

INVASIVE WEEDS : IMPLICATIONS FOR BIODIVERSITY

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ABSTRACT

The concept of weediness is discussed in relation to the origins and evolution of weeds and popular definitions of what constitutes a weed are appraised. A distinction is drawn between the attributes of a successful weed within arable ecosystems and those of colonising and invasive species. It is conjectured that successful invasion involves an element of opportunism enabled by chance introduction, colonisation and naturalisation within degraded habitats. Naturally disturbed habitats such as riparian and aquatic environments are particularly prone to invasion as are forests subject to indiscriminate exploitation. A consequence of alien invasion is that of reduced biodiversity. Arable ecosystems however are more likely to suffer reduced biodiversity as a consequence of agricultural intensification rather than invasion *per se*. It is concluded that a major factor influencing successful invasion is pre-adaption of ecological niche.

INTRODUCTION

'If evolutionary success is measured in terms of the number of individuals, reproductive output, area of the world's surface occupied, the range of habitats occupied and the potential for maintenance of the species then weeds are the most successful members of the plant Kingdom' (Baker, 1974). Plants referred to as weeds have assumed widespread occurrence as a direct result of the activities of man. However, although weeds owe their success to the activities of man the agriculturalist, without such activity they would be ousted if natural succession were allowed to occur. Consequently weeds exhibit a fugitive existence within the dilemma of successional habitats. So if weeds are entirely dependent on man, from where did they originate? It is widely believed that many of our contemporary weeds originated from naturally disturbed habitats e.g. salt marshes, sand dunes, mountain screes etc. Hence, prior to the origins of agriculture weeds displayed a somewhat restricted distribution. Subsequent vegetation destruction enabled further colonisation and weed expansion to occur and it is from these naturally disturbed and man-made 'scars' that many of our weeds of cultivation have arisen.

Definitions

'A plant is a weed if in any specified geographical area its populations grow entirely or predominantly in situations markedly disturbed by man, without of course being deliberately cultivated' (Baker, 1965). Whilst such a definition is directly applicable to agricultural situations and facilitates the inclusion of 'volunteer crops as weeds' it doesn't accentuate the potential impact of weeds on biodiversity within natural/semi-natural habitats. Perhaps of wider application is that definition offered by Navas (1991) in that a weed is 'a plant that

forms populations that are able to enter habitats cultivated, markedly disturbed or occupied by man and potentially depress or displace the resident plant populations which are deliberately cultivated or are of ecological and/or aesthetic interest'.

Godinho (1984) found it impossible to define satisfactorily the term 'weed' or the German equivalent 'unkraut'. Implicit in these terms are two separate meanings - (i) a plant that grows spontaneously in environments modified by man, and (ii) an unwanted plant. She overcame this difficulty using the French terminology of 'adventice' and 'mauvaise herbe'. Likewise, in the U.K. the term 'adventive' has been employed to designate non-naturalised aliens from the native flora. As such these 'newcomers' have often been ignored at peril rather than considered an integral component of the flora. However, not all alien invaders are successful and it is only in retrospect that their invasiveness become apparent. More recently Cronk & Fuller (1995) differentiated between invasive plants and those more typically encountered within man-made agricultural habitats. Thus they defined invasive plants as 'alien plants spreading naturally (without direct human assistance) in natural or semi-natural habitats, to produce a significant change in terms of composition, structure or ecosystem processes'. Stirton (1980) coined the term 'plant invader' to accentuate their capacity to spread aggressively and cause rapid, often irreversible changes in the landscape. However, as indicated not all invasive species pose a threat, for although *Impatiens capensis*, *I. parviflora* and *I. glandulifera* are naturalised aliens it is the latter that is considered most invasive (Williamson, 1996) whilst the native *I. noli tangere* is scarce (Stewart *et al.*, 1994).

What makes a successful weed?

Baker (1974) lists the attributes of the 'ideal' weed; fortunately there are no current contenders. These characteristics may be simplified and summarised as non-exacting germination requirements, discontinuous germination, rapid switch from vegetative to reproductive development, self compatible but not completely autogamous, high fecundity, extended seed production, efficient dispersal mechanism, phenotypic plasticity and competitive ability. These attributes may be further expanded and extrapolated in relation to agrestals to include seed dormancy and persistence, short generation time, genetic plasticity and ploidy, responsivity and tolerance of high fertility while Bazzaz (1986) has identified the physiological traits that may confer success in early successional habitats.

Baker (1974) suggests that the possession of a number of these desired attributes may confer 'major weed' status whereas those which possess relatively few exhibit 'minor weed' status. Consequently 'major weeds' are released from restrictions imposed by the environment. The development of a 'general purpose genotype' strategy allows a greater flexibility in response to environmental heterogeneity, albeit the introduction of *Digitalis purpureum* and *Chrysanthemum segetum* into N. America have been restricted to acid soils (Baker, 1986). Conversely the introduction of *Parthenium hysterophorus* from N. America into India has indicated a 'major weed' status free from restriction imposed by climatic, biotic or edaphic factors. Attributes of potential invasive species together with conditions conducive to invasion have been summarised by Di Castri (1990) and Beerling (1995). It is of interest that *Bromus tectorum* appears not to conform to the principle of invasive species in that it lacks innate dormancy and fails to form a persistent seedbank, germination occurring synchronously in response to available moisture. Its ability to pre-empt exploitation of the root environment over winter enable it to exclude native species. Over grazing and disturbance of potential sites facilitates an opportunistic strategy in that seed fecundity greatly

exceeds available sites for occupation (Young & Longland, 1996). Similar observations are reported for *B. sterilis* in that seed output may exceed the number of available sites by a factor of at least $\times 2$ (Froud-Williams, 1983). Conversely, Mortimer *et al.*, (1993) have indicated that *B. interruptus* is less ecologically fit to survive within arable environments which may have contributed to its extinction (Perring & Farrell, 1983).

GENETICS OF WEED INVASIONS

The ability to set seed by autogamy is widespread amongst weed species, providing the opportunity for a single individual to initiate a colony, even after successful weed control measures. Clearly the likelihood of successful invasion is enhanced in species of broad ecological tolerance, resulting in a range of ecotypes. Genetic variability in virtually autogamous species aids establishment in a newly colonised area where self-fertilisation is of immediate value for population expansion from a single or few individuals. Studies of genetic variation in weeds and other colonising species have indicated a number of shared genetic features that may contribute to their success (Brown & Marshall, 1981). Breeding system is the most important factor influencing genetic variation within and among populations (Loveless & Hamrick, 1984). Autogamy, important in the establishment of weed populations results in fewer genotypes and reduced levels of heterozygosity (Brown & Burdon, 1987). As a consequence predominantly autogamous species tend to be genetically uniform but highly differentiated from one another. Limited genetic variation may be the result of genetic bottlenecks associated with repeated episodes of colonization, extensive clonal propagation, inbreeding and the relative homogeneity of agro-ecosystems. Conversely, genetic diversity among weed populations is fostered by multiple seed introductions, habitat longevity, environmental heterogeneity, outbreeding and hybridization with other taxa (Barrett & Richardson, 1985).

In many parts of the world the weed flora is composed of alien species. Successful colonisation will depend on the degree of pre-adaptation to the new environment, the number of immigrants and the availability of 'safe sites'. Such events of colonisation often result from long-distance (inter-continental migration) involving one or few individuals. As a consequence of such 'founder effects' introduced populations may be genetically depauperate in comparison with their source of origin (Warwick, 1991), particularly in the absence of sexual reproduction. Despite this many examples of aquatic invasions involving considerable range extensions have resulted from limited genetic diversity as a consequence of clonal propagation. For example *Eichhornia crassipes* exhibits the rare polymorphism of tristylly, such that in its native range of Amazonia, long, mid and short styled morphs occur. However, in many parts of its adventive range, only mid-styled morphs occur suggesting limited introductions (Barrett, 1979) and subsequent clonal propagation. A similar example may be cited for *Salvinia molesta* which, coupled with an expression of phenotypic plasticity, facilitates further range extension through fragmentation or consolidation depending on environmental conditions (Room, 1983).

Apomixis (production of viable seeds without fertilization whereby the progeny are genotypically identical to the parent) offers a means for consolidation of successful genotypes. Examples of apomictic invasive weeds include *Chondrilla juncea*, *Chromolaena odorata* and *Hypericum perforatum* (Barrett & Richardson, 1985). The lack of sexual reproduction is clearly not disadvantageous to successful colonisation and invasion as

witnessed by examples of the aquatic weed *Elodea canadensis* and the riparian *Fallopia japonica*, neither of which produce seed in their adventive range. Nonetheless, sexual reproduction has facilitated range extension through the formation of more vigorous genotypes, sterile but vegetatively vigorous genotypes e.g. *Salvinia molesta*, hybrid swarms e.g. *Raphanus sativus* x *R. raphanistrum* and new species e.g. *Spartina anglica*. The latter has provided one of the most striking examples of weed origins this century (Gray *et al.*, 1991). *Spartina maritima* ($2n = 60$) a native of W. European coasts hybridised with *S. alterniflora* ($2n = 62$) following its introduction from N. America in 1829. The sterile hybrid produced was later referred to as *S. townsendii* ($2n = 62$) and spread rapidly colonising mudflats more successfully than either parent. However, around 1890 an amphidiploid ($2n = 122$), subsequently referred to as *S. anglica*, was recorded in the River Itchen, Hampshire, and spread so rapidly that it ousted the native *S. maritima* and the introduced alien *S. alterniflora*. Whilst this did not pose an initial threat to existing plant communities it has resulted in habitat alteration with possible consequences for other life forms and may pose a threat to *Zostera noltii* (Stewart *et al.*, 1994).

NATURE OF WEED INVASIONS

Groves (1986) has postulated that there are three main stages in the invasion process, namely introduction, colonisation and naturalisation. Factors restricting weed invasion have been reported as barriers to dispersal and availability of suitable sites. Examples of the former include geographical features such as oceans and mountains, their importance now diminished as a result of increased inter-continental travel. Habitat availability too has been modified by the expansion of crops to the areas formerly unsuitable for their cultivation. For example the progressive spread of a number of characteristically warm-season weed species including *Datura stramonium*, *Abutilon theophrasti* and *Xanthium strumarium* has been associated with the expansion of maize and soybeans in Ontario (Weaver, 1985). It is possible that similar events could be witnessed with the greater acreage and northern extension of maize production in the U.K. Potential invasive species include *Amaranthus retroflexus* and *Echinochloa crus-galli*.

The introduction of new world crops such as maize, tobacco and other solanaceous species into the mediterranean basin has further contributed to weed invasiveness. Native weed species are typically senescent during the season when these crops are cultivated, facilitating niche exploitation by introduced aliens such as *Solanum eleagnifolium*. This species exhibits a range of regenerative strategies viz. therophytic, chamaephytic, hemicryptophytic and geophytic (Guillerm *et al.*, 1990).

Weed invasions have typically been associated with human activity, whether deliberate or unintentional. Escapes from Botanic Gardens have provided some of the most notorious examples both within the U.K. and abroad. For example the cosmopolitan distribution of *Salvinia molesta* has been closely correlated with introductions to Botanic Gardens. Thus following its introduction to the Bogor Botanic Gardens in Indonesia in December 1950 it has become widely naturalised in rice paddies throughout S.E. Asia. Garden escapes in the UK include the aquatic *Crassula helmsii* (Dawson, 1994), the riparian species *Fallopia japonica* (Connolly, 1977) and *Heracleum mantegazzianum* (Tiley *et al.*, 1996).

Weeds may be considered as specialists and non-specialists, the former include the crop

mimics (mimetic weeds) and are totally dependent on man for their survival. Changes in agricultural practice can and have had profound consequences for their decline and demise. Conversely, the non-specialists are adapted to periodically disturbed sites and owe their success to seed dormancy and dispersal. Arable weeds (agrestals) rely almost entirely on biotic agencies for dispersal whereas ruderals have well developed mechanisms for abiotic dispersal. Consequently, agrestals are adapted for dispersal in time (through dormancy and development of a persistent seedbank) whereas ruderals are selected for dispersal in space. It is the latter group that are well adapted as colonising species, enabling invasion from often insubstantial origins.

Nonetheless, the role of man in promoting and extending the distribution of weeds cannot go unnoticed. Consequently, many weeds of the New World are of Eurasian origin, while perhaps surprisingly fewer examples of the converse have occurred. Exceptions include *Datura stramonium*, *Amaranthus* spp. Whilst species continue to be introduced and possibly increase in status others have undoubtedly declined. Thus Salisbury (1961) has suggested that 'the British flora is not an event but a process that is continuing both with respect to accretions and diminutions' (see for example Clement & Foster, 1994; Perring & Farrell, 1983; Ryves *et al.*, 1996).

Patterns of Weed Invasion

Following initial colonisation a lag phase has often been reported although this has been inferred as a possible aberration of sampling procedure (Cousens & Mortimer, 1995). Nonetheless, populations may suffer episodic decline as witnessed for *Sisymbrium irio* following the Great Fire of London in 1666. Conversely *Chamerion angustifolium* appeared to benefit following widespread burning during the London blitz in the 1940's. Likewise *Elodea canadensis* underwent a period of decline following range expansion after its initial discovery in the Grand Union Canal at Foxton Locks, Leicestershire. Reasons for the meteoric rise of introduced aliens have been attributed to the absence of natural predators and pathogens during their introduction. Notable examples include *Opuntia stricta* and *Chondrilla juncea* following their introduction in Australasia. However, Cook (1990) suggests that this is a simplistic explanation for aquatic invasive species.

Impact of Weed Invasions

In a recent review Randall (1996) suggested that weed invasions may adversely affect ecosystem processes, displace native species and hybridise with native species to modify the gene pool. Altered ecosystem processes include effects on sedimentation, erosion, frequency of fire, hydrological and nutrient cycling. Within the fynbos shrublands of South Africa, invasion by alien woody species has implications for extinction of native species, increased risk of fire, destabilized water catchment areas and hence increased erosion and reduced aesthetic quality (Le Maitre *et al.*, 1996). Increased sedimentation of maritime habitats has been associated with the evolution of *Spartina anglica* in the U.K. Increased risk of fire has been implicated with the invasion of the Great Basin rangelands in North America (Mack, 1981). This may further accentuate displacement of native vegetation. Such displacement may result from the introduction of seemingly innocuous species. For example whilst *Alliaria petiolata* is confined to hedgerows in its native range it has come to dominate the forest ground floor in N. America. Reasons for elimination of the native vegetation may result from direct competition or release of allelochemicals (Nuzzo, 1993). Similar

observations have been expressed following the introduction of *Isatis tinctoria* (Young & Evans, 1976) although restricted to single naturalised site in the UK (Perring & Farrell, 1983). Likewise, the apparently benign *Lythrum salicaria*, occasionally encountered on riverbanks in the U.K., has displaced many wetland species in N. America (Malecki *et al.* 1993). In the U.K. the impact of *Rhododendron ponticum* on the forest understorey vegetation is well documented (Abbott & Milne, 1995). Possible reasons for its success as an invasive species include prolific seed production, efficient dispersal, tolerance of a wide range of climatic variables, unpalatability, competitive ability, ability to regenerate vegetatively even after fire (Cronk & Fuller, 1996). Similar attributes have been identified for *Clematis vitalba*, which is considered to be an innocuous climber in the U.K. but can have a devastating effect on forest ecosystems in New Zealand.

Weeds know no taxonomic boundaries and are represented by all phylla. Although the predominant weeds are angiosperms some of the 'worlds worst weeds' include algae and pteridophytes. Habitat modification may contribute to their success and subsequent suppression of associated species. Eutrophication of irrigation channels has contributed to the spread of filamentous algae to the detriment of submerged aquatic vegetation. *Pteridium aquilinum*, albeit native to the U.K. has assumed widespread distribution in the uplands as a consequence of improved drainage for agricultural purposes. *Pteridium* is not grazed to any extent owing to its lack of palatability and toxicity to livestock and hence its canopy greatly suppresses understorey vegetation (Marrs, 1987). In some instances man-created habitats such as canals and railways, have fostered weed colonization and hence have contributed to bio-diversity. The development of the latter have contributed to the expansion of a number of invasive species including *Conyza canadensis*, *Senecio squalidus*, *Oenothera biennis* and where abandoned *Buddleia davidsonii*. Nonetheless invasions are typically associated with reduced biodiversity (Beerling, 1995).

Hybridization with native species

Hybridization events between native and introduced weeds are well documented, e.g. *Senecio cambrensis* and *Galeopsis tetrahit*, but perhaps of greater concern is the potential for hybridization between crops and weeds. Of notable mention is that involving genetically modified organisms such as herbicide resistant crops. Already, feral populations of oilseed rape are invasive weeds of roadside verges and have the potential to hybridise with related cruciferous weeds. Commercial release of genetically modified crops in the UK is likely in the imminent future, most probably these crops will be engineered for resistance to the non-selective herbicides glufosinate ammonium and glyphosate. For immediate consideration are genetically modified crops of sugarbeet, oilseed rape and potato. In common with conventional crops genetically modified crops are potentially capable of hybridisation with wild relatives. The risk of gene flow between cultivated and wild species has been reviewed by Raybould & Gray (1993) and Rogers & Parkes (1995). Three possible outcomes, viz minimal, low and high probability of gene flow between domesticated and wild relatives are exemplified by potato, oilseed rape and sugarbeet respectively (Raybould & Gray, 1993). Crops with close weedy relatives are more prone to gene transfer than crops in which domestication has resulted in ecological and reproductive isolation (Ellstrand & Hoffman, 1990). Gene exchange between domesticated and wild relatives could result in increased weediness as exemplified by weed beets (Boudry *et al.*, 1993).

Evidence from pollen dispersal suggests that transgene movement between genetically

modified oilseed rape (*Brassica napus*) and feral populations (Timmons *et al.*, 1996) and wild species is inevitable (Mikkelsen *et al.*, 1996). Indeed, the potential for hybridisation between oilseed rape and its wild relatives *Brassica campestris*, *B. napus*, *B. oleraceus* and *Sinapis arvensis* (Raybould & Gray, 1993) and *Hirschfeldia incana* (LeFol *et al.*, 1996) has been documented. Under UK conditions it is considered likely that *B. rapa* would hybridise most readily with *B. napus* as the maternal parent (Scheffler & Dale, 1994) albeit *B. rapa* produced a greater frequency of hybrid seed (Jorgensen & Andersen, 1994).

Transgenes may spread either from direct seed spillage resulting in volunteer and feral populations or via pollen transfer and hybridisation with native species. The ecological consequences of escape by genetically modified crops is discussed by Rogers & Parkes (1995) in terms of competitiveness in agricultural environments and invasiveness in semi-natural habitats. They concluded that genetically modified crops are unlikely to pose any greater threat than escape by conventional crops or feral populations and will be influenced by ecological fitness of the domesticates, but could have implications for wildlife through factors such as toxicity and allergenic effects.

IMPLICATIONS FOR CONSERVATION OF WEEDS

Recent reviews of invasive weeds have focused attention on their impact on semi-natural vegetation, especially that considered of conservation value. Compared with habitats such as chalk downland, heath and bog communities, agro-ecosystems have received scant attention from a conservation perspective. Indeed arable weed floras are a much despised and greatly maligned community. Nonetheless, they too may suffer from intense inter-specific competition as a result of agricultural intensification which favours particular taxa. The realisation that a number of formerly prolific species are now under threat of elimination has prompted recent research on their conservation (Hodgson, 1991).

Pre-adaptation of plants as weeds may have resulted from the possession of particular attributes that confer success in nutrient-rich habitats subject to periodic disturbance. Consequently such species have become adapted to agricultural practices over the millenia. Although agriculture has been characterised by continuous and gradual change, temperate agriculture has undergone a most dramatic revolution during the last half century. The traditional role of inversion tillage and crop rotation for weed control have denied any single species from assuming dominance and have maintained a weed flora diverse in species composition. The alternation of spring and autumn-sown crops, broad-leaf and graminaceous have contributed to a range of weeds of varying growth habits and life-histories. The season of planting is the most important factor influencing species composition, whilst drilling date, crop and varietal selection provide ancillary sieves. Increased dependence on inorganic fertilizers have resulted in a weed flora poor in species composition but highly responsive to nitrogen availability. Differential response to nitrogen application has been demonstrated in the former East Germany by Mahn (1984). Increasing nitrogen from 40 - 120 Kg N/ha benefitted nitrophilous species such as *Stellaria media* and *Galium aparine* through increased biomass, but disadvantaged less responsive species such as *Lamium amplexicaule*.

Likewise, the advent of herbicides may have been anticipated to affect species composition. Prior to the introduction of selective growth regulator type herbicides (phenoxyalkanoic acids) arable weed floras were dominated by dicotyledonous species. Yet, even after some

fifty years of use, susceptible species such as *Papaver rhoeas* are reasonably frequent as evident from their occurrence in break crops such as oilseed rape (Froud-Williams & Chancellor, 1987). Presumably either seed persistence is long-lived or herbicides play a minor role in their population survival. Nonetheless, it has been conjectured that herbicides have contributed to a displaced successional process whereby susceptible broad-leaved species have been displaced by less susceptible and indeed ultimately resistant grass-weeds (Froud-Williams, 1988). Thus, the history of herbicide development has been one of adjustment to changing weed flora composition, mecoprop introduced to control those broad-leaved species non-susceptible to 2,4-D and MCPA, benzoic acids introduced for *Polygonum* spp., hydroxy benzonitriles for *Matricaria* spp., and fluroxypyr for *Galium aparine*. As the incidence of broad-leaved species diminished, substituted ureas were required for the increased problem posed by *Alopecurus myosuroides*. This herbicide induced plagiosere has necessitated the development of specific graminicides to address the increased incidence of grass-weeds in both broad-leaf and graminaceous crops. A possible consequence of chemical control has been that of a weed flora rich in species density but poor in species diversity. Subsequent developments have largely been in response to problems of resistance created by over-reliance on individual herbicides.

However, work by Mahn & Helmecke (1979) indicated that although species dominance relationships changed in response to herbicide application to cereals over a five year period, species composition was virtually unaffected. Likewise, in a Canadian study initiated in 1947, Hume (1987) reported that no species sensitive to 2,4-D had been eradicated whilst some susceptible species including *Thlaspi arvense* were no less frequent. A recent survey of the weed flora in Danish arable fields conducted between 1967-1970 and 1987-89 compared frequencies of sixty seven common weed species of cereals and grass-leys (Andreasen *et al.*, 1996). The comparison showed that the occurrence of common species had generally declined since the earlier surveys. *Anagallis arvensis* and *Silene noctiflora* had declined considerably, possibly as a consequence of intensive herbicide use.

Conversely, resistance to herbicides may have contributed to domination of some grass-weeds in the absence of tillage (Hume *et al.*, 1991). However, Derksen *et al.*, (1993) failed to detect an increased association between annual grass-weeds and zero-tillage despite earlier predictions of Froud-Williams *et al.*, (1981) albeit greater infestations (including *Bromus tectorum*) were observed following zero-tillage (Blackshaw *et al.*, 1994, Légère *et al.*, 1994). In the UK a reduction in intensification of tillage as a consequence of increased reliance on herbicides for weed control has contributed to the invasiveness of *Bromus sterilis* and various umbelliferous species including *Anthriscus sylvestris* and *Heracleum sphondylium* from arable field margins (Theaker *et al.*, 1995; Rew *et al.*, 1996). Gaps in the herbicide spectrum have further contributed to the invasiveness of *Conium maculatum* and *Lactuca virosa* in oilseed rape, whilst regular displays of *Papaver rhoeas* in this crop is testimony to the importance of a persistent seedbank.

Implications of various agricultural practices for endangered arable weeds have been reported by Wilson *et al.* (1990). In essence, season of planting will greatly affect species composition, for germination of *Adonis annua* is synchronous in the autumn whereas that of *Silene noctiflora* is confined to spring. Relative competitive ability of the sown crop will further influence the potential for survival in that *Ranunculus arvensis* is less adversely affected by winter wheat than w. barley. Differential susceptibility to herbicides renders *Scandix pecten-veneris* more susceptible than *Chrysanthemum segetum*, while most species

evaluated were adversely affected by nitrogen with the exception of *Lithospermum arvense*. It is notable that the only examples of extinction of arable weeds have resulted from improvements in crop seed hygiene.

CONCLUSIONS

A number of biological attributes contribute to the invasiveness of weeds and include ecological physiological and genetic factors. However, such attributes are not necessarily synonymous with those characteristics associated with the expression of weediness, especially of those species specialised as weeds. Thus lack of sexual reproduction, habitual inbreeding, lack of innate dormancy and failure to form persistent seedbanks would appear not to preclude invasiveness. The introduction of alien species free of their natural pathogens and predators would appear to contribute to population expansion whilst degraded environments free of competition facilitate invasion. In particular the ability to exploit ecological niche as a consequence of pre-adaption would appear to aid their spread. The deliberate or accidental introduction of aliens has not always resulted in invasiveness as evident from the failure of numerous wool aliens to become naturalised. Climatic factors too have an important role in range extension of weed species and global climate change may have important implications for weed invasiveness and biodiversity (Froud-Williams, 1996). Nonetheless, the most important factor is that of dispersal by man, often with catastrophic consequences for native vegetation. The introduction of *Chromolaena odorata* for control of soil erosion is one such example. However, man has not only disseminated species beyond their native range, but has modified the habitats into which they are introduced to the benefit of the newcomers and the detriment of the residents.

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