Biological Invasions: a Global Perspective
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CHAPTER 20

Ecological Control of Invasive Terrestrial Plants

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20.1 INTRODUCTION

Methods of controlling terrestrial invasive plants have evolved as land use systems changed and diversified over time. But the aim of control has always remained the same—namely, to limit the number of plant propagules in the long term to a level tolerable to human activities. Rarely has eradication been a management aim. In this chapter I shall review some of the ways by which populations of invasive plants have been deliberately limited. I define ecological control of an invasive plant as the planned use of one or several methods of control when integrated with an understanding of the dynamics of the ecosystem in which the plant occurs. Control methods used in agricultural ecosystems usually simplify the system. Ecological control methods in natural systems, on the other hand, aim to maintain or even enhance biological diversity in the longer term.

In this chapter I shall discuss, using examples from invaded natural vegetation wherever possible, the different methods of control in terms of their relative importance in reducing plant populations. Case histories of three groups of invasive plants will be presented in relation to ecological aspects of their control: firstly, *Hypericum perforatum* in temperate grasslands; secondly, a group of *Eupatorium* (*Chromolaena*) species which invade areas of subtropical forests; and thirdly, some invasive tall shrubs in mediterranean-climate shrublands. From these and other examples I shall present some general principles for more effective control of invasive terrestrial plants in natural ecosystems.

20.2 METHODS OF CONTROL

In this section I discuss the different methods of control of invasive plants as they apply to natural areas. Wherever possible, my examples will be drawn from those identified by the contributors to national symposia (Groves and Burdon, 1986; Kornberg and Williamson, 1986; Macdonald *et al.*, 1986; Mooney and Drake, 1986).

One method to control invasive terrestrial plants is to prevent their entry to a country or region. Such a method is a policy of exclusion enacted by parliamentary legislation (Navaratnam and Catley, 1986). The method is presumably effective in limiting the number of invasive plants entering a country, although I have been unable to obtain figures on the numbers and identities of invasive plants which reach an entry point but are then detected and thereby excluded. This method does not usually keep out 'new' species of known taxonomic identity unless they are especially troublesome in another country. Even then, legislation may not prevent their entry, as in the case of various *Hieracium* species native to Europe and known to be invasive in Canada and in New Zealand but which have yet to reach Australia (Groves, 1986).

An allied method of legislative control for invasive plants is to declare them 'noxious' once they have entered a country. Whilst in theory this method gives management authorities the legal power to control growth and reproduction of such plants, in practice it seems neither to reduce the rate of spread of an invasive plant nor to lead to more effective control (Moore, 1971; Amor and Twentyman, 1974). A. M. Gill (personal communication) showed how ineffective this control method has been for the European plant *Hypericum perforatum* over the timespan of its invasion of southeastern Australia. Legislation concerning noxious plants is being revised currently in several regions to take this point into account, especially for plants invading non-agricultural land. How effective the revised legislation will be remains to be assessed.

Both these legislative methods of control are usually retrospective but I believe the emphasis to be changing gradually to become more forward-looking as more attempts are made to predict the potential of a plant to spread and be invasive (see, for example, Medd and Smith, 1978; Williams and Groves, 1980; Gunn *et al.*, 1981; Patterson, 1983). A change has also occurred as knowledge of the biology of invasive plants moves from a regional to an international perspective, as has occurred as a result of this SCOPE programme.

Physical methods of control include the planned mechanical or manual cultivation of invaded land or the manipulation of fire regimes to benefit indigenous species at the expense of invasive species. Cultivation of land to control invasive species mechanically is usually inappropriate to natural areas, although it has been used very effectively for millennia in agricultural areas. Hand-pulling of invasive plants is often practised and has the potential to be effective—as, for instance, in the control of the South African shrub *Chrysanthemoides monilifera* in urban parks in southern Australia (see later). Manual slashing of the Australian shrub *Hakea sericea* has been effective as a physical method of control in conjunction with burning of South African mountain fynbos. Hand-pulling and slashing have been completely ineffective, however, in controlling *Rhododendron* in British nature reserves (Usher, 1986).

The planned use of fire is usually a preferred method to conserve natural plant communities and to control the growth of undesirable plants invading those communities (Christensen and Burrows, 1986). For these two groups of plants alterations in the different components of the fire regime (Gill, 1975) will have different consequences. Fires at too frequent an interval often favour plant invasion. Generally, frequent fires favour resprouting perennials over non-sprouting species, disadvantage plants which rely solely on seed stored on the plant, promote grasses and forbs over dicotyledonous plants and may reduce species diversity (Vogl, 1977). Baird (1977) attributed the spread of the South African grass *Ehrharta calycina* in eucalypt woodland at King's Park, Perth, in part to fires every one or two years.

Watsonia species are iridaceous components of the South African fynbos which have invaded parts of southern Australia and New Zealand (Parsons, 1973), especially the species *W. bulbillifera*. Another species, *W. pyramidata*, was shown to be more prominent in autumn-burned vegetation in South Africa (Kruger, 1977). On the basis of this observation, burning of areas invaded by *W. bulbillifera* in Australia and New Zealand in seasons other than autumn should limit its invasiveness, especially if season of burning can be combined with other control methods.

Manipulation of fire intensities can also be used to control invasions. For instance, in areas of South African fynbos invaded by woody Australian acacias, fires of high intensity will increase the invasiveness of these shrubs because they possess a high proportion of soil-stored hard seeds which are stimulated to germinate by the rupturing of the testa induced by the high fire temperatures. Fires of lower intensities may benefit the indigenous component of the vegetation, especially the proteaceous element, and thereby reduce the invasiveness of the introduced leguminous element in the flora.

The most effective method of control of invasions by fire can often be to try and greatly reduce its frequency. In the example discussed earlier on the effects of fire frequency, Baird (1977) also found that in one area unburnt for 15 years the number of clumps of the invasive *Ehrharta calycina* gradually decreased from 115 to six. This result thus has the potential to change the almost self-perpetuating cycle of increased fire frequency and decreased fire intensity leading to increased colonization by *E. calycina* to one of a greatly reduced fire frequency and decreased colonization by the invasive species. In general, hard-seeded legumes, species with wind-dispersed seeds and bulb- and corm-producing plants will be at a disadvantage on infrequently burnt reserves. The effectiveness of this control method depends on the interaction between time since the last fire, the lifespan of the invasive plant and its propagules and the successional status of the invaded community. The South African plant *Senecio pterophorus* has short-lived wind-dispersed seeds. When previously grazed land in the Adelaide Hills, South Australia, was reserved for nature conservation, *S. pterophorus* rapidly dominated open areas no longer grazed by sheep. But after 10–15 years without fire a tree cover established and *S. pterophorus* plants no longer dominated the more shaded understorey. Whilst the plant is still present in the area, it is no longer as invasive as it once was because of the changed environmental conditions induced by less frequent fire (P. M. Kloot, personal communication). Generally, frequent fires keep a natural community in an early successional stage; infrequent fire may enable a community to change and this change may be unsuited to the growth of invasive species such as *S. pterophorus*.

Fire remains the cheapest form of management available to conserve and perpetuate natural plant communities. The different components of a fire regime—frequency, season and intensity—may be used effectively to retain the natural element and control the invasive element in the flora of a nature reserve.

Chemical methods of control are used widely to control the growth and development of invasive plants, although their use in areas set aside for natural values is less extensive than in agriculture, and even less desirable. Control of invasive plants by herbicide application is usually short term and directed at individual 'target' species. For example, *Chrysanthemoides monilifera* is sprayed regularly with herbicide in a hill reserve in southern Victoria whilst no control is directed at plants of the invasive grass genus *Ehrharta*. Spraying of one invader may well be leading to its replacement by a second plant also capable of outcompeting the indigenous species. Regular spraying with herbicides seems to have kept the invasive European shrub *Cytisus scoparius* from spreading further in Barringon Tops National Park in eastern Australia until reductions in funding halted the spraying programme. The subsequent extensive spread of the invader through the eucalypt woodland can be dated from this temporary cessation in chemical control (see also Macdonald *et al.*, this volume). For this leguminous species a control programme which does not lead to a reduction in the input of new seed into the store of dormant but viable seed in the soil will be ineffective in the long term. To reduce the level of *C. scoparius* cover by spraying with a herbicide will be effective if it allows for regeneration of native tussock grass (in the short term) or of native trees (in the long term), but it may not necessarily be effective in reducing the number of long-lived seeds in the soil.

Some invasive plants such as blackberry (*Rubus fruticosus* sp. agg.) provide food and refuge for invasive animals, such as foxes and rabbits in Australia and New Zealand. Spraying of blackberry with herbicides may reduce the suitability of the habitat for these introduced animals in the short term but the high and increasing costs of herbicides and the cost of application in difficult terrain usually means that continuity of spraying is interrupted and the invasion returns. Application of herbicides for blackberry control has the added disadvantage that because blackberries often occur densely along watercourses the chances of chemical contamination of waterways is thereby increased. I conclude that chemical control may be effective in limiting newly discovered infestations which have yet to spread, e.g. of *Onopordum tauricum* in Victoria (W. T. Parsons, personal communication). On the other hand, chemical control of already widespread invasive plants in nature reserves is often expensive, usually ecologically undesirable and rarely, if ever, effective in the long term, unless integrated with other methods of control.

The deliberate promotion of growth of indigenous plants to compete with and thereby control invasive plants is inadequately researched. It is a control method widely used in pasture research to promote the growth of desirable species which then better compete with the undesirable species. This imbalance in research effort can lead to the situation where a plant such as *Hypericum perforatum*, when invasive in pastures, can be controlled by competition from desirable pasture species such as *Trifolium subterraneum* and/or *Phalaris aquatica* (see later); *H. perforatum* can, however, remain dominant in more natural vegetation in reserves adjoining pasture lands because little is known of the characteristics of indigenous species which may compete effectively with the invader. Some *Eupatorium* spp. may be controlled by shading from indigenous tree species if the shading effect continues beyond the active reproductive output of the invader, as can occur in northeastern India (see later).

Because of the agronomic bias in most previous research on this control method, the index of competition is usually measured as the enhanced yield of plant or livestock product, whereas in the context of invasions in nature reserves, numbers of propagules per unit area of land or volume of soil may be of greater ecological significance. The method has the advantage that the controlling effects are expressed over a much longer time period than, say, are the effects of chemical control. It is an ecological aspect of control of invasive plants which is in need of much more research effort. If this enhanced research can include a study of rooting characteristics of the competing species, the results may be even more applicable to the management of biological invasions.

Biological methods to control invasive terrestrial plants have sometimes had a spectacular success in the long term. The control of *Opuntia* spp. by *Cactoblastis cactorum* in various countries (e.g. Mann, 1970, for Australia; Zimmermann *et al.*, 1986, for South Africa) is probably the best known example of success. Zimmermann *et al.* (1986) even considered that the present distribution, as well as abundance, of three invasive *Opuntia* species in South Africa was determined to a large extent by pressure from imported insect herbivores. The method is not without risks, however (see, for example, Howarth, 1983), although these risks are minimized by careful specificity testing before release in regions such as Australia and California. I know of no documented cases where a natural enemy after its deliberate introduction to control an invasive plant has caused a reduction in the population of a native congener of that plant, although such cases are known for the biological control of insects (Howarth, 1983). Programmes for biological control of genera such as *Convolvulus, Rubus, Rumex* and *Solanum* will need to carefully assess economic benefits against biological risk.

Results of a recent survey of biological control of invasive plants, both terrestrial and aquatic, show that only between 25 and 40% of programmes could be considered effective (Julien, 1982). When the method has been successful, density or cover measurements of the invasive plant have decreased as a result of the planned release of introduced or native arthropods or fungi or both.

Sometimes this reduction has been quantified, sometimes not. Success is usually attained when the effects of the invasive plant no longer exceed a 'threshold' level which may be economically, agronomically or, more rarely ecologically based. Research programmes on biological control commonly ignore increases in cover or numbers of the species replacing the invasive one (but see, as an exception, Huffaker and Kennett, 1959, for *Hypericum perforatum* control in California). This deficiency has the potential to lead to one invasive plant replacing another, as with several other methods of control (see earlier).

For plants invading nature reserves where low-cost control and minimal disturbance are important considerations, biological control methods have a considerable and continuing role to play. When effective, biological control is the ideal method, but it is not always effective and rarely is it predictable. A greater effort at evaluation, in ecological terms, of the successes and failures in the biological control of a range of invasive plants may help to overcome this deficiency from which formulation of a theoretical basis for the method can commence (see e.g. Crawley, 1986 and this volume).

The theme developed in this section has been that although individual control methods are sometimes effective at controlling invasive plants, a combination of control methods carefully timed to coincide with critical stages in the reproductive cycle of the plant will be even more effective. Such control is increasingly being termed 'integrated' control (see, for example, Kluge *et al.*, 1986), following the terminology developed for systems for invertebrate control. For my purposes, I prefer to use the term 'ecological' control for those methods not only attuned to the plant's life cycle but also to the dynamics of the ecosystem in which it occurs.

20.3 SOME EXAMPLES OF ECOLOGICAL CONTROL

In the three case histories which follow I shall develop the concept of ecological control further and endeavour to show that control methods which result in a more diverse ecosystem, such as the planned use of fire, competing plants and/or biological control, may make control of terrestrial invasive plants more effective in the long term and more ecological. Mechanical or chemical control methods seem to have the opposite effect of making the invaded ecosystem simpler. Whilst the latter may be desirable in an agroecosystem it is less desirable in the natural ecosystems which are the subject of this volume.

20.3.1 Control of *Hypericum perforatum*

The 200 or more species of *Hypericum* (family Clusiaceae) generally are distributed world-wide in temperate and subtropical regions. Several species with large, bright yellow flowers are valued as garden plants and some for their herbal properties. Because of these two sets of characteristics, *Hypericum* species have been introduced deliberately to regions where several have become naturalized and invasive. Of this latter group, *H. perforatum*, native to a large area of Europe, western Asia and northern Africa, is a particularly invasive perennial species of temperate grasslands and woodlands. It reproduces vegetatively, both from crowns and rhizomes, and sexually from seeds (Campbell and Delfosse, 1984); each plant of *H. perforatum* produces an average of about 30000 seeds (Salisbury, 1942; Tisdale *et al.*, 1959; Parsons, 1973), which are small, sticky and dormant. Genetically, *H. perforatum* is variable, with several hybrids of different ploidy levels known (Robson, 1968). Its breeding system is almost entirely apomictic (Robson, 1968). The species is very variable (Robson, 1968), especially in leaf width.

Hypericum perforatum was brought to the east coast of North America in 1793, to California 100 years later (Tisdale *et al.*, 1959), and to British Columbia soon after (Harris *et al.*, 1969). It is known to have been introduced deliberately to Australia in the 1880s (Parsons, 1973), although A. M. Gill (personal communication) showed that multiple introductions of the plant were highly probable; certainly it was cultivated in Melbourne in 1858 and in Adelaide in 1859. The plant is widespread on both islands of New Zealand (Healy, 1972, Campbell and Delfosse, 1984). *H. perforatum* was introduced to South Africa as a contaminant in seed from Australia in 1942 (Stirton, 1983) and at the end of the 19th century to Chile from Argentina (Villanueva and Fauré, 1959). The genetic identity of the material introduced to these different regions is unknown.

H. perforatum presence reduces the capacity of grasslands to provide grazing for livestock and it alters grassland composition. The plant has been of considerable economic importance to the western USA and southeastern Australia, where formerly productive areas have been abandoned and land use has sometimes been changed radically.

To be effective in the long term, control programmes for *Hypericum perforatum* need to reduce seed production to close to zero; in the short term, reduction in growth of *H. perforatum* and thereby reductions in replenishment of root reserves are essential for control. Some control methods seemingly have no effect on *H. perforatum* populations. As most of the introductions of *H. perforatum* predate the implementation of quarantine procedures, legislation enacted subsequently seeks only to prevent the importation of new and possibly different genetic material to a region. *H. perforatum* is a declared noxious plant in several countries, and in Australia at least this form of legislative recognition seems to have done very little if anything to slow its rate of spread or to bring about a more effective level of control (A. M. Gill, personal communication). Cultivation of invaded land is not an effective control method on its own, even in arable areas (Davey, 1917). Burning increases, rather than decreases, the density of the plant (Dodd, 1920; Moore and Cashmore, 1942), although it may temporarily reduce growth and destroy some seeds (Campbell and Delfosse, 1984). These various methods, considered either alone or together, thus appear to have no effect on limiting the numbers of seeds produced by *H. perforatum* per unit area or on reducing reserves in the root system.

Application of herbicides to stands of *Hypericum perforatum* may reduce growth and seeding of the plant, depending on time of application and level of active ingredient (a.i.) in the herbicide mixture. The present recommendation, based on results from pasture research, is to use either 2, 4-D ester applied at the rate of 3.36 kg a.i./ha at early flowering (late spring) or glyphosate (1.68 kg a.i./ha) applied in summer or early autumn before annual pasture species germinate (Campbell and Delfosse, 1984). This recommendation may affect associated plants to varying extents and may not be appropriate to situations where values other than agronomic ones are important, as in nature reserves. The effectiveness of these recommendations is based on reductions in percentage ground cover of *H. perforatum* after 2 years (Campbell *et al.*, 1979); I can find no results for concomitant reductions in the level of seeding of *H. perforatum* in response to herbicide application or any results for a period longer than 2 years.

The growth of *Hypericum perforatum* may be controlled in pasture by competition from other plants, especially from a mixture of subterranean clover (*Trifolium subterraneum*) and perennial grasses (Moore and Cashmore, 1942). Four and a half years after sowing various pasture species into land heavily infested with *H. perforatum*, Moore and Cashmore (1942) showed that the number of *H. perforatum* plants was reduced by 96% on plots containing the winter-growing *T. subterraneum* and by 64% of the level on an unsown 'control' on plots containing the summer-growing *T. repens*. A perennial grass such as *Phalaris aquatica* was more effective in reducing yield of *H. perforatum* than was the annual grass *Lolium rigidum* over 4 years of measurements in New South Wales. Moore and Cashmore attributed control by this means to shading of the procumbent shoots of *H. perforatum* by the dense canopy of *T. subterraneum* produced in winter. More probably, as Clark (1953) has suggested, the mature plants of *H. perforatum* are being controlled by perennial grasses in summer when competition for moisture is severe, and seedlings of *H. perforatum* are being shaded in winter by a dense canopy of *T. subterraneum*.

A more extreme form of competition imposed on *H. perforatum* plants is to radically change land use of the invaded area from either grassland or woodland to a plantation of *Pinus radiata* which, when canopy closure is reached in 10–12 years, completely shades *H. perforatum*. As a plantation of *P. radiata* lasts about 40 years, it is an effective long-term control method used in several regions, especially northeastern Victoria (Parsons, 1973). Planting of *P. radiata* has the obvious disadvantage, however, that the natural ecosystem is obliterated for ever—one invader is replaced by another with economic value, as in the deliberate promotion of growth of *T. subterraneum*. Use of indigenous species to control *H. perforatum* populations has not been evaluated experimentally, although in southern Australia the indigenous perennial grass *Themeda australis* is able to suppress *H. perforatum* growth (Davey, 1919).

Attempts to control *H. perforatum* by the introduction of insects from the plant's region of origin date back to 1919 when a search began in England for potential biological control agents. Ten insect species were subsequently introduced to Australia from both England and southern France and six are known to have been released in Australia between 1930 and 1940 (Campbell and Delfosse, 1984). Of these insects, only the chrysomelid *Chrysolina quadrigemina* from southern France survived in sufficient numbers to cause significant damage to *H. perforatum* in grassland areas. The adult *C. quadrigemina* exerts its controlling effect by completely defoliating the plant in spring, whilst in late autumn and winter its larvae feed on the young buds and leaves. Various of the other insects introduced attack different parts of the plant but in Australia they have relatively minor effects on plant density at other than a local level. The same insect has been the most successful biocontrol agent for *H. perforatum* subsequently in the western USA (Huffaker, 1967; Dahlsten, 1986), Canada (Harris *et al.*, 1969), Chile (Villanueva and Fauré, 1959) and South Africa (Stirton, 1983), whilst in New Zealand, *C. hyperici* has survived better than *C. quadrigemina* (Harris *et al.*, 1969) and in Hawaii the gall midge *Zeuxidiplosis giardi* seems to be the main controlling agent (Davis and Krauss, 1967; Julien, 1982).

The long-term effects of release of *C. quadrigemina* in Californian rangelands containing *H. perforatum* were followed for up to 10 years by Huffaker and Kennett (1959). These rangelands were probably composed originally of perennial grasses and forbs which were replaced largely by annual plants as a result of overgrazing by domestic livestock (Clements and Shelford, 1939). At the time of insect release (early 1946; Huffaker, 1967) the percentage cover of *H. perforatum* plants varied between 26 and 51% depending on site (Figure 20.1), with other plant cover being from other invasive plants, some legumes and a group of annual forage grasses. As a result primarily of the winter feeding of the larvae of *C. quadrigemina* (cf. adult beetles feeding for a shorter period in spring–summer), Huffaker and Kennett (1959) measured a substantial reduction in *H. perforatum* cover to almost zero in a period of 4–5 years and a concomitant increase in cover of all other plant groups, especially of annual forage grasses. At one site in Humboldt County the native perennial grass *Danthonia californica* increased in cover. At no site did other noxious plants show any consistent increases as *H. perforatum* cover decreased. The larvae of *C. quadrigemina* kept the plants of *H. perforatum* defoliated from midwinter through to early spring of each year and hence root reserves were progressively depleted. With further time from release, the seed crop (number and yield?) was also depleted, although Huffaker and Kennett (1959) give no quantitative data on this aspect. We may conclude that entomological control of *H. perforatum* has been highly successful in California. In fact, St John's wort has been removed from the state's list of primary noxious plants.

In regions other than California the success rate of entomological control has not been as satisfactory, however (Huffaker, 1967). At most Californian sites

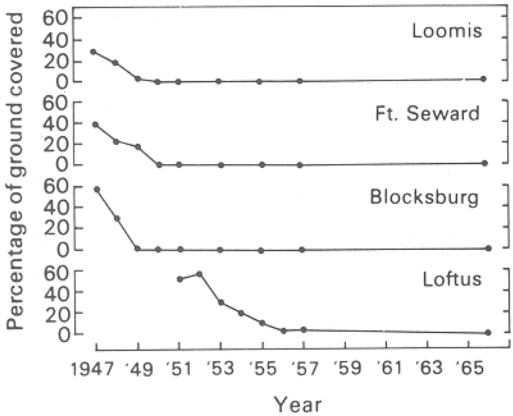

Figure 20.1. Reduction in ground cover of *Hypericum perforatum* by *Chrysolina quadrigemina* at four sites in California for the period 1947 to 1966 (redrawn from Huffaker, 1967)

nearly all plants died as a result of a single severe attack by *C. quadrigemina* larvae and a very high degree of control of *H. perforatum* (namely, greater than 99%) was maintained over 16 years of measurement (1950–1966) at three sites (Figure 20.1) (Huffaker, 1967). Huffaker claimed an 80–90% level of control to be satisfactory because domestic animals can feed on light infestations without ill effect and thereby help to maintain a low plant density. In southeastern Australia the level of mortality of *H. perforatum* was much less (about 54% averaged over 16 sites) and Huffaker attributed this significant difference to the differing incidence of summer rainfall in the two regions (Figure 20.2). Absence of summer rain in many areas of California, as represented by Loomis, Alderpoint and Redding (Figure 20.2), kills *H. perforatum* plants already defoliated by *C. quadrigemina* larvae. Summer rainfall in southeastern Australia, as represented by Myrtleford, Benalla and Mudgee (Figure 20.2), promotes regrowth of the defoliated plants and enables them to survive. The insects were imported originally from Mediterranean France to southeastern Australia and then were sent to California after at least 10 years' acclimatization in Australia. Obviously, the insect's phenology was still attuned to a typical summer-dry mediterranean-type climate. Huffaker observed a greater level of success for *C. quadrigemina* in South and Western Australia, as represented by Clare and Dwellingup (Figure 20.2), because these regions are much more summer-dry than are northeastern Victoria and southern New South Wales. In these latter regions the plant continues to be a major invader of nature reserves and national parks, such as Kosciusko.

H. perforatum increased initially in grasslands in several regions of the world from the sites to which it was introduced deliberately because it was able to invade ground made bare as a result of overgrazing by domestic stock. The

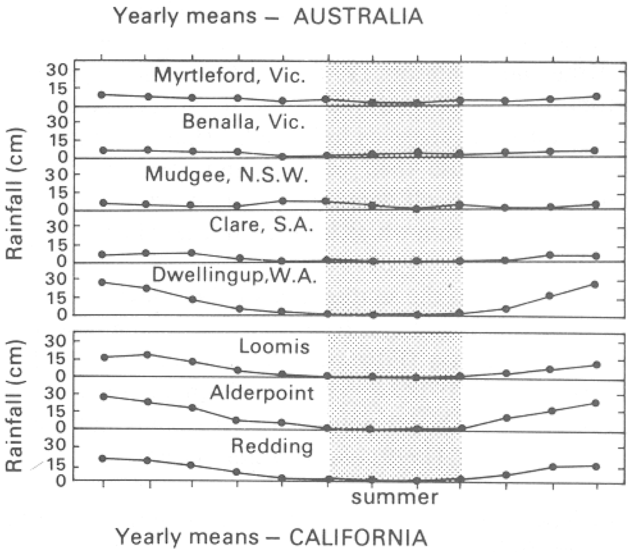

Figure 20.2. Patterns of annual rainfall, as long-term averages at five locations in southern Australia and three in California, all representative of regions invaded by *Hypericum perforatum*. Periods of summer rainfall have been synchronized and centred to show contrasts (redrawn from Huffaker, 1967). Entomological control has been highly successful at Clare, Dwellingup, Loomis, Alderpoint and Redding (see text)

perenniality, profuse seeding and deep root system of *H. perforatum* enabled it to compete successfully with annual grasses and forbs and to become dominant within about 20 to 30 years from its time of naturalization. Because seeds of *H. perforatum* may remain viable in soil for at least 20 years or longer (A. M. Gill, personal communication), *H. perforatum* has the capacity to germinate and reinvade an area should there be significant reductions in vegetative cover at any time over this long period. Clark (1953) commented appropriately concerning *H. perforatum* in plantations of *P. radiata* that '*Hypericum* is generally the last plant to be excluded by the pines and the first to reappear' (p. 98). In the temperate-climate regions which *H. perforatum* has invaded, I conclude that control will always be more effective if it arises from the long-term interaction between the effects of one or several natural enemies and of competing perennial plants as modified by appropriate grazing regimes and by the incidence of summer rainfall.

20.3.2 Control of *Eupatorium* spp.

Three species of the genus *Eupatorium* (family Asteraceae), all originating in Central or South America, are common invaders of formerly forested land in subtropical regions. The three species are *Eupatorium odoratum* (syn. *Chromolaena odorata*, King and Robinson, 1970a), *E. adenophorum* (syn. *Ageratina adenophora*, King and Robinson, 1970b) and *E. riparium* (syn. *Ageratina riparia*, King and Robinson, 1970b). Although the three species have been assigned recently to two different genera as indicated, I shall consider them collectively whenever possible, because their ecology and their invasive properties are basically similar. They are all perennials, usually with woody rootstocks and upright branching stems from which large quantities of wind-dispersed seeds are produced.

E. odoratum is native to the southeastern USA, Mexico and the West Indies south to Argentina and is widely adventive in Africa and Southeast Asia. It has been introduced to Nigeria (Edwards, 1977), India (Kushwaha *et al*., 1981), Thailand (Zinke *et al*., 1978, as cited in Ramakrishnan *et al*., 1981), the Phillippines, Sumatra and Natal, South Africa (Erasmus and van Staden, 1986b). Contrary to Holm *et al.*, (1979), *E. odoratum* is not yet known to occur in Australia.

The species depends both on sexual and vegetative reproduction for increase. In north eastern India it can produce as many as 48000 seeds per plant (Kushwaha *et al*., 1981). Seeds of *E. odoratum* apparently do not survive in soil for long although there is some evidence for seed dormancy (Erasmus and van Staden, 1986b). *E. odoratum* is variable (Edwards, 1977; Edwards and Stephenson, 1974).

E. adenophorum was introduced deliberately from Mexico to Maui in about 1864 as an ornamental and it now occurs on all the other major Hawaiian islands except Kaui (Bess and Haramoto, 1972). It also occurs in Australia on the northern coast of New South Wales (Auld and Martin, 1975) and in Queensland (Dodd, 1961). For this region, Auld (1969) showed that there was about a 75% chance of the occurrence of a dense population of *E. adenophorum* in areas which had a combination of steep land ($>20°$), no tree cover and an annual rainfall greater than 1900 mm. *E. adenophorum* also occurs in India (Ramakrishnan and Misra, 1981), the northern region of New Zealand, Nigeria, the Philippines, Thailand, Trinidad (Holm *et al*., 1979) and California (Auld, 1972).

Population increase in *E. adenophorum* occurs by both sexual and vegetative reproduction. *E. adenophorum* is an apomictic triploid which forms seeds by agamospermy (Holmgren, 1919, as cited by Auld and Martin, 1975). Seeds (cypselas) germinate in late summer in New South Wales (Figure 20.3) (Auld and Martin, 1975) and they have an absolute requirement for light (Auld and Martin, 1975), so that germination is effectively limited to sites free from plant competition. Seedlings have a high relative growth rate and are fully established within 8 weeks of germination. New vegetative growth begins as resprouts from the crown of the plant with the first sustained rains in summer (Auld and Martin, 1975). In India invasion occurs in early successional vegetation up to 6 years from clearing of forest; mortality of seedlings reached 100%

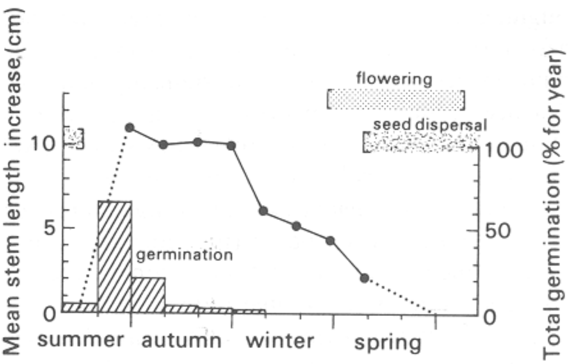

Figure 20.3. Seasonal growth and germination of *Eupatorium adenophorum* in eastern coastal Australia. Monthly increase in stem length, monthly germination and length of flowering and seed dispersal periods are shown (redrawn from Auld and Martin, 1975)

in vegetation older than this and mortality of vegetative resprouts followed a similar pattern (Ramakrishnan *et al*., 1981). As for *E. odoratum* (see earlier), *E. adenophorum* is also variable (Ramakrishnan *et al*., 1981), albeit by different environmental and genotypic means.

E. riparium, another invasive species in the genus co-occurs with *E. adenophorum* in eastern Australia (Auld and Martin, 1975) and northeastern India (Ramakrishnan *et al*., 1981). It is an herbaceous perennial with a scrambling habit. It is rarely as troublesome as *E. adenophorum* and, at least in Australia, has a more restricted distribution although it was introduced much earlier.

In most countries in which *Eupatorium* species occur, their presence reduces stocking capacity of grazing land and restricts the movement of stock and machinery. They reduce carrying capacity because they compete with more desirable pasture plants and they contain aromatic chemicals which make the foliage unpalatable to cattle (Ramakrishnan and Misra, 1981). In south east Asia generally, the presence of *Eupatorium* spp. can arrest secondary succession of former forested land which was cleared for short-term cropping; only by lengthening the slash-and-burn cycle can their deleterious effects be overcome (Ramakrishnan *et al*., 1981). *E. odoratum* is highly flammable and thus its presence increases the chance of fire which may further retard secondary succession. *Eupatorium* spp. can limit early growth in plantations of forest tree species, of coconuts in Sri Lanka and of other tropical tree crops (Anon., 1977).

Control of *E. adenophorum* by cultivation is feasible in some arable situations because its root system is usually confined to the top 40 cm of soil (Auld and Martin, 1975). These authors assessed the potential for root segments cut from different positions on the plant to regrow. They showed that only cuttings which included part of the crown regrew and that regrowth took place only from crown tissue. Thus ploughing which 'uproots' the crown of the plant can be an effective control method for agricultural land, but slashing of shoot growth above the level of the crown will be ineffective. Because of the difficulty of uprooting crowns on steep land, and hence of limiting regrowth, most mechanical control methods have had only limited success in the control of this species (Auld and Martin, 1975) and are usually not applicable to nature reserves.

Herbicidal control of *E. odoratum* has been investigated because of the plant's economic impact on plantation cropping (Erasmus and van Staden, 1986a). Triclopyr, if applied at the time of year and rate recommended, caused at least a 90% mortality of shoots in a dense infestation. Erasmus and van Staden considered that such a result would appreciably decrease the detrimental effect of *E. odoratum* on desirable plantation species as well as reduce its potential as a fire hazard. The level of shoot mortality obtained would undoubtedly cause a major decrease in seed production, but the extent of that reduction was not measured.

Many chemicals have been used to control dense populations of *E. adenophorum* in pasture (Auld, 1972). Auld and Martin (1975) concluded that progress on an effective chemical control programme for *E. adenophorum* was restricted by the requirement for high volume application of herbicides and by seasonal variability in results: their conclusion probably holds for *Eupatorium* spp. generally and especially when considered in the ecological context of this review.

Competing plants have been shown to control the growth and reproduction of *Eupatorium* spp. in two ecosystems. On land cleared permanently for grazing *Eupatorium* invades poor quality pasture dominated by species such as *Axonopus affinis* (carpet grass). More productive grasses such as *Pennisetum clandestinum* (kikuyu) need to be established during spring when the probability of effective rainfall is low and before *Eupatorium* seeds germinate in late summer (Auld and Martin, 1975). As *Eupatorium* seeds require light to germinate (Erasmus and van Staden, 1986b) and seedlings can tolerate a shading level of as much as 10% of full sunlight (Auld and Martin, 1975), the growth of pasture grasses must be early and substantial to limit growth of *Eupatorium* shoots in this way. Growth of *Eupatorium* spp. may also be controlled in the long term by shading by the canopy of tree species either regenerating naturally or planted as tree crops. This is an effective 'natural' control method provided that the duration of the forested stage is longer than the viability of seeds in the soil or, in the case of *E. adenophorum*, root crowns. In northeastern India the period of tree cover required is at least 20 years (Ramakrishnan *et al.*, 1981).

Biological control of *E. adenophorum* has been tried with some success in Hawaii (Bess and Haramoto, 1959, 1972,), Australia (Dodd, 1961) and India (Rao *et al.*, 1981) using primarily a tephritid gall fly *Procecidochares utilis*. This fly was introduced from Mexico to Hawaii in 1945 and its progressive effects in reducing the abundance of *E. adenophorum* on Maui especially have been studied over a 22-year period (Bess and Haramoto, 1959, 1972). The same insect was introduced from Hawaii to eastern Australia in 1952 (Dodd, 1961) and to India in 1963 (Rao *et al.*, 1981). On Maui the release of *P. utilis* has led to substantial reductions in the invasiveness of *E. adenophorum* in the long term. No regrowth of the plant has occurred on areas from which it was freed between 1950 and 1957 (Bess and Haramoto, 1972). In general, the degree of control achieved is related to rainfall—control on Maui has been good in low rainfall areas but negligible in higher rainfall areas, where mowing and herbicide applications are still necessary.

In both eastern Australia and India *P. utilis* seems to have been less effective at limiting *Eupatorium* numbers than in Hawaii because, when introduced to these former regions, *P. utilis* has been parasitized by several native hymenoptera (Dodd, 1961). Apparently concurrently with the establishment of *P. utilis* in Australia, the fungus *Cercospora eupatorii* appeared, possibly arriving as a contaminant of a consignment of gall flies from Hawaii (Dodd, 1961). *C. eupatorii* is specific to *Eupatorium* and is damaging to seedlings especially; it is native to America (Dodd, 1961). Attack of seedlings by this fungus is probably a factor limiting further spread of the plant in southern Queensland. The fungus is now being evaluated as a candidate organism for introducion to South Africa to control *E. odoratum* (M. J. Morris, personal communication). In Australia *Eupatorium* is also attacked by a native crown-boring beetle of the genus *Dihammus*, which can weaken plants to the point where pasture species can compete successfully in most open, dry situations. Biological control of *Eupatorium* has been more effective in situations such as on Maui where growth of pasture grasses (e.g. *Pennisetum clandestinum*) has also exerted a controlling effect.

Control of *Eupatorium* spp. by any means depends on achieving substantial reductions in seed numbers and in the amount of regenerative tissue in root crowns. Despite the considerable literature on *Eupatorium* control (Anon., 1977), I can find no data on these critical measures. Bess and Haramoto (1959) presented data on the comparative growth in height of *E. adenophorum* plants infested with *P. utilis* in relation to the developmental stage of the fly; they showed that infestations of shoots by *P. utilis* led to a reduction in height growth (Figure 20.4) but the relationship of this reduction to seed output is not clarified. Erasmus and van Staden (1986b) showed that application of some herbicides could cause 100% mortality in *E. odoratum* shoots in the short term. Where control was less than 100%, the relationship between incomplete shoot mortality and seed production is not clear, nor are the longer term consequences of the treatment on growth and reproduction of the species apparent. Only in the documented case of *E. odoratum* and *E. adenophorum* in different-aged communities in northeastern India have these data been collected (Table 20.1). These results show a complete reduction in seed production after more than 5 years for *E. odoratum* and after 10 years for *E. adenophorum* as the forest reverts to its former state. Substantial reductions in plant density took longer to occur in these systems, from which we may conclude that established plants of each species may be long-lived.

I conclude that the most effective ecological control for *Eupatorium* spp., at least in eastern Australia, as in India, may be to allow the invaded land to revert to

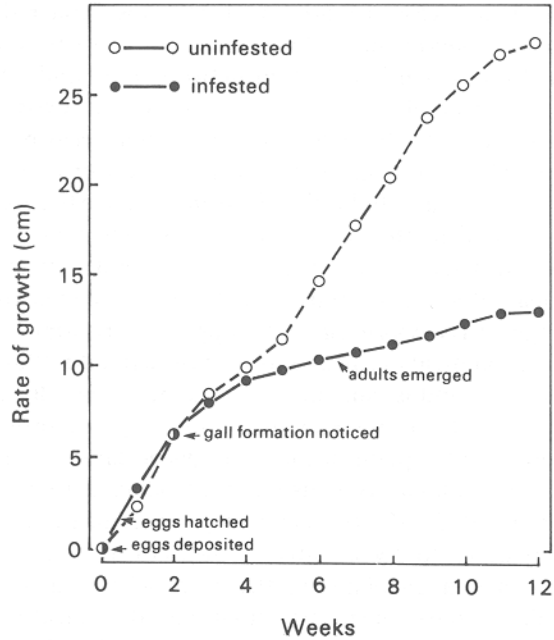

Figure 20.4. Comparative height growth of plants of *Eupatorium adenophorum* infested or not infested with the fly *Procecidochares utilis* grown in a glasshouse. The duration of the developmental period of the fly is shown (redrawn from Bess and Haramoto, 1959)

Table 20.1. Reproductive characteristics of *Eupatorium adenophorum* (*a*) and *E. odoratum* (*o*) in 'fallows' of different ages in northeastern India (from Table 3 of Ramakrishnan and Misra (1981) and Table 3 of Kushwaha *et al.* (1981) respectively)

	Age of 'fallow' (years)								
	1		3		6	5	10		15^{+}
	a	*o*	*a*	*o*	*a*	*o*	*a*	*o*	*a*
Plants/m²*	8	2	28	5	24	35	2	3	3
Capitula/m²	536	428	1988	14635	1287	910	62	—	—
Seeds/m²	33768	12818	123256	436185	79794	13975	3782	—	—

*Excluding seedlings
$^{+}$20-year fallow measured and similar to 15 years for *a*

subtropical forest and/or to deliberately plant in chosen indigenous tree species to compete with other invasive plants such as *Cinnamomum camphora* or *Baccharis halimifolia*.

20.3.3 Control of *Acacia longifolia* and *Chrysanthemoides monilifera*

The two previous case histories have involved essentially one-way movements of invasive plants; my next case history is more a two-way exchange. In this section I shall review the ecology and control of several woody shrubs native to two regions of mediterranean-type climate. Some southeastern Australian species in the widespread genus *Acacia* (Mimosaceae) are invasive in South Africa, whilst two subspecies of the South African species *Chrysanthemoides monilifera* (Asteraceae) are invasive in southeastern Australia. The main coastal species of *Acacia* being displaced by *C. monilifera* ssp. *rotundata* is the structurally similar *Acacia longifolia* (Weiss and Noble, 1984a), which is itself strongly invasive in South African shrubland (Stirton, 1983), which, in turn, may contain *C. monilifera* ssp. *monilifera* as a common component.

Acacia longifolia varies in eastern Australia, especially in phyllode width and growth habit. Two distinct varieties are recognized, viz. *A. longifolia* var. *longifolia* (Sydney golden wattle), a tall shrub of coastal forests, and *A. longifolia* var. *sophorae* (coastal wattle), a low, bushy spreading shrub of coastal sand dunes. There is some doubt as to the taxon present in South Africa (Weiss, 1983) as var. *sophorae* is itself variable. The var. *sophorae*, although originally introduced deliberately to South Africa in the 1820s and 1830s (Shaughnessy, 1980) was first identified as an invasive plant only as recently as 1945 from a riverine occurrence (Boucher and Stirton, 1983), possibly because it can be confused in the vegetative state with *A. cyclops* and/or *A. saligna*. Despite the long time since its introduction, the distribution of *A. longifolia* is still 'relatively restricted' (Boucher and Stirton, 1983, p. 47). *A. longifolia* has also been introduced to several regions of the Americas and is naturalized in Uruguay, Argentina and California, but apparently not invasive there (Boucher and Stirton, 1983).

Two (ssp. *monilifera* and ssp. *rotundata*) of the six subspecies of *Chrysanthemoides monilifera* described from southern African material (Norlindh, 1943), have been introduced to Australia at various times. *C. monilifera* seems to be invasive only in Australia—I can find no reference to its occurrence elsewhere. *C. monilifera* ssp. *monilifera* occurs in coastal areas of Australia from about Sydney, New South Wales, to Streaky Bay in western South Australia (H. McBeth, personal communication), as well as in Tasmania and as isolated occurrences in southwest Western Australia and at inland sites in northern Victoria and southwestern New South Wales (Lane, 1984).

C. monilifera ssp. *rotundata* was introduced to Stockton, near Newcastle, in 1908 (Gray, 1976) whence it has both spread naturally and been planted deliberately (to stabilize sand dunes and to revegetate areas following mining) northwards and southwards of the original site along the eastern coastline of New South Wales and Queensland. The subspecies is now an invasive plant of major importance to nature conservation in this region, where it may co-occur with *C.*

monilifera ssp. *monilifera* on coastal dune systems, but usually seaward of the latter. Some hybridization may occur between the two subspecies (Weiss, 1983), but is of apparently limited occurrence both in South Africa and Australia.

Both species invade disturbed areas of natural vegetation where they may displace indigenous plants. Both species produce large numbers of long-lived dormant (hard) seeds which may be stored in the soil. Wildfires in both countries occur periodically and are usually of a sufficiently high intensity to stimulate the soil-stored seeds to overcome dormancy, to germinate prolifically and thereby to ensure seedling establishment. Alternatively, in the absence of fire, germination may occur after weathering of the fruits. Seeds of both species are also dispersed naturally by birds in both countries. It seems then as though *Acacia longifolia* and *Chrysanthemoides monilifera* are almost ecological analogues of one another in South Africa and Australia respectively, the only really significant difference for their control being that *C. monilifera* spp. *rotundata*, and to a lesser extent ssp. *monilifera*, are also able to regenerate by resprouting after fire.

Both species may be controlled mechanically—slashing of mature *Acacia longifolia* shrubs and some hand-pulling of young plants in South Africa, and hand-pulling, especially of seedlings, of *Chrysanthemoides monilifera* in south-eastern Australia, as mentioned earlier. These methods reduce the numbers of plants and if hand-pulling follows a fire, the method is probably effective at reducing the numbers of soil-stored seeds as well.

An appropriate fire regime can control *C. monilifera* effectively. For instance, Lane and Shaw (1978) showed that if a prescriptive fire of low intensity followed a wildfire of higher intensity, the plant density of *C. monilifera* ssp. *monilifera* was greatly reduced. Weiss (1983) advocated a similar fire regime to control *C. monilifera* in coastal New South Wales, provided the second fire could be timed before the commencement of flowering of the seedlings induced to germinate by the first fire. In this way, the numbers of soil-stored seeds could be considerably reduced. Alternatively, Weiss (1983) suggested an application of herbicide, either applied broadly over an invaded area or as a 'spot' spray, to replace the first fire. The use of a high-intensity fire followed by a second has yet to be tried for *A. longifolia* in South Africa.

As at March 1978 no herbicide was registered for chemical control of *A. longifolia* in the Cape Province (Stirton, 1983). Chemical control of *C. monilifera* is registered and recommended in Australia and involves a range of herbicides, dilution rates and methods of application (Cooney *et al.*, 1982; Love, 1984) to either mature plants or to seedlings. Profuse germination may follow such treatments and seedlings establish densely. Continued control measures are then needed for the next 3 or 4 years to reduce the seed supply in the soil if the method is to be effective on its own.

C. monilifera seedlings appear to establish only poorly on areas where competition from dense grasses and herbs is present, such as *Lomandra longifolia* (Weiss and Noble, 1984a); conversely, they are very vigorous in the absence of competition, e.g. on rocky outcrops, cliffs and pathways (Lane, 1984) and as initial colonizers after disturbance. When seedlings of both *A. longifolia* and *C. monilifera* were grown together in pots, *C. monilifera* was found to be more competitive than *A. longifolia* and this competitive advantage was lessened, but not reversed, under conditions of water stress (Weiss and Noble, 1984b). Apart from these results little is known of the characteristics of indigenous plants which may be successful competitors against either species.

A biological control programme for *Acacia longifolia* has been commenced by South Africa (Neser and Kluge, 1986) and a programme on *Chrysanthemoides monilifera* will commence shortly. In each case there is optimism about the chances for success (see, for example, Neser and Morris, 1984, for *C. monilifera*). One of the most hopeful candidates for *C. monilifera* control is a group of tephritid flies in the genus *Mesoclanis* (Munro, 1950) which render the seeds inviable while they are still on the mature shrubs.

Weiss and Milton (1984) provided an excellent quantitative basis to assess the effectiveness of any control programme (see Table 20.2). They tested the thesis that the reproductive output of the invader is higher than the indigene, using *A. longifolia* and *C. monilifera* in both Australia and South Africa. *A. longifolia* had about a thousand-fold fewer viable seeds in Australian soil than in South Africa and conversely, *C. monilifera* had about fifty-fold less viable seeds in South African soil than in Australia, although the number of whole seeds of *C. monilifera* in soil was similar in the two countries. Thus the level of predation of buried seeds was greater for *C. monilifera* in South Africa (see also Noble, this volume). For *A. longifolia* in Australia fewer seeds were incorporated into the soil seed pool because they had been preyed upon earlier in the life cycle. If control programmes for these two groups of plants, especially those integrating different control methods (Groves, 1984), could all be assessed in terms of the differential reproductive outputs presented in Table 20.2, then a truly ecological basis for control of invasive plants could be formulated.

Table 20.2. Reproductive characteristics of *Acacia longifolia* and *Chrysanthemoides monilifera* ssp. in Australia and South Africa (modified from Table 1 of Weiss and Milton, 1984)

	A. longifolia		*C. monilifera*	
	Australia	South Africa	Australia	South Africa
Main flowering time	Aug.–Oct.	July–Sept.	Apr.–Aug.	June–Sept.
Ripe seeds/m^2	364	2923	4450	2160
Soil seeds/m^2				
fragmented	25	—	6380	2352
whole	7.5	7600	2475	2320
viable	5.6	7370	2030	46

20.4 SUMMARY AND CONCLUSIONS

Of the invasive plants considered in the preceding sections some common attributes emerge.

1. They have nearly all been introduced deliberately and usually because of their perceived value to horticulture. The only exceptions seem to be the accidental introductions of *Hypericum perforatum* to South Africa and of *Chrysanthemoides monilifera* ssp. *rotundata* to Australia, although the latter was then spread deliberately because of its perceived value for sand stabilization.
2. Because they have usually been introduced many times, some genetic variation occurs, which may be expressed both morphologically and physiologically.
3. All species are early colonizers of disturbed sites in their countries of origin.
4. Their seedlings have a high growth rate which can be reduced substantially by shading.
5. Plants produce large numbers of seeds early in their life cycles and a proportion of seed is usually dormant.
6. They can reproduce vegetatively from perennial rootstocks once they are established, with the apparent exception of *Acacia longifolia*.
7. The leaves of *H. perforatum* and *E. adenophorum* can be toxic to domestic herbivores.

These plants thus have many of the characteristics of invasive plants generally (see Noble, this volume). Given these attributes in common, what aspects of their control may also be general? I shall present four principles of control which seem to be general for invasive plants in nature reserves.

1. One aspect of control, and a recurring theme throughout this review, is that only rarely is one control method effective in limiting the numbers of propagules of invasive plants per unit area. A rare exception seems to be the entomological control of *Opuntia* spp. by *Cactoblastis* and this successful case history has been so widely quoted as to give an incorrect interpretation for the success of entomological control methods generally. More often, as the case histories presented previously show, it has been a combination of methods which has led to effective control of terrestrial invasive plants. Examples of a conscious integration of methods for control of invasive plants in natural systems are few (see Kluge *et al.*, 1986) and even more rarely is such an integrative approach itself integrated with the dynamics of the natural ecosystem being invaded.
2. Control methods which simplify the ecosystem and reverse the trend towards diversification of the system seem to be more prone to subsequent invasion by other groups of invasive plants, the end result of such actions being to replace one invasion with another. On this basis control methods which add to diversity, e.g. a marked reduction in fire frequency, deliberate promotion of

competing plants, use of arthropods and/or fungi, have the potential to produce an ecosystem which may be better able to resist further invasion.

3. Once initiated, control methods have to be maintained (see also Macdonald *et al.*, this volume). This need for continued action has not always been recognized and a short-term interruption to a control programme can have disastrous consequences in the longer term, e.g. as with chemical control of *Cytisus scoparius* in a national park in eastern Australia (see earlier).
4. An aspect of previous research on control of invasive plants is that the monitoring of control is sometimes inadequate, either because it is not done at all or else it is done for too short a time. A further deficiency is that often the index measured may not always be the critical one by which to assess the effectiveness of control in ecological terms. As a previous section showed, a control programme which measures reduction in yield of an invasive plant such as *Hypericum perforatum* may be appropriate in pasture research but one which measures the number and viability of seeds per unit volume of soil and the change in cover of associated species (see Huffaker and Kennett, 1959) may be more appropriate for *H. perforatum* control in a nature reserve.

Invasions have been occurring naturally for millennia. This chapter has been concerned with a few more recent invasions of plants not indigenous to the region being invaded. As reserves of natural ecosystems become increasingly the only remnants of vegetation types formerly widespread, a study of invasive plant control becomes more urgent if those ecosystems are to be retained and conserved for the future. In this contribution I have assessed internationally the present status of research on some examples of invasive plant control in three regions—temperate grassland/woodland, subtropical forests and mediterranean-climate shrublands. If other plant invasions in other regions are to have a similar potential for successful control a major requirement is to know more of the ecology of the species or species aggregate in its country of origin. For obvious reasons researchers in biological control have been better able to contribute to such knowledge. But legislators, appliers of herbicides and manipulators of vegetation dynamics also need to be more international in their approach to a control programme for terrestrial invasive plants. I hope this review may be catalytic in bringing about such a widening of outlook and approach to all controllers of invasive plants.

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