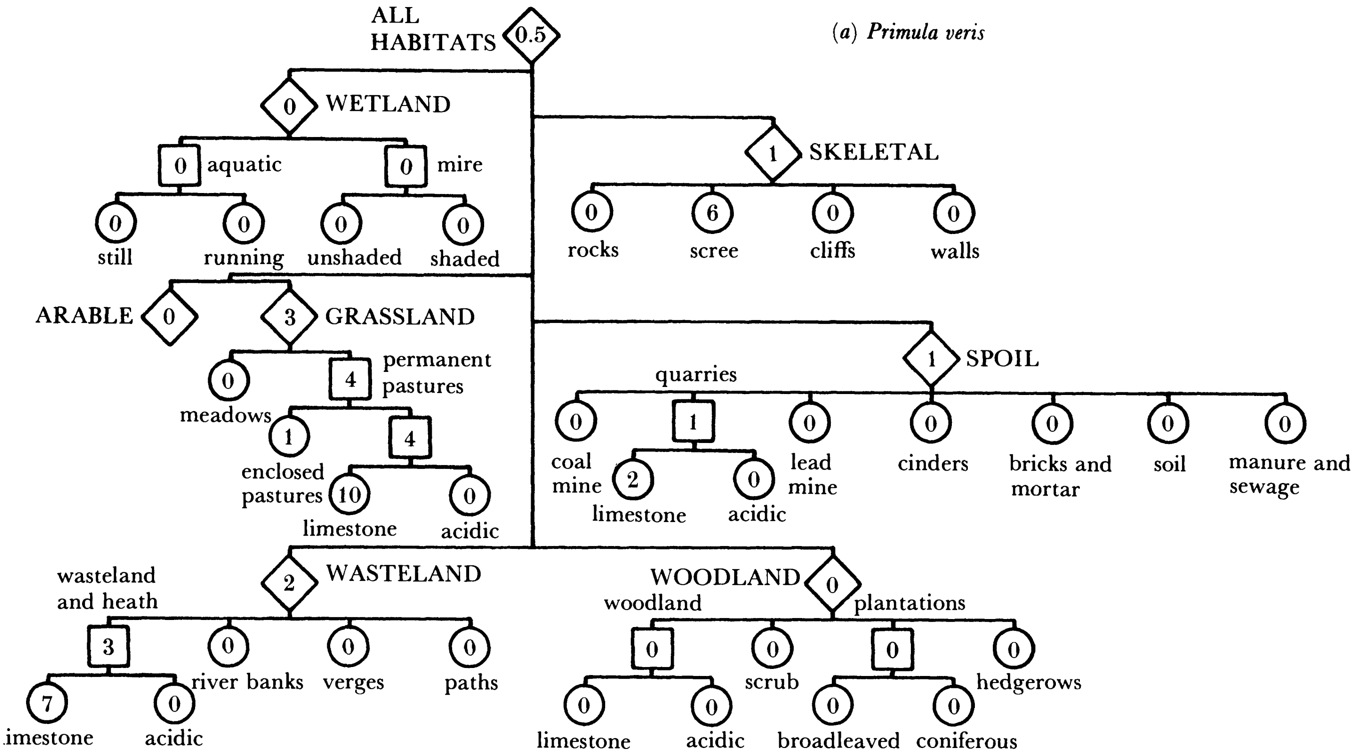


FIGURE 1. The survey area, showing major geological boundaries. The approximate extent of urban development is shown by squares. Key to geological formations: CL, Carboniferous Limestone; MG, Millstone Grit; CM, Coal Measures; ML, Magnesian Limestone; BS, Bunter Sandstone. The position of the survey area in Britain is shown by the inset.

immediately evident. In figure 2, a low capacity for spread is apparent in *Primula veris* and *Danthonia decumbens*, which have remained almost exclusively confined to habitats that are part of the more ancient countryside. In contrast, *Matricaria matricarioides* and *Chamerion angustifolium* have achieved high frequencies in several of the recent, man-made habitats grouped together under the general title of 'spoil' on the right-hand side of the habitat diagram.

(*b*) *Laboratory screening experiments*

To attempt to identify any distinctive features of colonizing species within the Sheffield flora, an effort has been made to compare the characteristics of groups of species broadly classified with respect to their capacity to colonize spoil habitats. Some of the information needed for these comparisons, such as the abundance of the species in the region as a whole or the affinity for soils of high pH, was available from the vegetation survey itself. Additional characteristics, such as life history, life-form and shoot morphology were obtained from published sources (e.g. Clapham *et al.* 1962). A further source of information was a series of large-scale laboratory screening procedures conducted in parallel with the vegetation survey, with the objective of compiling standardized comparative data on the physiological characteristics of the commoner flowering plants of the Sheffield region. In this paper, use will be made of screening data describing the relative growth rates of seedlings in productive conditions (Grime & Hunt 1975), measurements of the dormancy and response to temperature and irradiance of seeds (Grime *et al.* 1981) and estimates of nuclear DNA content here used as a predictor of minimum length of the cell cycle (Bennett 1971) and shoot phenology (Grime & Mowforth 1982; Grime 1983).



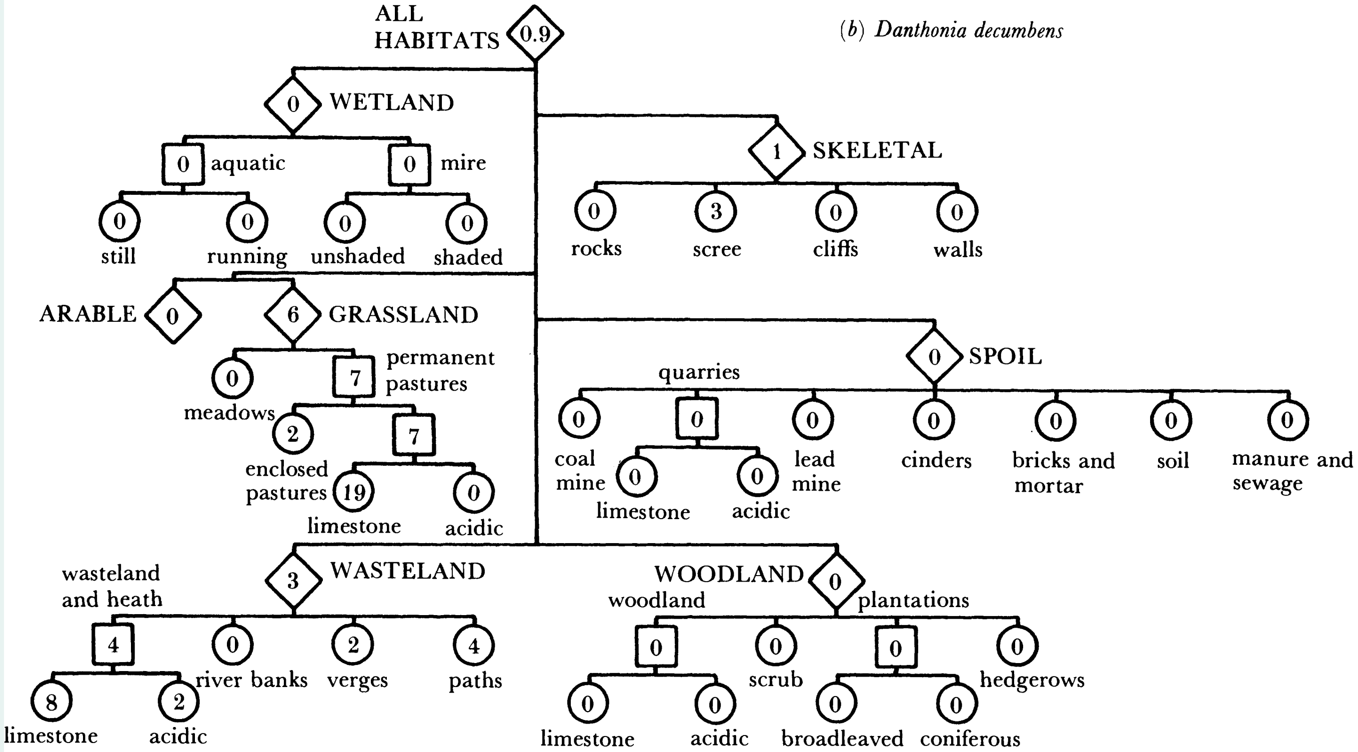


Figure 2a, b. For description see p. 642.

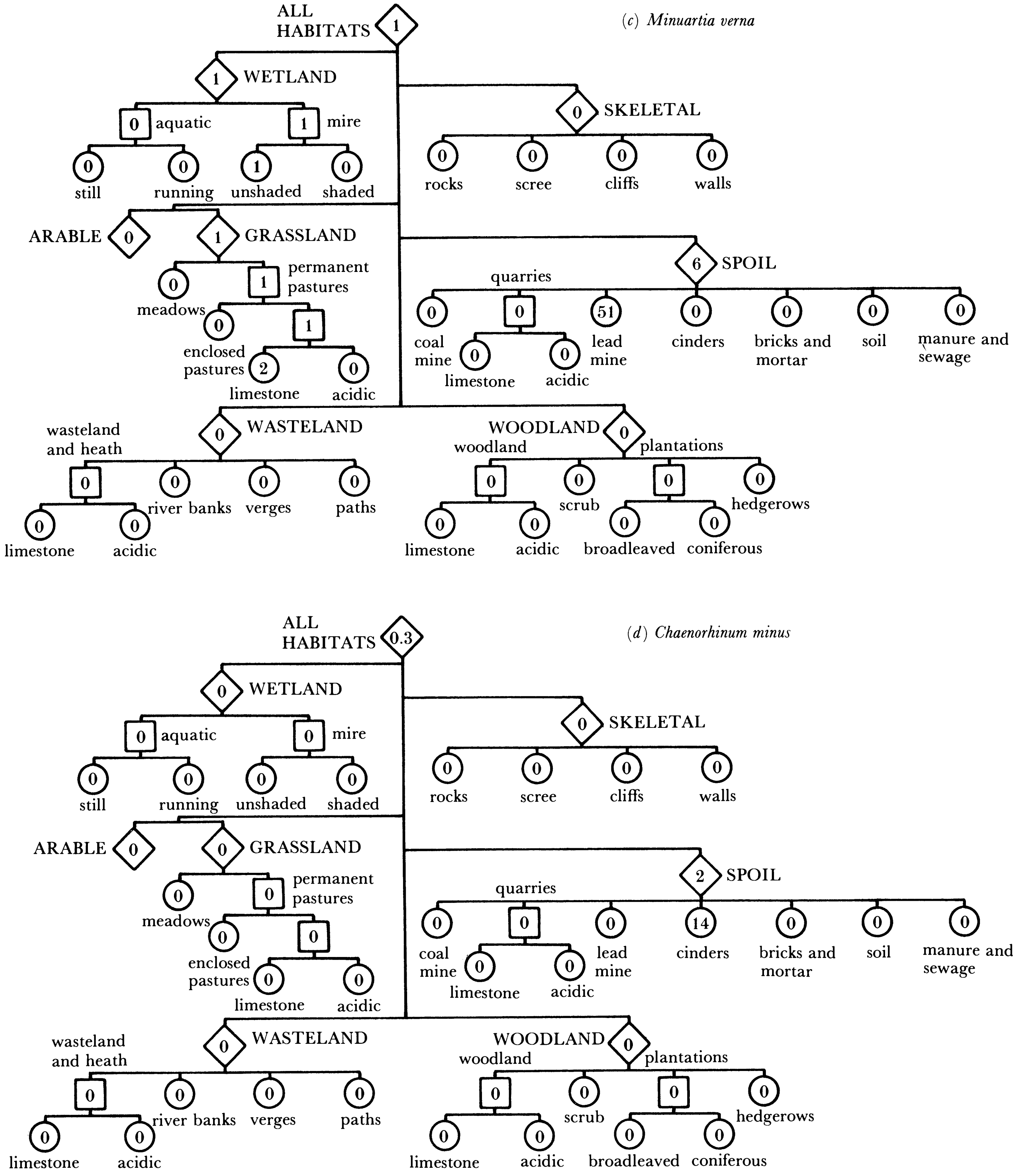
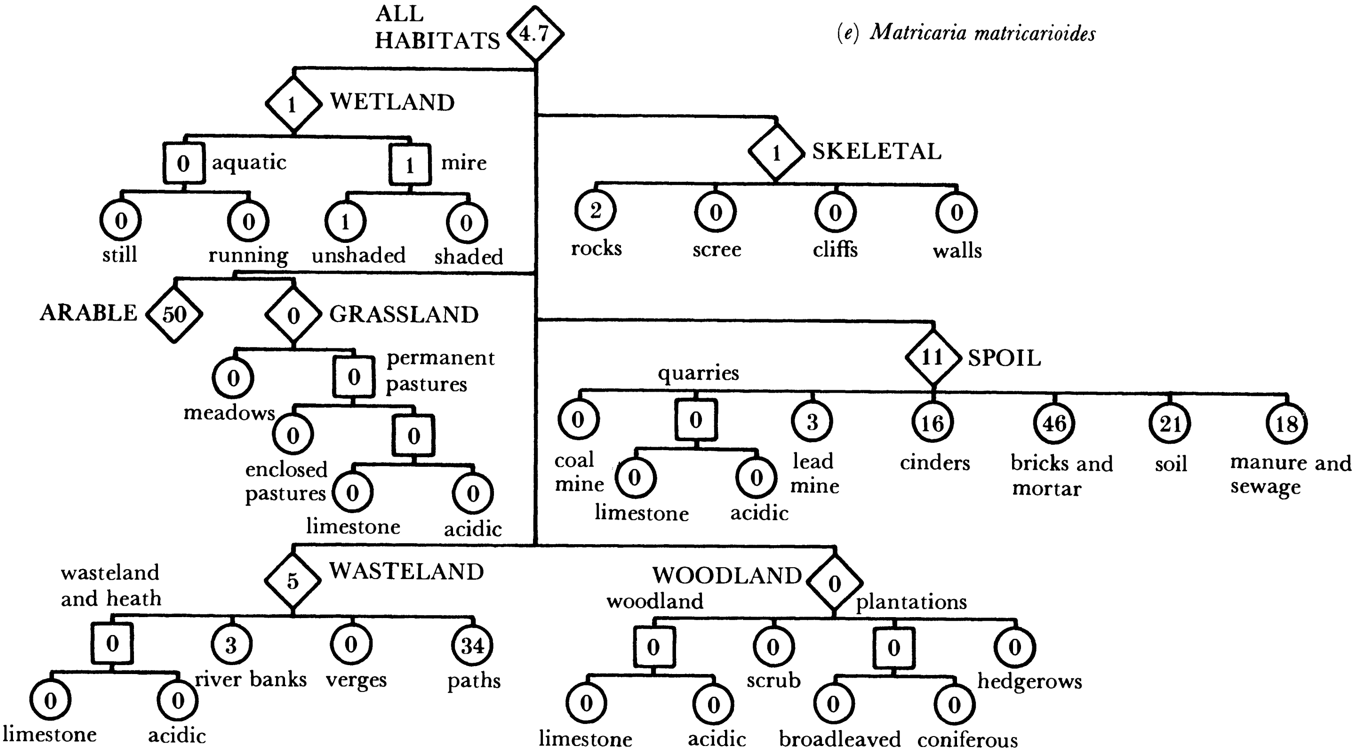
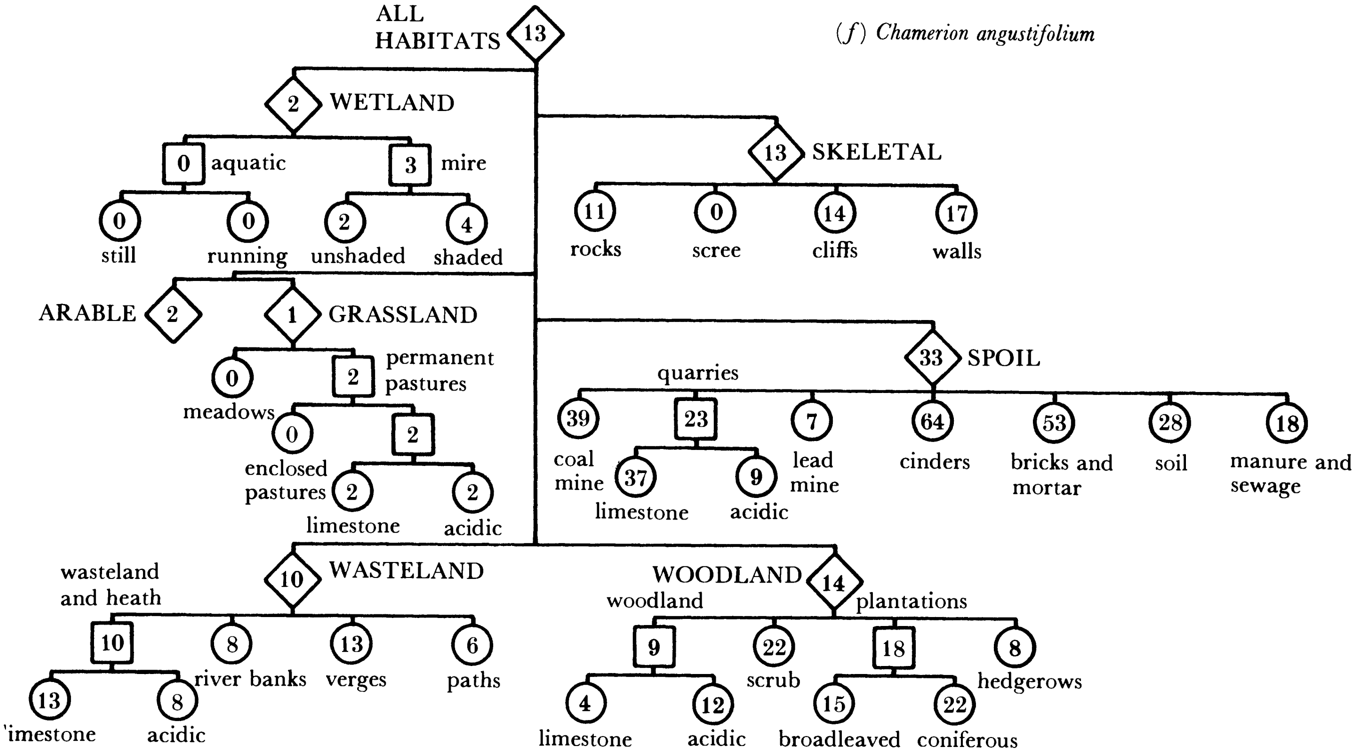


FIGURE 2*c*, *d*. For description see p. 642.



(*e*) *Matricaria matricarioides*



(*f*) *Chamerion angustifolium*

FIGURE 2. The frequency of occurrence of six herbaceous species in each of the major habitats of the Sheffield region. Values indicate the percentage of samples that contain the species.

Results

(*a*) *Species of high frequency of occurrence on spoil*

As a result of variation in the age, size, geographical location, soil properties, neighbouring vegetation and, not least, past and continuing impacts of man, spoil habitats and their plant communities vary considerably through time and space. Nevertheless it is instructive to identify the species that occur most frequently in spoil habitats as a whole and to review their characteristics. In table 1, the twenty most common vascular plants of spoil habitats in the Sheffield region are listed. With the exception of two species of *Senecio*, all are perennial, herbaceous plants and over half are grasses. Perhaps surprisingly, members of the Compositae make up as little as 25% of the list and the wind-dispersed category is represented by only six species. Also included in table 1 is an 'index of colonization', which expresses the frequency with which each species is recorded on spoil as a function of its frequency in the region as a whole. The index of colonization (CI) is calculated as:

Table 1. The 20 most common vascular plant species of spoil habitats in the Sheffield region

(*F*, percentage of spoil samples containing the species; CI, index of colonization; A, annual; P, perennial; G, grass; C, composite; W, wind-dispersed. The brackets for *Poa annua* denote the fact that annual and perennial phenotypes of this species occur in the Sheffield region.)

		F	CI	A	P	G	C	W
1.	*Holcus lanatus*	36.4	2.0	.	+	+	.	.
2.	*Chamerion angustifolium*	32.8	2.6	.	+	.	.	+
3.	*Agrostis stolonifera*	32.0	1.8	.	+	+	.	.
4.	*Dactylis glomerata*	29.4	1.6	.	+	+	.	.
5.	*Festuca rubra*	28.5	1.5	.	+	+	.	.
6.	*Agrostis capillaris*	26.0	1.4	.	+	+	.	.
7.	*Poa annua*	24.9	2.0	(+)	(+)	+	.	.
8.	*Poa pratensis*	24.8	1.7	.	+	+	.	.
9.	*Arrhenatherum elatius*	24.1	1.7	.	+	+	.	.
10.	*Poa trivialis*	23.5	1.1	.	+	+	.	.
11.	*Tussilago farfara*	23.5	4.1	.	+	.	+	+
12.	*Taraxacum officinale*	22.0	1.8	.	+	.	+	+
13.	*Deschampsia flexuosa*	18.3	0.9	.	+	+	.	.
14.	*Cerastium fontanum*	18.2	2.0	.	+	.	.	.
15.	*Plantago lanceolata*	17.3	1.8	.	+	.	.	.
16.	*Cirsium arvense*	16.1	2.4	.	+	.	+	+
17.	*Elymus repens*	14.4	1.6	.	+	+	.	.
18.	*Trifolium repens*	14.2	1.5	.	+	.	.	.
19.	*Senecio vulgaris*	14.2	3.6	+	.	.	+	+
20.	*Senecio squalidus*	13.7	4.2	+	.	.	+	+

$$\text{CI} = \frac{\text{percentage occurrence on spoil}}{\text{percentage occurrence in all habitats}}.$$

With the exception of the calcifuge grass *Deschampsia flexuosa*, all of the species listed in table 1 have CI values greater than 1.0, indicating their capacity for differential population expansion in at least some spoil habitats. However, since most of the CI values fall below 3.0, it is quite clear that the commonest species on spoil are plants of high abundance in the region as a whole. It is worthy of note that high CI values are conspicuous among the five composites.

(*b*) *Species with a high index of colonization*

An index of colonization of spoil habitats was calculated for each of the 282 species that were recorded in more than 0.25% of the samples of the vegetation survey. In table 2, the species with the highest colonization indices are identified. These species provide a marked contrast with those listed in table 1. With the exceptions of *Senecio squalidus*, *Senecio vulgaris* and *Tussilago farfara*, none of these plants is of common occurrence on spoil nor within the vegetation survey as a whole. Only one grass, *Desmazeria rigida*, is represented and over half the species are members of the Compositae. Twelve of the twenty species in table 2 are annual plants and the same number have an efficient mechanism of dispersal by wind. Close inspection of the ecology of the species in table 2 reveals that many are specialists exploiting particular types of spoil. This is exemplified in figure 2 by *Chaenorhinum minus*, a species of cinder tips and railway ballast, and *Minuartia verna*, which is virtually confined to the spoil heaps of disused lead workings. Further examples are *Senecio viscosus* and *Linaria vulgaris*, both associated with cinders, *Erigeron acer* and *Desmazeria rigida* (limestone quarry debris) and *Chenopodium rubrum* (manure heaps and sewage waste).

TABLE 2. THE 20 VASCULAR PLANT SPECIES ATTAINING THE HIGHEST INDICES OF COLONIZATION IN SPOIL HABITATS OF THE SHEFFIELD REGION

(CI, index of colonization; *F*, percentage of spoil samples containing the species; A, annual; P, perennial, G, grass; C, composite; W, wind-dispersed.)

		CI	*F*	A	P	G	C	W
1.	*Chaenorhinum minus*	6.3	1.9	+	.	.	.	+
2.	*Senecio viscosus*	5.5	5.5	+	.	.	+	+
3.	*Minuartia verna*	5.3	5.3	.	+	.	.	.
4.	*Linaria vulgaris*	4.9	3.4	.	+	.	.	+
5.	*Sonchus asper*	4.9	3.4	+	.	.	+	+
6.	*Erigeron acer*	4.6	2.3	+	.	.	+	+
7.	*Chenopodium rubrum*	4.3	3.0	+	.	.	.	.
8.	*Desmazeria rigida*	4.3	1.7	+	.	+	.	.
9.	*Atriplex prostrata*	4.2	5.5	+	.	.	.	.
10.	*Senecio squalidus*	4.2	13.7	+	.	.	+	+
11.	*Tussilago farfara*	4.1	23.5	.	+	.	+	+
12.	*Crepis capillaris*	3.9	7.8	+	.	.	+	+
13.	*Artemisia vulgaris*	3.8	9.1	.	+	.	+	.
14.	*Senecio vulgaris*	3.6	14.2	+	.	.	+	+
15.	*Solidago virgaurea*	3.5	2.1	.	+	.	+	+
16.	*Artemisia absinthium*	3.4	1.7	.	+	.	+	.
17.	*Cardamine hirsuta*	3.4	2.7	+	.	.	.	.
18.	*Epilobium ciliatum*	3.3	5.2	.	+	.	.	+
19.	*Tripleurospermum inodorum*	3.1	7.8	+	.	.	+	.
20.	*Reynoutria japonica*	3.0	0.6	.	+	.	.	+

(*c*) *The relation between frequency in the region as a whole and ability to colonize spoil habitats*

In table 3, all the species present in more than 0.25% of the survey samples have been separated into classes reflecting their frequency in the Sheffield region; the ability of each class to colonize spoil has been examined by means of the index of colonization. As we might expect from the pattern already detected in table 1, a significantly ($p < 0.05$) higher proportion of the species in the highest frequency class have an index of colonization exceeding 1.0. A

Table 3. A comparison of spoil colonization by vascular plant species classified with respect to their frequency of occurrence in the Sheffield region

(Statistical significance of results, tested by χ^2, indicated in tables 3–13 by standard conventions: **, $p < 0.01$; *, $p < 0.05$; (*). $p < 0.1$; n.s., not significant.)

frequency (%) in Sheffield region (all habitats)	index of colonization < 1.0	⩾ 1.0	
< 1.0	55	42	n.s.
1.0–1.9	53	20	*
2.0–3.9	27	26	n.s.
> 3.9	19	40	*
all species	154	128	

smaller proportion of spoil colonists is evident among the less frequent species, but this relation is clearly not a simple one in that the lowest frequency class contains a considerable number of colonists. The explanation for this is to be found in table 2, which shows that many of the specialist spoil colonizers are relatively uncommon plants.

(*d*) *Edaphic tolerance and spoil colonization*

The spoil habitats of the Sheffield region provide an extraordinary array of substrates, including those that are highly acidic (gritstone quarries and coal-mine heaps), calcareous (limestone quarry heaps and lead-mine spoil) or with pH values exceeding 8.0 (brick and mortar rubble). In table 4, most of the commoner species of the region have been classified with respect to the mode of their soil pH ranges and the proportion of colonizing species has been calculated for each class. The results show that although spoil colonists include both calcicoles and calcifuges, a significantly higher proportion are plants associated with soils of high base status.

Table 4. A comparison of spoil colonization by vascular plant species classified with respect to the mode of their soil pH distributions

(Soil pH determinations are based upon samples at field capacity taken from the 0–30 mm zone of the soil profile.)

mode of soil pH range	index of colonization < 1.0	⩾ 1.0	
< 6.0	59	24	*
6.0–6.9	63	45	n.s.
> 6.9	22	59	**
all species	144	128	

(*e*) *Relation of plant size, life-history and life-form to spoil colonization*

Table 5 reveals no general relations between plant size, as indicated by the maximum height attained by the leaf canopy, and capacity to colonize spoil habitats. From table 6, however, it is clear that, although the majority of spoil colonists are polycarpic perennials, a significantly higher proportion of the common ephemerals of monocarpic perennials of the region have indices of colonization exceeding 1.0. When the same species are classified with respect to life-form (Raunkiaer 1934) no distinctive pattern is established except that therophytes are shown to include a significantly enlarged proportion of spoil colonists (table 7).

TABLE 5. A COMPARISON OF SPOIL COLONIZATION BY VASCULAR PLANT SPECIES CLASSIFIED WITH RESPECT TO THE HEIGHT OF THE LEAF CANOPY OF THE ESTABLISHED PLANT

height of leaf canopy	index of colonization	
mm	< 1.0	⩾ 1.0
< 250	35	42 n.s.
260–500	31	24 n.s.
510–750	32	31 n.s.
> 750	17	16 n.s.
all species	115	113

TABLE 6. A COMPARISON OF SPOIL COLONIZATION BY VASCULAR PLANT SPECIES CLASSIFIED WITH RESPECT TO LIFE HISTORY

	index of colonization	
life history	< 1.0	⩾ 1.0
ephemeral or monocarpic perennial	18	47 **
polycarpic perennial	126	81 n.s.
all species	144	128

TABLE 7. A COMPARISON OF SPOIL COLONIZATION BY VASCULAR PLANT SPECIES CLASSIFIED WITH RESPECT TO LIFE-FORM

life-form	index of colonization	
(Raunkiaer)	< 1.0	⩾ 1.0
therophytes	13	41 **
geophytes	12	4 n.s.
hemicryptophytes	104	65 n.s.
chamaephytes	8	10 n.s.
phanerophytes	8	8 n.s.
all species	145	128

(*f*) *Seedling relative growth rate and spoil colonization*

Estimates of the relative growth-rate of seedlings under standardized productive growth-room conditions over the period of 2–5 weeks after germination (Grime & Hunt 1975) are available for 119 of the commoner species of the Sheffield region. In table 8, these data are used to compare the proportion of colonizing species in three growth rate classes. Species colonizing spoil are under-represented in the lowest growth rate class and form a high proportion of the most rapidly growing species. Although both these features of the data marginally fail to be confirmed statistically, a clear trend is evident and is consistent with a large body of evidence linking high relative growth rate with the capacity to exploit fertile disturbed habitats (Bradshaw *et al.* 1964; Parsons 1968; Higgs & James 1969; Grime & Hunt 1975).

(*g*) *Nuclear DNA amount and spoil colonization*

Recently, variation in nuclear DNA amount between plant species has been used as a convenient marker for variation in development characteristics such as minimum length of the cell cycle (Bennett 1971), and the rate and timing of leaf growth in the spring (Grime & Mowforth 1982; Grime 1983; Grime *et al.* 1985). In table 9, species for which estimations of nuclear DNA content are available have been compared with respect to the proportion of colonizing species. The ability to exploit spoil habitats is more common, where the 2*C* nuclear DNA amount falls in the range 2.0–9.9 pg per nucleus. Above and below this range the proportion of colonizing species is reduced. These findings are consistent with evidence associating low DNA amounts with slow rates of plant development under temperature-dependent conditions of the early spring (Grime *et al.* 1985) and linking high DNA amounts to inflexibly slow rates of cell division (Bennett 1971). The intermediate nuclear DNA amounts of the majority of the colonizing species in this study appear to represent a compromise ensuring the potential for rapid development under a relatively wide range of climatic conditions.

TABLE 8. A COMPARISON OF SPOIL COLONIZATION BY VASCULAR PLANT SPECIES CLASSIFIED WITH RESPECT TO THEIR MEAN RELATIVE GROWTH RATES

(Growth rates measured in a productive, controlled environment during the phase 2–5 weeks after germination.)

seedling relative growth rate	index of colonization		
wk^{-1}	< 1.0	$\geqslant 1.0$	
< 1.0	25	11	(*)
1.0–1.4	23	34	n.s.
> 1.4	8	18	n.s.
all species	56	63	

TABLE 9. A COMPARISON OF SPOIL COLONIZATION BY VASCULAR PLANT SPECIES CLASSIFIED WITH RESPECT TO NUCLEAR DNA AMOUNT

2*C* nuclear DNA amount/pg	index of colonization < 1.0	$\geqslant 1.0$	
< 2.0	29	17	n.s.
2.0–9.9	40	54	n.s.
> 9.9	25	9	n.s.
all species	94	80	

(*h*) *Flowering and spoil colonization*

Table 10 examines the colonizing ability of the common angiosperms classified according to the season and duration of the flowering period. No pattern is evident with respect to the timing of flowering, but it is established that the proportion of colonizing species rises with increasing length of the flowering period.

For those species for which adequate data are available, a classification has been attempted with respect to breeding system (table 11). As we might expect from previous investigations (Baker & Stebbins 1965), colonizing plants form a high proportion of the category described as 'mainly inbreeding or apomictic'. However, perhaps the most significant feature of the data is the clear evidence that, under the conditions prevailing in spoil habitats of the Sheffield region, outbreeding has not proved to be a significant barrier to colonization in a large number of species.

TABLE 10. A COMPARISON OF SPOIL COLONIZATION BY VASCULAR PLANT SPECIES CLASSIFIED WITH RESPECT TO FLOWERING PERIOD AND DURATION OF FLOWERING

(a) flowering period	index of colonization < 1.0	index of colonization ⩾ 1.0
Jan., Feb. or Mar.	9	11 n.s.
April	18	12 n.s.
May	27	28 n.s.
June	47	37 n.s.
July onwards	29	29 n.s.
all species	130	117

(b) duration of flowering months	index of colonization < 1.0	index of colonization ⩾ 1.0
< 2	52	20 *
2–3	45	37 n.s.
3–4	18	28 n.s.
> 4	16	31 (*)
all species	131	116

TABLE 11. A COMPARISON OF SPOIL COLONIZATION BY FLOWERING PLANT SPECIES CLASSIFIED WITH RESPECT TO BREEDING SYSTEM

breeding system	index of colonization < 1.0	index of colonization ⩾ 1.0
outbreeding	69	49 n.s.
mainly outbreeding	49	43 n.s.
mainly inbreeding or apomictic	19	32 n.s.
all species	137	124

(i) *Wind-dispersal and spoil colonization*

In table 12 the proportion of colonizing species is compared between groups classified according to the presence or absence of an efficient mechanism of seed or spore dispersal by wind. This is a conservative classification, in which only species capable of drawing a considerable benefit from air currents are described as wind-dispersed. A greater proportion of colonizing plants is evident among the wind-dispersed species and the data fall only marginally below the level required to establish a statistically significant departure from the colonizing performance of all common species. Although table 12 provides this useful confirmation that wind dispersal is sometimes correlated with colonizing ability, it is salutary to observe that wind-dispersed species are outnumbered by 3:1 among the species with a colonizing index greater than 1.0.

(j) *Seed characteristics and spoil colonization*

Extensive information on the seed and germination characteristics of the flowering plants of the Sheffield region (Grime *et al.* 1981) has been used in an effort to detect any attributes that are related to colonizing ability. A higher proportion of small-seeded species are colonizers

TABLE 12. A COMPARISON OF SPOIL COLONIZATION BY VASCULAR PLANT SPECIES CLASSIFIED WITH RESPECT TO THEIR CAPACITY FOR EFFECTIVE WIND-DISPERSAL

wind-dispersal	index of colonization < 1.0	$\geqslant 1.0$
+	18	34 (*)
–	136	94 n.s.
all species	154	128

of spoil, but many exceptions to this general trend are apparent (table 13). No significant relations could be found between colonizing ability and the capacity of freshly collected seeds to germinate immediately. The responses of seeds to temperature and to level of irradiance were not consistently related to the capacity to colonize spoil habitats.

From data and criteria of the kind described in Thompson & Grime (1979), a majority of the common flowering plants of the Sheffield region have been classified according to the types of seed bank they are known to develop. From the data summarized in table 14, it is apparent that colonizing ability is not restricted to species in which all or most of the seeds germinate soon after release (seed bank type I). Some of the most successful colonists of spoil habitats, e.g. *Agrostis capillaris*, *Plantago lanceolata*, *Chenopodium rubrum* and *Atriplex prostrata*, have seeds capable of long-term survival in the soil (seed bank type IV).

TABLE 13. A COMPARISON OF SPOIL COLONIZATION BY FLOWERING PLANT SPECIES CLASSIFIED WITH RESPECT TO SEED MASS

seed mass / mg	index of colonization < 1.0	$\geqslant 1.0$
< 0.5	51	68 n.s.
> 0.5	80	46 n.s.
all species	131	116

TABLE 14. A COMPARISON OF SPOIL COLONIZATION BY FLOWERING PLANT SPECIES CLASSIFIED WITH RESPECT TO TYPE OF SEED BANK

(See text for definitions of types.)

seed bank	index of colonization < 1.0	$\geqslant 1.0$
nil or type I	23	23 n.s.
type II or III	58	47 n.s.
type IV	40	47 n.s.
all species	121	117 n.s.

DISCUSSION

Where the objective in studies of plant colonization is to analyse the process by which a species expands its geographical range, there is much to recommend the traditional approach of mapping historical records (Salisbury 1932). However, it may be argued that the role of colonization extends far beyond the limited perspective afforded by studies of the spread of plants new to a particular region. The approach adopted in this paper is based on the assertion that colonizations are also, and more importantly, an integral part of the rapid changes in the relative abundance of common plants that are responsible for the continuing transformation (many would say deterioration) of the British flora (Ratcliffe 1984). Here, it is contended that analyses of the circumstances and characteristics of spoil colonization provide a valuable probe with which to examine the processes involved in the profound vegetation changes that are occurring in a wide range of habitats in response to increasing habitat disturbance and changing land management.

(*a*) *The role of seed and spore dispersal mechanisms in colonization*

In tables 2 and 12 there is strong evidence that an unusually high proportion of the species that possess an efficient mechanism of wind dispersal are capable of invading spoil habitats. In species such as *Senecio viscosus*, *Chaenorhinum minus* and *Erigeron acer*, wind dispersal is correlated with the ability of some comparatively uncommon species to exploit specific types of 'open' habitat occupying only a small proportion of the landscape. However, several additional sources of evidence suggest that these phenomena should not be regarded as proof of the limiting role of seed dispersal mechanisms in spoil colonization. In the first place, account must be taken of the fact that dispersal of some of the rarer wind-dispersed spoil plants, e.g. *Chaenorhinum minus*, has taken place along linear routes, such as railway tracks, along which their spread has been accelerated by passing vehicles (Arnold 1981). Secondly, it is evident (table 12) that many of the most effective spoil colonists have seeds that have no well-defined mechanism of dispersal and that tend to accumulate in large numbers in the soil. This observation suggests that access to spoil sites in many instances is independent of the mobility of the seed and occurs through transfer with soil, in the spoil itself, on human feet or in the tread of vehicles' tyres. Finally, doubt concerning the importance of dispersal mechanisms is cast by the fact that the most effectively dispersed component of the vascular flora, namely the pteridophytes, is conspicuous by its virtual absence (Grime 1985) from the spoil habitats of the Sheffield region.

(*b*) *The role of Salisbury's 'infection pressure' in colonization*

From tables 1 and 3 there is evidence supporting the hypothesis of Salisbury (1953) that rapid rates of colonization are more likely in species which have exceeded some critical level of abundance. This result suggests that, for many common plants of the Sheffield region, transport in soil or by other means is sufficient to ensure spoil colonization providing that the output of disseminules is sufficiently high.

(*c*) *Colonization in an ecological and evolutionary context*

If effective colonization depends primarily on the release of numerous propagules, we may suppose that colonizing ability will be dependent, in turn, on high population densities and high reproductive capacities. Hence it is no surprise to find (table 1) that the most frequent colonists of spoil habitats in the Sheffield region are fast-growing, perennial herbs of high fecundity, such as *Holcus lanatus* and *Chamerion angustifolium*, or prolific ephemerals such as *Poa annua* and *Senecio squalidus*. It is of critical importance, however, to recognize that it is only in comparatively recent times that the British landscape has supported extensive populations of such nutritionally demanding early-successional plants. The success of these particular colonizing species has been determined to a major extent by eutrophication and increasingly disruptive effects on vegetation that arise from agriculture, forestry, mineral extraction, urban expansion and recreation. In terms of plant strategy theory (Grime 1974, 1979; Leps *et al.* 1982), these vegetation changes represent a shift away from slow-growing, stress-tolerant plants with modest reproductive schedules, and towards ruderal and competitive strategists. Recently, Hodgson (1986*a*, *b*, *c*) has drawn attention to the fact that, according to their estimated degree of evolutionary advancement (Sporne 1980, 1982), families of angiosperms differ in their capacity to contribute to the expanding sector of 'ruderals' and 'competitors'. In figure 3, a consequence of this phenomenon is evident in the correlation established between estimates of the evolutionary advancement of the major dicotyledon families of the Sheffield region and the mean indices of spoil colonization of their constituent species.

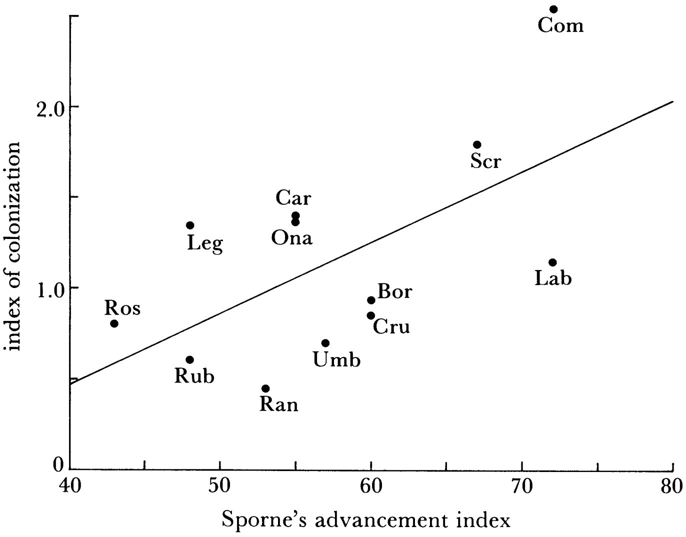


FIGURE 3. The relation between an index of the evolutionary advancement of dicotyledon families and an index describing the capacity of the families to colonize spoil habitats of the Sheffield region. Each index of colonization is a mean of values calculated for all species present in more than 0.25% of the survey samples. Key to families: Bor, Boraginaceae; Car, Caryophyllaceae; Com, Compositae; Cru, Cruciferae; Lab, Labiatae; Leg, Leguminosae; Ona, Onagraceae; Ran, Ranunculaceae; Ros, Rosaceae; Rub, Rubiaceae; Scr, Scrophulariaceae; Umb, Umbelliferae. Correlation coefficient $r = 0.6067$ ($p < 0.05$).

I am particularly grateful to my colleagues, Dr J. G. Hodgson and Dr R. Hunt, for permission to use unpublished survey data, and to Mrs J. M. L. Mackey, Mrs N. Ruttle and Mr S. R. Band for assistance in the preparation of the manuscript. This research was supported by the Natural Environment Research Council.

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Discussion

M. J. Crawley (*Department of Pure and Applied Biology, Imperial College, London*). I have two questions. First, a statistical point: had Professor Grime carried out two-way contingency analysis, a good many more of his results would have been significant (especially the results on breeding systems). Second, why are there so few aliens in his top twenty colonists and top twenty invasion coefficient species?

J. P. Grime. On the first point, I deliberately used conservative statistical analytical methods. On the second: the key to success is ability to colonize small areas of disturbed ground in a landscape with established vegetation. Species already abundant in adjacent habitats will have the greatest advantage.

Sir Richard Southwood, F.R.S. (*Department of Zoology, South Parks Road, Oxford OX*1 3*PS*, *U.K.*). Research carried out on vegetation at Silwood Park with Dr V. K. Brown confirms that aliens are largely concentrated in newly disturbed field sites.

J. L. Harper, F.R.S. (*Unit of Plant Population Biology, University College of North Wales, Bangor, Gwynedd, LL*57 2*UW*, *U.K.*) I can see the appeal of Professor Grime's C–S–D model, but it seems difficult to make it operational. Clearly the plotting of values on a triangle in the way proposed implies only two degrees of freedom. Any point on the C–S–D triangle determined by values of C and S immediately fixes the position with respect to D. In Professor Grime's triangle, the axes are given in percentages so that any point on the triangle adds up to 100% of something. What is this quantity, and how can we measure it and allocate it between C, S and D?

I worry, as Professor Grime knows, about the use of the word 'stress' in ecology. For the physicist it is a 'force per unit area'. Does the word bear any corresponding precision in ecology? I am also becoming unhappy with the usage of the word 'disturbance' in ecology. Again, it is not easy to see how it can be made operational. Is there some way in which a forest fire, the track of a bulldozer, a rabbit's burrow or a falling raindrop can be compared quantitatively as environmental forces? If we have to measure 'disturbance' by the response of the organisms, there is danger of a circular argument. Ideally, I suspect, we should aim to measure and compare the effects of various forces on individual fitness. Is this feasible?

J. P. Grime. May I refer Professor Harper to the descriptions of the triangular model and the definitions of stress and disturbance contained in two publications (Grime 1974, 1977). These emphasize that C–S–D is a *theoretical* model which proposes that the intensity with which plants compete for resources in vegetation is inversely related to the intensity of the constraints on plant production (stress) and the intensity with which plant biomass is destroyed (disturbance). It is inevitable and quite proper therefore that the axes of the model describing the theoretical relationships between intensities of C, S and D should add up to 100%.

The value of a theoretical model depends upon the extent to which it explains phenomena and generates testable predictions. On both these counts the C–S–D model is proving its value, not least in identifying major traits in life-history, physiology and biochemistry (now over twenty in number) which vary in relation to the axes of the model.

Professor Harper asks for an operational development of the C–S–D approach. This has been taking place over the last twelve years with the result that it is now possible to begin to analyse vegetation in terms of the frequencies and functional characteristics of component strategies (Grime 1984). Operational methods are already available where estimates of stress and disturbance are required. Stress in a stand of vegetation is inversely related to productivity, measurable as dry matter produced per unit area of ground per annum and disturbance can be estimated as dry matter destroyed per unit area of ground per annum.

In recent years, Professor Harper has contested the usefulness of most of the key words in my ecological vocabulary. 'Competition' was the first to fall from grace, 'stress' and 'strategy' have been castigated and now, alas, 'disturbance' has become a cause for concern. I readily concede that these terms have proved unnecessary in the increasingly specialized studies of plant demography and morphology advocated by Professor Harper. With many other ecologists, I remain attached to a terminology that can assimilate information from all fields of ecological research and can play its part in the development of a general conceptual framework for plant and animal ecology.

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Sir Richard Southwood, F.R.S. I think we need a four-sided diagram with two axes, because we need to define 'stress' in the habitat by means of something like Livingstone's bioclimatic index, taken together with productivity. This, on one axis, with disturbances on the other, would give a broad specification of the ecological situation.

R. N. Mack (*Washington State University, U.S.A.*). The terms 'colonization' and 'invasion' appear to be being used inconsistently. Does Professor Grime discriminate between them and does he separate them in this work? Would he agree that not all plants invade, but all colonize?

J. P. Grime. My paper was largely about species that colonize disturbed, relatively eutrophic habitats. The species that invade undisturbed ecosystems are usually those with longer life and slower growth.

A. J. Gray (*Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset BH*20 5*AS, U.K.*). Colonizing species are those that habitually establish themselves in transient or disturbed habitats. Invaders are a wider group, including species that can establish in undisturbed situations. Colonizers are thus a subset of invaders, specializing in disturbed situations.

A. Gibbs (*Research School of Biological Sciences, Australian National University, Box* 475 *P.O., Canberra A.C.T.* 2601, *Australia*). You related colonizing ability to major taxonomic group, but surely the scale was confounded by the number of other variables?

J. P. Grime. I established a broad correlation with Sporne's index. Recent angiosperm history seems to have allowed the development of attributes we now find predisposing to success in colonizing disturbed situations.