Biological Invasions: a Global Perspective
Edited by J. A. Drake *et al.*

CHAPTER 2

Patterns, Extents and Modes of Invasions by Terrestrial Plants

VERNON H. HEYWOOD

2.1 INTRODUCTION

The botanical traveller soon becomes aware of the fact that there is scarcely a region in the world where the vegetation has not been disturbed to some degree by man's activities, usually leading to the introduction of alien species. The extent and pattern of these invasions varies widely from one part of the world to another and it is the aim of this paper to seek any regularities or generalizations that might be made concerning either the geography, origins or taxonomic affiliations of the invader species. As Harper (1977) notes, man has introduced a new order of magnitude into distances of dispersal, and through the transportation, by accident or design of seeds or other propagules, through the disturbance of native plant communities and of the physical habitat, and by the creation of new habitats and niches, the invasion and colonization by adventive species is made possible.

In some cases the invaders make their presence felt only too conspicuously, as in the Mediterranean Basin where much of what until 200 years ago was regarded as native vegetation is in fact man-modified, such as the matorral, garrigue, etc. Ellenberg (1979) observes that the reason that he travelled to Peru and other tropical countries was to study 'real nature' but after several months of field work he could not fail to discover traces of man's impact there too, even in the Amazonian rainforest area. Human influence was apparent too in the remote highlands and lonely dry valleys of the Pacific slopes. The ecosystems of the Andes are far from being untouched nature and Mediterranean people introduced their agropastoral system into tropical mountainous countries where similar landuse systems had been practised for thousands of years previously.

A global survey of the pattern and extent of invasion by terrestrial plant species is bound to be anecdotal to a degree because of the extreme diversity in the sources and in reliability of the available data. Apart from the obvious lack of a fixed geographical starting point for a global overview, the main factor that makes my task virtually impossible is the lack of data and the wide inconsistency of those that can be traced in the literature. For many parts of the world, notably in temperate regions, Floras or catalogues listing native plants exist and often analyses of adventive or weed species. However, the terms used and the criteria employed (when they can be determined) vary widely between these surveys. As discussed below, the situation in many parts of the tropics and subtropics is much more difficult in that few Floras or handbooks exist and those that do are usually highly incomplete.

As Webb (1985) in a perceptive paper on the criteria for presuming native status notes, 'Most Floras make some attempt to distinguish between native and introduced species though some of them do so half-heartedly. But their authors seldom disclose the evidence which has led them to their decision, and all too often it would appear that the assignment has been made by copying from earlier works or on essentially intuitive grounds.' This problem is also discussed by Smith (1986) in connection with annual species of *Bromus* in Europe and South west Asia.

In reviewing literature for this paper, I have become acutely conscious of the difficulties of interpreting the available data because of either failure to distinguish between different categories of introduction—between native and introduced weeds, between casual and established (naturalized) weeds and/or aliens and so on. Invaders have been termed aliens, immigrants, exotics, adventives, neophytes, xenophytes or simply introduced species. Invaders may be native to the region or country but not to the community in question. Naturalization of species may occur within their native country or region but outside their natural geographical range (Robinson *et al.*, 1986; Robin and Carr, 1986). Two useful definitions are: 'Plant invaders are alien plants that invade and oust native vegetation' (Stirton, 1979) and 'Aliens... can be exotic species (plants introduced from overseas) as well as indigenous species (...native species) that have successfully taken up residence in plant communities in which there is good reason to believe that the species are newcomers' (Williams, 1985, citing Michael, 1981). Mack (1985) regards as an invader any taxon entering a territory in which it has never occurred before, regardless of the circumstances (e.g. transoceanic migrations). All entrants even if they fail to establish will be regarded as invaders, including recurring Holocene migrations. The term weed, however, is a value judgement.

There is a long-recognized connection between habitat disturbance or environmental alteration by humans and the invasion and spread of aliens. The invasion process is divided by Groves (1986) into three main stages: introduction, colonization and naturalization. Introduction itself is a function of dispersal and Berg (1983) distinguishes between dispersal and successful (and effective) dispersal, i.e. followed by establishment, since only successful dispersal can bring about distributional and evolutionary change. He quotes Fosberg: 'Transport without establishment has no significance.' Colonization depends in turn not only on successful dispersal but on successful reproduction. And this according to

Stebbins (1971) depends on a compromise between the often conflicting demands of three separate processes—diaspore production, plant dispersal and establishment which in turn depend on a whole series of factors such as pollination biology, seed production, predation, size, vigour, longevity, storage, germination requirements, seedling vigour, establishment and so on.

Invasions can proceed without any apparent disturbance, as in the case of pines from temperate biomes which are repeatedly introduced into tropical and subtropical areas, an example being *Pinus radiata* in Australia which was found to invade native eucalyptus forest from adjacent populations (Burdon and Chilvers, 1977).

Another problem stems from the different criteria used, implicitly or explicitly, in the application of the terms: for example the term neophyte (or neosynanthropic plant) is regarded by some as post-Columbian, as followed, for example, by *MedChecklist* (Greuter *et al.*, 1986) whilst archaeophytes are those that were present in the area concerned before that time. Even this dividing line is disputed—*MedChecklist* uses 'before the end of the fifteenth century' while Webb (1985) proposes 'about A.D. 1550, when as a result of voyages of discovery, plants from America and Asia came flooding in an unprecedented scale'. Neophytes, are on the other hand, regarded by some authors as much more recent introductions (cf. Dafni and Heller, 1982). Also archaeophytes are sometimes regarded as part of the native flora (as in *MedChecklist*) while others consider native plants as those which either evolved *in situ* or which arrived in the area concerned before the beginning of the Neolithic period or which arrived there subsequently by a method entirely independent of human influence.

These, then are some of the factors that have to be taken into account in trying to interpret the literature on invasions on a global scale. It has to be noted, however, that it is only in the case of selected countries or regions such as Australia, Europe, North America, South Africa, New Zealand, that the literature is sufficiently detailed for such problems to be really troublesome. Usually the difficulty is simply lack of information of any depth or quality. A major source of information is the very large weed literature, which I have used extensively. As we have already seen, however, not all weeds are invaders and in any case weed information for many parts of the world is sadly defective.

2.2 TAXONOMIC PATTERNS: NAMES AND NUMBERS

It is evident from what we noted above about the floristic literature that it is virtually impossible to give a reliable estimate as to the numbers of taxa worldwide that can be regarded, however loosely, as invaders. Theoretically this could be done by making a country-by-country survey of the whole world and listing those species that have been recorded as invaders or aliens and then editing the result. Alas this is no more feasible than attempting to calculate the total numbers of native species, let alone aliens, due to the gaps in the floristic

Table 2.1. Distribution of plant species throughout the world (after Heywood, 1985a)

	Flowering plants	Fungi	Ferns	Mosses
Worldwide	250 000	120 000	12 000	14 000
Tropical	160 000	90 000	11 000	9 000
Tropical Africa	30 000	20 000	1 000	1 500
Tropical Asia	35 000	20 000	6 000	2 000
Tropical America	95 000	50 000	5 000	4 000
Europe	11 500	—	150	1 100

literature. We can, however, present some figures and make some extrapolations or approximations from these.

Firstly, some statistics on the numbers of species in the various groups of plants are needed to provide a context. These are summarized in Table 2.1. It should be noted that even these estimates are disputed and the figures for tropical groups are the least reliable. Toledo (1985) in a review of Latin American floristics suggests higher figures for the New World tropics than are normally accepted and the figures for individual countries also vary quite widely. If has been suggested that there are up to 50 000 species of angiosperms in Brazil while other estimates put the figure at no more than 30 000. What is evident, however, is that the greatest floristic richness is found in regions where our knowledge of the flora is least studied.

Perhaps we should note in passing that when it comes to aliens numbers of species are not necessarily an indication of the extent to which the vegetation of the area is invaded or otherwise affected since species vary widely in their invasive capacity, aggressiveness, degree of spread and permanence and their interaction with the natural ecosystem. The literature is full of examples of single species which have shown dramatic spread and major impact on plant communities (see below).

The only global assessments of aliens are a few publications on weeds, notably Holm *et al.*, *The World's Worst Weeds* (1977). In this valuable compendium it is suggested that certainly fewer than 250 plant species have become important weeds of the world (as judged by one particular set of criteria) and they list the 18 most serious weeds in approximate order of their troublesomeness to the world's agriculturalists. These are listed below. Those marked with an asterisk are regarded as a group apart since they are not only cited more often than other world weeds but are ranked as the greatest troublemakers in the largest number of crops.

*1. *Cyperus rotundus*
*2. *Cynodon dactylon*
*3. *Echinochloa crusgalli*

*10. *Chenopodium album*
*11. *Digitaria sanguinalis*
*12. *Convolvulus arvensis*

*4. *Echinochloa colonum*
*5. *Eleusine indica*
*6. *Sorghum halepense*
*7. *Imperata cylindrica*
8. *Eichhornia crassipes*
9. *Portulaca oleracea*
13. *Avena fatua* etc.
14. *Amaranthus hybridus*
15. *Amaranthus spinosus*
16. *Cyperus esculentus*
17. *Paspalum conjugatum*
18. *Rottboellia exaltata*

Looking through this list many will be surprised not only by inclusions but by omissions. Certainly such a list does not closely relate with those species that are considered to be the most important invasive species in terms of their effect on vegetation. It should be noted that 10 of the 18 species are grasses, most of them tropical.

Attention must be drawn to bracken (*Pteridium aquilinum*) which has been described as either the world's worst weed or the most successful pteridophyte, depending on one's interests. It is the most widely distributed of pteridophytes and with the possible exception of some annual weeds it is probably the most widely distributed of vascular plants (Page, 1976). It became established in many open forest communities long before the advent of man or his agriculture although its frequency of occurrence and spread has, of course, been greatly expanded as a result of man's activities. It has been estimated that the rate of spread of dense bracken communities is 2% per annum. Some of the reasons for bracken's success as a 'permanent ecological opportunist' are its high disease resistance, low palatability to herbivores, its allelopathic effect on competing species, the effectiveness of the long distance dispersal by it minute spores, its legendary vegetative lifespan (up to hundreds of years), its tolerance of burning, its wide edaphic and climatic tolerance and its broad cytological and genetical variability (see Smith and Taylor, 1986).

In *A Geographical Atlas of World Weeds* by Holm *et al.* (1979) it is noted that the agricultural literature suggests that up to 5000 species of plants have been recorded as weeds but this is now regarded as an unrealistic estimate. After years of intensive study, Holm *et al.* consider that a reasonable estimate of the number of weeds of agriculture is of the order of 8000. Unfortunately their *Atlas* is not analysed but for the purposes of this paper we have organized the lists into families in order of number of contained species and also into those genera containing 10 species or more in descending order. These analyses are given in Appendixes 2.1 and 2.2. Clearly the statistics cover a mixture of both introduced and indigenous species but as we have noted above, indigenous species are often invasive in plant communities in their native territory. From these analyses it will be seen that the leading two families are the Compositae (Asteraceae) with 224 genera and 830 species and the Gramineae (Poaceae) with 166 genera and 753 species, which is what a quick perusal of the literature would suggest. The Papilionaceae comes a good third with 87 genera and 415 species followed by a cluster of 11 families with over 100 species each, Euphorbiaceae, Lamiaceae, Brassicaceae, Convolvulaceae, Cyperaceae, Solanaceae, Apiaceae, Rosaceae, Scrophulariaceae, Polygonaceae and Malvaceae. More than half the remaining families contain 10 weed species or fewer, 44 of them with one species only. It is clear that weediness occurs very selectively amongst the angiosperms. In terms of monocotyledons versus dicotyledons the division is 1193:6218 species. In the gymnosperms the leading families in this regard are the Pinaceae with 32 species (20 of them *Pinus* spp.) and Cupressaceae with 15 species.

Looking at the genera, *Cyperus* and *Euphorbia* head the list with 81 and 80 species respectively, followed by *Solanum* (66), *Polygonum* (62), *Panicum* (57), *Ipomoea* (57), and *Acacia* (53).

Considering the high-ranking families, Asteraceae and Poaceae, they represent 13% and 12% of the species total respectively. Similar high percentages have been recorded in the alien flora of individual regions such as California where Raven and Axelrod (1978) report the naturalized flora to contain 674 species of which 137 (20%) are grasses and 112 (16.5%) are Asteraceae. For North America as a whole Rollins and Al-Shehbaz (1986) have analysed the herbaceous weed species and of the 460 species in 253 genera, the Compositae (with 69 species), the Cruciferae (with 52 species) and the Gramineae (with 52 species) far outrank any other family. In an overview of European weeds as exemplified by a comparison of the agrestal floras of Finland, Austria and Italy, Holzner and Immonen (1982) found that the weediest families were the Compositae with 16% of all the weed species of the three countries, followed by the Gramineae (13%), Leguminosae (13%), Cruciferae (7%), Caryophyllaceae (7%), Labiatae (6%) and Polygonaceae (5%). In the west Mediterranean 50% of the weed species belong to four families, the Compositae, Papilionaceae, Gramineae and Cruciferae (Guillerm and Maillet, 1982). The figures for Italy (which are almost certainly an underestimate) given by Franzini (1982) are a total of 466 species belonging to 51 families with the leading families being: Papilionaceae 17%, Gramineae 14%, Compositae 16%. In a review of the weed flora of South Africa, Wells and Stirton (1982) give the following figures (based on the first national weed list of South Africa by Harding *et al.*, 1980):

Exotic weeds	78 families	284 genera	503 species
Indigenous weeds	75 families	211 genera	381 species

The plant families containing most weed species (introduced and indigenous) were: Asteraceae (86 and 70), Poaceae (85 and 40), Fabaceae (50 and 22), Solanaceae (21 and 7), Cactaceae (17 and 3), Brassicaceae (16 and 11), Onagraceae (12 and 3), Rosaceae (11 and 7). Another analysis by Wells *et al.* (1983), confirmed by a further and larger sample (Wells *et al.*, 1986), indicated that 50% of the plants introduced to South Africa belonged to four families: Poaceae, Fabaceae, Asteraceae and Solanaceae (in that order) with the Brassicaceae also supplying many species that are marginally invasive. However, if one considered only the so-called transformer species (i.e. those that transform habitats or landscapes) about 50% belong to three families: Fabaceae, Myrtaceae and Pinaceae (in that order) with a substantial part of the remainder belonging to the Cactaceae, Poaceae, Proteaceae, Salicaceae and Solanaceae.

It is not possible to quote comparable figures for tropical countries since complete analyses have not been made. Some indication can, however, be obtained from partial listings.

It is not perhaps surprising that in general terms the largest angiosperm families supply such a large percentage of the world's aliens or invader species. To a large degree the very features that have been responsible for the evolutionary success and diversity of these families are those that have been responsible for their successful spread and establishment as aliens.

The Compositae (Asteraceae) are regarded as one of the most advanced families from an evolutionary point of view and few families contain such an abundance of weedy species, many of which are extremely successful and have spread especially through temperate areas of the world (see Table 2.2). Their success derives largely from the development of biological features which both ensure survival under adverse conditions and a high reproductive rate. They possess a complex series of integrated reproductive biological features in the pseudanthial capitula. The aggregation of reduced flowers into heads, their geitonogamous breeding system, often with superimposed agamospermy, a series of complicated dispersal mechanisms involving involucral bracts, capitular scales, wings, tubercles, hooks, spines, pappus scales, bristles and parachutes, and the streamlined single-seeded pseudofruits (cypselas) developed from an inferior ovary have all contributed to their success. Their diversity of habit, too, is reflected in those species that occur as invasive species—annual, biennial or perennial herbs, shrubs, trees are all

Table 2.2. Some weedy members of the Compositae (after Heywood *et al.* 1977)

Achillea millefolium—yarrow
Ambrosia artemisifolia—roman ragweed
Anthemis cotula—stinking mayweed
Bellis perennis—daisy
Centaurea nigra—lesser knapweed
Chrysanthemum segetum—corn marigold
Cirsium spp.—thistles
Cotula coronopifolia—brass buttons
Crepis spp.—hawk's beards
Hieracium spp.—hawkweeds
Leontodon spp.—hawkbits
Matricaria matricarioides—pineapple weed
Parthenium hysterophorus—wild feverfew
Senecio jacobaea—ragwort
Senecio vulgaris—groundsel
Sonchus spp.—sow thistles
Taraxacum officinale—dandelion
Xanthium strumarium—cockle bur

represented. Chemical factors are also important in their success in providing protection from overgrazing. The common groundsel (*Senecio vulgaris*) which produces between 50 000 and 60 000 cypselas per plant, with a germination frequency of over 80%, is well protected from the majority of potential herbivores by the presence in the leaf tissue of the plant of toxic levels of pyrrolizidine alkaloids (Heywood *et al.*, 1977).

The grasses are a major source of weeds in many parts of the world. Again a streamlined and highly evolved inflorescence containing reduced and aggregated flowers, coupled with a series of dispersal mechanisms in the flowers and associated parts, together with a diversity of habit has been largely responsible for their evolutionary success and diversification in general and their successful role as weeds and aliens in particular. Annual grasses are amongst the most noxious and invasive species in both temperate and tropical regions. Pantropical annual grass weeds include *Eleusine indica*, *Echinochloa* spp., *Roettboellia exaltata*, *Digitaria sanguinalis*, and *Setaria* spp. Perennial grasses are exceedingly difficult to eradicate and are highly competitive, making them amongst the most pernicious weeds in the world (Kasasian, 1971). Four perennial grasses which are especially important in the tropics are *Cynodon dactylon* (also grown as a lawn grass), *Imperata cylindrica*, *Paspalum conjugatum* and *Sorghum halepense*.

The rich representation of Leguminosae in weed floras and as successful invaders is again not unexpected in view of the large size of the family: 650 genera and 18 000 species (Polhill *et al.*, 1981) and its enormous diversity of habit. As Polhill *et al.* point out 'the Leguminosae are notably "generalists", ranging from forest giants to tiny ephemerals, with great diversity in their methods of acquiring the essentials of growth and in their modes of reproduction and defence'. It is significant that nearly a third of the 18 000 species are contained in only six genera—*Acacia, Astragalus, Cassia sensu lato, Crotalaria, Indigofera*, and *Mimosa*—all of which are characteristic of open and disturbed habitats. It may be noted that five of these genera rank highly in the list based on Holm *et al.* in Appendix 2.2, with *Acacia, Crotalaria* and *Cassia* in the first 25. The Leguminosae possess many unique features which have been responsible for their evolutionary and ecological success, not the least being their frequent ability to fix atmospheric nitrogen through the possession of *Rhizobium* in their root nodules—general in the subfamilies Mimosoideae and Papilionoideae although in only about 30% of species of Caesalpinoideae, especially in the *Dimorphandra* group of the Caesalpinieae and *Chamaecrista* in the Cassieae (see Corby, 1981). Malloch *et al.* (1980) in a review of mycorrhizae in vascular plants point out that in the Caesalpinoideae the Detarieae-Amherstieae, which often occur on infertile soils, probably always have ectotrophic mycorrhizae which may provide an alternative to root nodulation. Other major ectotrophic trees include Dipterocarpaceae, *Nothofagus*, *Eucalyptus* and *Quercus*, which like the Detarieae-Amherstieae are ecologically aggressive and have been successful in invading primarily or exclusively endotrophic forest in their respective ecological regions. Attention should also be focussed on the Leguminosae's remarkably successful pollination mechanisms and reciprocal co-evolution with Hymenoptera (Arroyo, 1981). Legumes have successful dispersal mechanisms and as Raven and Polhill (1981) comment the often pantropical distribution of genera and major groups reflects this. They point out that no fewer than 13 genera of legumes reached the Hawaiian Islands over water barriers as wide as any to be found in the world. Madagascar too has been repeatedly colonized by legumes at various stages of the family's evolution.

Several other so-called 'natural' families provide us with many examples of invader species, such as the Brassicaceae (Cruciferae), Apiaceae (Umbelliferae), Euphorbiaceae, Lamiaceae (Labiatae), Polygonaceae, Amaranthaceae, etc. Similar analyses could be provided to a greater or lesser extent of the adaptive syndromes of these groups in terms of their success as weeds and aliens. At the generic level too, many illustrative examples could be given but there is room here for only a few examples. A tropical example is the weedy amaranths. Of the 60 or so species of *Amaranthus* only a handful are nowadays used as crops (National Research Council, 1984) while 37 have been reported as weeds; several of them such as *A. viridis*, *A. spinosus*, *A. retroflexus*, and *A. hybridus* are serious weeds of pastures, crops, roadsides and even in urban areas. The seeds remain viable for long periods, some germinating after 40 years. Their ability to adapt to any environment and tolerate adverse conditions may be partly explained by their C_4 photosynthetic pathway as well as their abundant pseudocereal-type fruits.

Nearly all the literature is concerned with invasions by higher plants, especially the angiosperms and gymnosperms, although a number of ferns and allies, notably bracken (mentioned above) and species of *Equisetum* are also included. There are few recorded cases of invasion among bryophytes. One of the best documented examples is *Campylopus introflexus*, an American/southern temperate species that has spread rapidly in Britain and western Europe since the first British record in 1941 (Richards and Smith, 1975).

Although it may not appear to be directly connected with considerations of invasions by plants, mention must be made of the special taxonomic problems often posed by invading alien species. Quite simply the fact that the alien belongs to another flora frequently increases the possibilities of misidentification or misunderstanding. Several authors have drawn attention to the difficulties that can arise from these problems. This is especially true of what are termed 'critical' groups where even taxonomists are divided as to their correct classification. The absence of an agreed taxonomy as between countries or continents, for example, exacerbates the difficulties. North American taxonomists frequently adapt, for example, different generic classifications from those widely used in Europe and Raven and Axelrod (1977) sensibly advocate the use by Californian (and by implication other North American) botanists of the taxonomy and nomenclature worked out by Flora Europaea. A particular problem arises when both native and alien variants of the same species occur in the territory concerned as in the case of, for example, *Leucanthemum vulgare* in Britain where both native and introduced tetraploid races occur in addition to the diploid. Burtt (1986) draws attention to the practical problems that can arise from the incorrect identification of aliens as in the case of *Hypericum perforatum* where biological control in New Zealand proved unsuccessful until it was realized that it was the Mediterranean race involved. Recognition of these and similar problems has led us in Britain recently to propose the establishment of a Weed Identification Centre at Kew and Reading. Other related initiatives are the establishment of a European-Mediterranean Weed Flora and Computerized Database in association with the European Economic Community's Agro-Med programme.

2.3 THE EXTENT OF INVASIONS

Only very broad generalizations can be made about the global extent of invasions by terrestrial plants. Some idea can be obtained from looking at the figures for native and alien plants for different parts of the world. Table 2.3 gives such a selection although it has to be repeated that the data vary widely in their accuracy and comparability. Even so it is clear that in terms of species numbers alone there is wide diversity with the percentage of aliens in the flora ranging from a few per cent in some tropical regions to nearly 50% in New Zealand. But number of species is not necessarily a good measure of the extent of invasion since there are numerous cases of the disproportionate effect of single species such as *Casuarina litorea* in the Bahamas which Correl (1982) describes as undoubtedly the most

Table 2.3. Percentages of introduced species in selected floras

Country	Native species	Introduced species	Percentage introduced
Antigua/Barbuda	900	180	10
Australia	15–20 000	1500–2000	10
Sydney	1500	4–500	26–33
Victoria	2750	850	27.5
Austria	3000	300	10
Canada	3160	881	28
Ecuador Rio Palenque	1100	175	15
Finland	1250	120	10
France	4400	500	11
Guadeloupe	1668	149	9
Hawaii	12–1300	228	17.5–19
Java	4598	313	7
New Zealand	1790	1570	47
Spain	4900	750	15

successful alien plant, especially in coastal areas, creating dense shade and producing a toxic effect on most plants so that very few native plants are able to reproduce under it. Or *Andropogon pertusus* which in less than 100 years has become the commonest grass in lowland Jamaica (Adams, 1972). And the European shrubs *Cytisus scoparius* and *Ulex europaeus* which have become widely naturalized in the Nilgiri hills in Tamil Nadu province in South India (Nair and Henry, 1983) or bracken, *Pteridium aquilinum*, which is rampant on Horton Hills in the hill country of Sri Lanka. Or *Casuarina* and *Melaleuca* which have established themselves in natural communities in the Cape region of South Africa, and constitute a threat to their ecological balance. The recent explosion of the North American *Parthenium hysterophorus* in Egypt was apparently initiated from a single sowing in 1960 of a large area with impure grass seed imported from Texas (Boulos and el-Hadidi, 1984). And so the list of examples could continue for pages with examples from most parts of the world and from most bioclimatic regions.

The extent of invasion of a particular territory is closely linked with the history and mode of invasions that have occurred, especially those that are man-induced. This is discussed in Section 2.4. What has to be stressed is that the present pattern and extent of invasion is often the culmination of centuries if not thousands of years of change in the vegetation, usually caused directly or indirectly by man's action. This is all too clear when one considers the extent to which the original vegetation has been converted or modified for agriculture.

2.3.1 North temperate regions

In north temperate regions such as Europe the native vegetation has been largely destroyed or modified by deforestation, agriculture, grazing, urbanization and other of man's activities. In these regions non-active species have come to play a major role in our perception of the landscape. In Great Britain, for example, agriculture affects 80% of the land surface and most of the native vegetation had been destroyed or heavily altered already by 1700. Natural forest cover had been reduced to 5.4% in 1924 although the forested area was increased subsequently to 9.4%, largely due to the plantation of alien conifers (Ratcliffe, 1984). What is not perhaps realized is the extent to which the distribution of plant species can change over relatively short periods due to man's activities. The situation in the Netherlands as described by Mennema (1984) is so serious that he considers that plant geography as a subject can no longer be practised there. By comparing the products of the number of Netherland vascular plant species and the number of their localities before and after 1950, he found that 70% of the flora (not the species!) had disappeared. What is in many ways worse is that many wild species have been planted in educational flora parks and other man-made nature areas or along roadsides, and commercial nurseries have invested considerable sums of money in cultivating less common species for planting on roadsides or other nature areas. As a result genotypes and ecotypes have been introduced which are different from those that naturally belong to the areas concerned. Attention needs to be drawn to this dangerous practice which is now becoming widespread due to the actions of well-meaning but ill informed people. The consequences in terms of the invasion of communities and populations by not so much alien species as alien ecotypes is insidious. This is of course also a very serious danger in countless reafforestation projects where non-local if not exotic provenances have been employed.

2.3.2 Mediterranean-climate regions

In the Mediterranean Basin, most of the natural vegetation has been modified by man's activities, a process dating back thousands of years. Many of the plant communities are secondary and exist today in the form of matorral or garrigue as the result of human interference with the climax communities of oaks and pines (di Castri, 1981). These shrublands, which largely consist of invasive subseral species and often other more weedy elements depending on the state of degradation of the soil and vegetation, cover an immense area and constitute a third of the total vegetation. Much of the remaining forest cover in the Mediterranean is highly modified, especially by reafforestation or other forms of management and the oak forests in particular have suffered from the introduction of alien species, usually in the form of conifers, some of which can become invasive so long as man controls the regeneration of the natural oak climax forest. The pine forests themselves, which cover vast areas of the Mediterranean and sub-Mediterranean, are seldom climax communities but a replacement of the broad-leaved forest that man has destroyed over the centuries. With the exception of some montane forests these pinewoods are heavily modified in composition through the planting of species such as *Pinus halepensis, P. pinaster and P. sylvestris*. Indeed, in the west Mediterranean *P. halepensis*, the Aleppo pine, was considered to be introduced until pollen analysis revealed it to be native. Eucalypts have been extensively employed in reafforestation and in Spain cover nearly 80% of the acreage of broadleaves planted and represent nearly 10% of all reafforestation acreage (ICONA, 1984). The vigorous growth and competitive ability of several of the introduced species of *Eucalyptus* pose an increasing threat to the native residual vegetation.

In Australia, as Specht (1981) has observed, in the areas of mediterranean climate and vegetation, man through modern agriculture has managed to achieve in 50 years what has taken over 2000 years in the Mediterranean Basin. Little remains in its original form, having been replaced largely by fields of wheat and grazing land in all but the driest zones.

Likewise in the Cape region of South Africa, which is loosely mediterranean in climatic terms, the impact of man on the mediterranean-type scrublands on the more fertile soils has been such that little of the original vegetation remains. Intensive landuse has reduced the renosterveld from 36% of the area to 1% and today farmland and other non-native vegetation, plus urbanization covers over 50% of the southwest Cape region. Much of the remaining vegetation of the Cape region is threatened by the large numbers of alien species that have been introduced, often invading and replacing native plant communities. Particularly serious are the problems posed by the large number of woody plants, many of them of Australian origin. Counted amongst these are several wattles or acacias, especially *Acacia cyclops*, *A. decurrens*, *A. elata*, *A. longifolia*, *A. saligna*, as well as the stinkbean *Albizzia lophantha*, and *Eucalyptus cladocalyx*, *E. gomphocephala* and *E. lehmannii*. Other Australian tree invaders include several species of *Hakea* and from the Mediterranean Basin two species of pine, *Pinus pinaster* and *P. halepensis*. These invasive species often grow more strongly than the native scrub and have better powers of regeneration after fire with the result that the original communities are being largely replaced. This is especially true of the fynbos which are particularly susceptible to invasion. It is estimated that 60% of the natural vegetation of the fynbos has been replaced in this way. Major problems are caused by other introductions such as *Lantana camara*, one of the world's 10 worst weeds (*sensu* Holm *et al.*, 1977) which is toxic to livestock and has invaded the veld and agricultural or derelict land. Notorious too are the prickly pears (*Opuntia*), especially *Opuntia aurantiaca*, which is the most widespread and which is largely resistant to eradication by chemical or mechanical means.

In the mediterranean vegetation zones of Chile little remains of the natural vegetation today as a result of man's action over thousands of years and most of the remaining matorral communities are heavily modified by invader species.

2.3.3 Grasslands and pastures

The grassland and pastures of the world again owe their origin to a large extent to man's action, often dating back thousands of years and these areas are often rich in alien invaders, some of them deliberately introduced. As Williams (1985) reminds us the principal plants used to create Australia's sown pastures have been neophytes and their derivatives. The long history of planned plant introductions into northern Australia is reviewed by Mott (1986) in a paper on planned invasions of tropical Australian savannas. Fire has frequently played a major role in the creation of these pasture lands. In Australia Williams (1985) believes that the ease by which so many aliens have been able to invade so successfully and become part of the Australian landscape can be explained in part by the fire regimes of the Aboriginal populations for as long as 10 000 years. Fire too has been suggested as one cause of the extensive grassland communities of California; the European settlers upset the equilibrium of the landuse system involving fire established by the native Indians and so increased the scale and frequency of fires as a means of clearing forest and chaparral to open up ranges for grazing, agriculture and mining (Trabaud, 1981).

Whatever the nature of the original grassland in California, whether it was dominated by perennial grasses such as *Aristida*, *Poa*, *Stipa* or other plants, there can be no denying that today it is dominated by introduced annual grass species to such an extent that they have been considered as new and permanent members of the native flora on the grounds that they are unlikely now ever to be eliminated (Heady, 1977). Again in Africa the grassland ecosystems usually result from the destruction of the forest (with the exception of some savannas of edaphic origin) and are often maintained through the use of fire regimes and are frequently infested by alien invader species. Likewise in South America, the region of the great savannas, including the cerrados and campos of Brazil, and the llanos of Colombia and Brazil, covering 3 million square kilometres of barely usable land, are increasingly being seen as areas for exploitation leading to their invasion by weedy and pioneer species. Many of the ranch lands of South America have been produced by forest destruction after the European conquest. Similarly in Madagascar vast areas of the natural vegetation have been burned, since the Palaeo-Indonesians invaded the island, to provide pasture land for the zebu cattle. These pastures are poor in species and characterized by weedy species such as the pantropical *Imperata cylindrica* and *Heteropogon contortus*.

A general review of pasture weeds of the tropics and subtropics is given by Tothill *et al.* (1982). They concur with Moore (1971) in considering that woody weeds are by far the most important in native grazing lands in the semiarid/arid/subhumid tropics and subtropics. Many of these woody weeds are native species but there has also been invasion from exotics such as *Calotropis procera*, which has extended throughout tropical Asia and Africa into South America and is now spreading rapidly in northern Australia. Other invaders in Australia include *Acacia farnesiana*, *Mimosa* spp., *Cryptostegia grandiflora* and *Zizyphus mauritiana* which form dense thickets. The effects of woody invaders on the natural rangelands of south and southwest Africa have already been mentioned, whether by native or exotic species. Herbaceous weeds also affect tropical and subtropical pastures. A grass that is widespread and used for permanent pasture in various parts of the tropics, such as Florida, West Indies, Fiji, Malaysia, Guyana and Hawaii, is *Axonopus affinis*. It invades degenerate pasture of *Paspalum dilatatum*, *Trifolium repens* and *Pennisetum clandestinum*, leading to a decline in animal production (UNESCO, 1979). Even amenity grassed areas in the tropics are subject to severe invasions. In Brasilia, for example, the grassed areas in parks, gardens, etc., mainly comprise two species, *Paspalum notatum* and *Cynodon dactylon* and these are invaded by no fewer than 60 species belonging to 38 genera and 15 families (Gramineae 15 species, Compositae 10 species) and this is a common pattern in other areas of Brazil (Brandao Ferreira and Borges Machado, 1976).

2.3.4 Tropical forests

The widespread destruction or conversion of the primary forest ecosystem in both the dry and humid tropics has led to a whole series of secondary successional communities (when degradation has not proceeded too far) in which numerous invaders play a role—herbaceous weeds, grasses, shrubs and secondary trees. These successional stages can last for hundreds of years and have not been studied in detail. The human impact on the tropical forest differs in the major regions. Large-scale commercial logging has already been responsible for clearing out a large part of the forests of Africa and Southeast Asia. Additionally the introduction of large scale plantation crops such as sugar, rubber, oil palm, coffee, tea, etc., especially in the 19th century, has been the cause of massive deforestation. While few of these crops have themselves become weedy and invasive, the plantations have each attracted their own suite of weeds. The weeds of tea plantations, for example, are reviewed by Ohsawa (1982) and include herbs, lianas, shrubs, trees and even epiphytes. In Central and South America logging has so far been less serious a cause of deforestation or forest conversion than clearing and burning for cattle ranching together with slash and burn cultivation which when practised on a massive scale, especially by unskilled immigrants, can have a serious effect on the forest cover. Although weeds are not unknown in the relatively untouched forests of large areas of the Amazon, such ecosystems are perhaps amongst the least affected by invasion by higher plants.

A perhaps underestimated source of invaders in tropical forest ecosystems are the minor crops which are often cultivated by local peasants on an appreciable scale. A good example is cardamom (*Elettaria cardamomum*) which has become a serious invader of valleys in humid forests in Sri Lanka and South India, even in reserve areas where its cultivation is illegal.

2.3.5 A pattern of islands

Island ecosystems are a special case in terms of plant invaders and a good deal has been written about them. It is now accepted as highly probable that the flora of remote islands have been derived from long distance dispersal, the classic case being the Hawaiian Islands (Wagner *et al.*, 1985). However, by far the most devastating effects have been caused by man's introductions, accidental or deliberate, of plant species that have become serious invaders of the often fragile island ecosystems. The introduction of domestic animals has been another important factor since these not only affected the vegetation directly by grazing or browsing but were responsible indirectly for the introduction of many vigorous weeds and invaders through the imports of fodder plants and seeds.

The extent of invasion by alien species in island floras varies widely. Islands such as New Zealand, Hawaii and Madagascar are extreme examples with greatly modified vegetation and large numbers of introduced species. Patterns for the islands of the Indian Ocean, including Madagascar, the Mascareignes, Seychelles and Sri Lanka, are reveiwed by Renvoize (1979) while those of temperate island floras are considered by Moore (1979, 1983). Other useful contributions will be found in the symposium volume *Plants and Islands* (Bramwell, 1979).

2.4 MODES OF INVASIONS

Viewed globally it might seem impossible to seek out any overall pattern or trends in the invasion process by higher plants. There is a risk too that what appears to be a pattern is simply a reflection of our state of knowledge of different parts of the world. Nevertheless some regularities and generalizations do seem to emerge.

Historically one can often detect several distinct phases in the invasion process—for example, prehistoric man's effect on the vegetation, that of the early settlers, the period of colonial expansion, the phase of modern agriculture and most recently the massive degradation of the vegetation caused by the population explosion, coupled with the demand for increased resources and improved living standards. A detailed example of such a chronology is given by Harris (1965) in his outstanding ecological study on the Outer Leeward Islands (Antigua, Barbuda and Anguilla).

These do not all fit into exactly the same chronological pattern in different parts of the world but I shall consider the main phases briefly in turn, giving what I hope are representative examples. The emphasis will be on invasions which have been facilitated by man, either deliberately or accidentally, since these are by far the main source of recent introductions across the world. Human action has been responsible for the extension of range of native plants through habitat disturbance which, as Baker (1986) points out is invasion in only a technical sense. Clear cases of invasions are the many examples of native species which have been introduced with man's help into other parts of the country and often into communities where they were not known previously. But by far the most numerous invaders are those that have been introduced by some means of transport from foreign lands by man, his domesticated animals or machinery. The actual modes of entry are numerous and varied, ranging from packing material and soil around introduced plants to bird seed and clothing and footwear. As we shall see man has transported thousands of species of plants from one biogeographic region to another through the deliberate introduction of economically important plants such as crop or plantation species, timber trees, forage plants, or those of ornamental or amenity importance, often together with their accompanying weeds. This has been done on a massive scale and the extent is not perhaps appreciated until one takes a global view. There are few areas in the world where the consequences of this process are not strongly reflected.

The geographical source of these invaders is, therefore, often a reflection of the agricultural and economic history of the region concerned and of the mode of invasion. High percentages of invaders in North America and Austalia, for example, have come from Europe, western Asia and the Mediterranean Basin. These sources are understandable when one considers the pattern of colonization and the source of the human and animal introductions. The eastern and southern fringes of the Mediterranean Basin and the adjacent Mediterraneo-Irano-Turanian steppes of the Middle East are probably the largest source of weeds and the cradle of many that are common to temperate and warm-temperate zones of the world (Zohary, 1962). Outstanding members of such weed communities are annual species of Gramineae, Compositae, Leguminosae, Umbelliferae, Cruciferae, etc. This is partly explained by the long history of human modification of the vegetation of this region, dating back to at least 9000 BP and the origins of agriculture. This together with the climatic conditions and the nature of the soils has created a whole series of habitats that favour the evolution and spread of species with the characteristics that today we associate with weeds. Not surprisingly a large part of the synanthropic flora of countries such as Israel and Egypt is made up of species of Mediterranean origin or distribution, with again high percentages of grasses, composites, crucifers, legumes, etc. The number of alien weeds and invaders is, not surprisingly, small: Dafni and Heller (1982) record only 73 adventive species for Israel. In Egypt the occurrence of tropical weeds seems to be of recent date and a considerable number have recently been reported from the Nile basin. The winter and summer weed communities of Egypt were recently studied by Kosinova (1975) who found that summer weeds are predominantly of tropical distribution or origin while winter weeds are represented by species of Mediterranean origin or distribution.

2.4.1 The early historical and aboriginal phases

In a number of cases we have some information on the effects of aboriginal activities on the plant life of various parts of the world. For example the agricultural practices of the Arawaks and Caribs on the Leeward Islands is discussed in detail by Harris (1965). Widespread and naturalized aliens at this period (600–1500 AD) probably included guava, soursop and sweetsop. In Hawaii when the Polynesians arrived some 1600 years ago, they found the vegetation was virtually untouched by man. The Polynesians burned and cleared large parts of the lowlands for their crops; they also introduced pigs and rats with devastating consequences (see account in Wagner *et al.*, 1985). In Australia Groves (1986) notes that the first record of an introduction leading to a plant 'invasion' was tamarind *Tamarindus indica*, brought in by the Macassans on their annual visits to the northern shores of Australia for their own diet from about 1700 AD. In East Africa extensive agriculture was thought to have been introduced by Bantu-speaking peoples in 0–500 AD who caused widespread forest clearance. The main crops were probably sorghum, eleusine millet and bananas (Lind and Morrison, 1974). Possible introductions to southern Africa are considered by Wells *et al.* (1986) who point out that several of the early crop plants are themselves invasive there, such as *Cannabis sativa*, *Cocos nucifera*, *Jatropha curcas*, and *Pisidium guajava*. An elegant review of pre-Columbian plant migrations from lowland South America to Meso-America is given in a series of papers edited by Stone (1984). In pre-Columbian times grain amaranths *Amaranthus hypochondriacus*, was one of the basic food crops in the New World and thousands of hectares were cultivated in Aztec and Inca farmlands. It was the Spanish conquistadores who stopped its use as a staple (National Research Council 1984). Some of the earliest records of synanthropic plants come from the excavations of Egyptian prehistorical and historical settlements, most importantly from ancient tombs, from the Neolithic to the Coptic periods. A composite list of the synanthropic species identified from the various periods and dynasties is given by Kosinova (1974) from which it will be seen that numerous well-known invasive species are represented. What is evident from these and other sources is that many plant introductions took place in many parts of the world long before the effects of the European colonial phase were noted.

2.4.2 The European/colonial phase

The voyages of exploration and gradual settlement of the East and the New World by the European powers led to the most intensive and extensive invasions by higher plants that the world has witnessed. Although there had been some movement of plants by man prior to this along the trade routes, dating back many hundreds of years, it was the opening up of the tropics, in particular by the East India Companies, for the development of the spice trade especially, and the discovery of the New World leading to the great wave of post-Columbian exchanges of crop plants that was responsible for the major impact on the world's ecosystems. This was essentially a European-dominated phenomenon involving the great colonial powers such as France, Spain, Portugal, the Netherlands and most notably Britain, who eventually became the proprietors of some of the most important agricultural lands in the world. This phase has been aptly described in recently published account by Crosby (1986) 'ecological imperialism'.

The European colonization of Australia, to take a major example, has been described as an 'apocalyptic event' for Australian ecosystems. Since the settlement by the British in 1788 the flow of new plant material was almost uncontrollable. The sequence of events has been graphically summarized by Williams (1985):

> The first trickle of plants was represented mainly by species from Britain, few of which grew without massive and continuous disturbance of the native vegetation and soils. By the mid-1800s this trickle had become a torrent and by the 1880s it was a flood...

A similar pattern has been described for other countries. Globally the extent to which the vegetation has been destroyed or modified by the introduction of crop plants is closely related to the history of colonization. In the tropics of Asia the effects have been the most dramatic because of the extent and duration of the colonial period; in tropical Africa the consequences on the native ecosystems, although substantial, were less due to the later timing of the process. In Latin America, the early withdrawal of the colonial powers of Portugal and Spain and the minor involvement of Britain and other colonial countries has meant that the vegetation has suffered very much less than in other areas of the tropics. In the Caribbean, on the other hand, the sustained period of colonization has had devastating effects on the native plant life, especially through the widescale introduction of the plantation crops, notably sugarcane on which the local economies became dependent (see below).

2.4.3 The role of the botanic gardens

The early European botanic gardens, founded from the 16th century onwards in Italy, France, Britain, the Netherlands and so on, were responsible for a considerable amount of plant introduction for medicinal and ornamental and amenity purposes, as well as later for scientific study. However, it was the tropical botanic gardens which were used mainly as an instrument of colonization. They were created in many cases as instruments of colonial expansion and commercial development and played a major role in establishing the patterns of agriculture in several parts of the world, notaly in Southeast Asia (Heywood, 1985b, 1986). Great tropical botanic gardens that have been significant in this process include that of Pamplemousses in Mauritius (the first tropical botanic garden to be established in 1735), Buitenzorg (today the Kebun Raya, Bogor) founded in 1819 and which was responsible for the introduction of the oil palm (*Elaeis guineensis*) as a plantation crop in Southeast Asia from seedlings obtained from Mauritius in 1848; Peradeniya (1821) and its associated gardens at Gampaha and Hakgala in Sri Lanka and Singapore (1822) which along with Gampaha and the Royal Botanic Gardens at Kew were the source of the major rubber plantations in Southeast Asia (Holttum, 1970; Purseglove, 1959). Very many crop plants were introduced through these gardens, often in association with European botanic gardens in Britain, the Netherlands and France—cloves, chocolate, cinchona, tea, coffee, breadfruit and so on. These tropical gardens were often more to be regarded as staging posts or introduction centres than botanic gardens in the modern sense. The celebrated Royal Botanic Gardens of Calcutta were originally created as, in effect, a commercial nursery and indeed their founder Colonel Kyd called the place a botanic garden although no botany was to be practised there and he explicitly wrote that there would be none. Purseglove (1959) comments on a curious aspect of these gardens:

> It has always seemed strange to me that many of the world's major tropical plant products are produced largely in countries far removed from their region of origin, e.g. South American rubber in Malaya and Indonesia, South America cocoa in West Africa, South American quinine in the East Indies, African coffee in Brazil, cloves and nutmeg from the Moluccas in Zanzibar and Grenada respectively, sugar, banana and limes from South-East Asia in the West Indies, and

> vanilla from Central America in Madagascar. Obviously this cannot be attributed to any one particular reason and many factors are involved, including economics, available land and labour supply, technical skill in processing, suitability of the crop for plantation or peasant agriculture, etc. Nevertheless, one would have expected that a crop was more suited ecologically to its country of origin than to its new home. I suspect that one of the major reasons is that when a new crop has been introduced without many of its normal pests and diseases, it has more chance of flourishing and giving high yields. Many of the crops are introduced as seeds, which limits the number [of] pests and diseases they can carry with them, and this is further enhanced by the plant quarantine regulations now enforced in many countries. One can only contemplate what would happen to the Malayan rubber industry if the South American Leaf Blight (Dothidella ulei) were accidently introduced.

Just how important the colonial tropical botanic gardens were considered is indicated by the attitude of Sir Joseph Hooker, the celebrated onetime Director of the Royal Botanic Gardens, Kew, who regarded the economic revival of the West Indies as dependent on the wise application of botanical science. He had seen the emancipation of slaves, the rise and fall of the sugar industry and growing poverty, discontent and demoralization. In a letter in 1897 he wrote 'I am interested greatly in the W. Indian sugar situation... I had so much to do with the vegetable industries of the W. Indies when I was at Kew, that I cannot but feel deeply interested... I see nothing for it but the establishment of cheap Botanical Gardens, confined to economic plants, in the other colonies.' The quite remarkable influence of the network of British botanic gardens that stretched around the world and centred on Kew is described in Brockway's somewhat provocative study entitled *Science and Colonial Expansion. The Role of the British Royal Botanic Gardens* (1979). Another important historical study of the role of a colonial botanic garden, that of the Company's Garden, later the Cape Town Botanic Garden and now the Cape Town Public Gardens, is given by Shaughnessy (1986), and in particular its activities in the 1850s and 1860s in introducing and spreading Australian plants.

While human agencies have been responsible for the spread and maintenance of many of these introduced species, and the disturbance of the vegetation that had to take place before the crops or plantations could be established, only a limited number of the species involved have become invasive independently of man's continuing action in aiding their dispersal. It is often the crop and plantation weeds that create the problems rather than the cultivated plants. Man has provided the conditions suitable for invasion through these large scale agricultural activities and the surprise, perhaps, is that not more species have responded to the opportunities.

2.4.4 Recent changes in the spread and decline of invaders

In recent years, the changes caused by the impact of man on the environment as a result of modern agricultural methods, machinery, weedkillers, crop rotations, etc., has altered the agricultural landscape and has had an effect on the synanthropic flora, causing not only the increase of some weed species but the decline of others. In Sweden, for example, and other Nordic countries two of the most threatened species are *Agrostemma githago* and *Bromus secalinus*. The former is an archaeophyte, known from archaeological sites. It is at risk today because the germination biology of the seeds is not adapted to modern agricultural practices (see Svenson and Wigren, 1986). In Egypt, *Ceruana pratensis* (Compositae) was formerly a common weed along the Nile and in irrigation channels, especially in Upper Egypt, with records dating back to Pharaonic times. It is now extremely rare and on the way to extinction (Boulous and el-Hadidi, 1984).

There are several factors causing an increase in the availability of habitats suitable for successful colonization by exotic species. The accelerating trends in the deforestation of parts of South America, for example, mainly for cattle ranching, expansion of plantation crops such as coffee and cane, the introduction of plantations of exotic timber and firewood species, and the shortening of the fallow cycle in slash and burn cultivation which is itself extending considerably, are almost certain to have a major effect on the patterns of invasion and on the composition of the exotic flora. Already we can predict some of the candidate species for invasions since there is today a strongly developing interest in wider scale introduction of lesser known species of potential use in agriculture and forestry (National Research Council, 1975). Examples include the forgotten crops of the Incas such as oca (*Oxalis tuberosa*) which is second only to potato in the Andes. It is already a commercial crop in New Zealand ('yam') and as Vietmeyer (1986) puts it would like to sweep round the world if given modern attention.

As a plant conservationist I must confess to viewing the present situation with some alarm. So much of the world's vegetation has already been modified or destroyed by invasions, and we have become all to accustomed to accepting secondary or even artificial vegetation and landscapes as though they were today's norms. We must make strenuous efforts to safeguard as far as possible the remaining part of our native vegetation, a natural heritage that is under ever increasing threat.

2.5 SUMMARY AND CONCLUSIONS

There are few ecosystems in the world that have not been affected to a greater or lesser degree by invasions by terrestrial plants, especially flowering plants and conifers. Human intervention has been the major causal factor in these invasions, especially through the clearance of natural vegetation for agriculture and forestry and the subsequent invasions by weedy species. The extent of this habitat modification varies considerably in different bioclimatic regions—ranging from large scale transformation in many mediterranean-climate regions and in many island ecosystems, to relatively minor incursions in remote humid tropical forests. The species involved belong to a wide range of families but with notable concentrations in large 'natural' families such as the Asteraceae, Fabaceae and Poaceae which possess complex reproductive and dispersal mechanisms. Invasion of natural communities, in many parts of the world, by introduced plants, especially woody species, constitutes one of the most serious threats to their survival, although it is one that is not fully acknowledged by conservationists.

ACKNOWLEDGEMENTS

Many colleagues have assisted me with references or suggestions, especially J. Akeroyd, A. H. Bunting, D. Drennan, D. M. Moore, B. Pickersgill, P. H. Raven, W. Wagner. Their help is gratefully acknowledged.

REFERENCES

Adams, C. D. (1972). *Flowering Plants of Jamaica.* University of West Indies, Mona.

Arroyo, M. T. Kalin (1980). Breeding systems and pollination biology in Leguminosae. In: Polhill, R. M., and Raven, P. H. (Eds.) *Advances in Legume Systematics*, pp. 723–69. Royal Botanic Gardens, Kew.

Baker, H. G. (1986). Patterns of plant invasions in North America. In: Mooney, H. A., and J. A. Drake (Eds.), *Ecology of Biological Invasions of North America and Hawaii.* Springer-Verlag, New York.

Berg, R. Y. (1983). Plant distribution as seen from plant dispersal—general principles and basic methods of dispersal. *Sonderb. Naturwiss. Ver. Hamburg*, **7**, 13–46.

Boulos, L., and el-Hadidi, M. Nahil (1984). *The Weed Flora of Egypt.* American University of Cairo Press.

Bramwell, D. (Ed.) (1979). *Plants and Islands.* Academic Press, London.

Brandao Ferreira, M., and Borges Machado, J. (1976). Invasoras dos gramados do Distrito Federal. *An Soc. Bot. Brasil XXV Congreso Nacional de Botanica.* pp. 389–94. Recife.

Brockway, L. H. (1979). *Science and Colonial Expansion. The role of the British Royal Botanic Gardens.* Academic Press, New York. 215 pp.

Burdon, J. J., and Chilvers, G. A. (1977). Preliminary studies on a native eucalypt forest invaded by exotic pines. *Oecologia*, **31**, 1–12.

Burtt, B. L. (1986). Concluding remarks and the way ahead. *Proc. Roy. Soc. Edinburgh*, **89B**, 301–7.

Corby, H. D. L. (1981). The systematic value of leguminous root nodules. In: Polhill, R. M., and Raven, P. H. (Eds.), *Advances in Legume Systematics*, pp. 657–76. Royal Botanic Gardens, Kew.

Correll, D. S. (1982). Flora of the Bahamas Archipelago. Cramer, Vaduz.

Crosby, A. W. (1986). *Ecological Imperialism. The Biological Expansion of Europe, 900–1900.* Cambridge University Press, Cambridge. 368 pp.

Dafni, A., and Heller, D. (1982). Adventive flora of Israel— phytogeographical, ecological

and agricultural aspects. *Pl. Syst. Evol.*, **140**, 1–18.
di Castri, F. (1981). Mediterranean—type shrublands in the world. In: di Castri, F., Goodall, D. W., and Specht, R. L. (Eds.), *Ecosystems of the World 11. Mediterranean-type Shrublands*, pp. 1–52. Junk, The Hague.
Ellenberg, H. (1979). Man's influence on tropical mountain ecosystems in South America. *J. Ecol.*, **67**, 401–16.
Franzini, E. (1982). Italy. In: Holzner, W. and Numata, M. (Eds.), *Biology and Ecology of Weeds*, pp. 245–56. Junk, The Hague.
Greuter, W., Burdet, H., and Long, G. (1986) *MedChecklist*, Vol. 3. OPTIMA, Berlin and Geneva.
Groves, R. H. (1986). Plant invasions of Australia: an overview. In: Groves, R. H., and Burdon, J. J. (Eds.), *Ecology of Biological Invasions*, pp. 137–49. Cambridge University Press, Cambridge.
Guillerm, J. L., and Maillet, J. (1982). West Mediterranean countries of Europe. In: Holzner, W., and Numata, M. (Eds.), *Biology and Ecology of Weeds*, pp. 227–44. Junk, The Hague.
Harding, G. B., Stirton, C. H., Wells, M. J., Balsinhas, A., and van Hoepen, E. (1980). A first national weed list for southern Africa. Cited in Wells M. J., and Stirton, C. H. (1982).
Harper, J. L. (1977). *Population Biology of Plants*, Academic Press, London.
Harris, D. R. (1965). *Plants, Animals, and Man in the Outer Leeward Islands, West Indies.* Univ. Calif. Publ. Geogr. 18.
Heady, H. F. (1977). Valley grassland. In: Barbour, M. G., and Major, J. (Eds.), *Terrestrial Vegetation of California*, pp. 491–514. Wiley, New York.
Heywood, V. H. (1985a). *Times Higher Education Supplement*. 19 March, p. 13.
Heywood, V. H. (1985b). Botanic Gardens and taxonomy—their economic role. *Bull. Bot. Survey India*, **25**, 134–47.
Heywood, V. H. (1986). *Botanic Gardens as Resource and Conservation Centres.* Commonwealth Science Council (in press).
Heywood, V. H., Harborne, J. B., and Turner, B. L. (Eds.). (1977). *The Biology and Chemistry of the Compositae.* London, Academic Press. xiv + 1189 ps.
Holm, L., Pancho, J. V., Herberger, J. P., and Plucknett, D. L. (1979). *A Geographical Atlas of World Weeds*, Wiley, New York.
Holm, L. G., Plucknett, D. L., Pancho, J. V., and Herberger, J. P. (1977). *The World's Worst Weeds*, University Press Hawaii, Honolulu.
Holttum, R. E. (1970). The historical significance of botanic gardens in S.E. Asia. *Taxon*, **19**, 707–14.
Holzner, W., and Immonen, R. (1982). Europe: An overview. In: Holzner, W., and Numata, M. (Eds.), *Biology and Ecology of Weeds*, pp. 203–26. Junk, The Hague.
ICONA (1984). *Inventario Forestal Nacional ICONA. Años 1965 a 1974.* Madrid.
Kasasian, L. (1971). *Weed Control in the Tropics.* Leonard Hill, London.
Kosinova, J. (1974). Studies on the weed flora of cultivated land in Egypt. 4 Mediterranean and tropical elements. *Candollea*, **29**, 281–95.
Kosinova, J. (1975). Weed communities of winter crops in Egypt. *Preslia*, **47**, 58–74.
Lind, E. M. and Morrison, M. E. S. (1974). *West African Vegetation.* Longman, London.
Mack, R. M. (1985). Invading plants: their potential contribution to population biology. In: White, J. (Ed.), *Studies on Plant Demography*, pp. 127–42. Academic Press, London.
Malloch, D. W., Pyrozynski, K. A., and Raven, P. H. (1980). Ecological and evolutionary significance of mycorrhizal symbiosis in vascular plants. *Proc. Nat. Acad. Sci.*, **77**, 2113–18.
Mennema, J. (1984). The end of plant geography in the Netherlands. *Norrlinia*, **2**, 99–106.

Michael, P. W. (1981). Alien plants. In: Groves, R. H. (Ed.), *Australian Vegetation*, pp. 44–64. Cambridge University Press, Cambridge.
Moore, D. M. (1979). Origins of temperate island floras. In: Bramwell, D. (Ed.), *Plants and Islands*, pp. 66–85. Academic Press, London.
Moore, D. M. (1983). Human impact on island vegetation. In: Holzner, W., Werger, M. J. A., and Ikusima, M. (Eds.), *Man's Impact on Vegetation*, pp. 237–46. Junk, The Hague.
Moore, R. M. (1971). Weeds and weed control in Austalia. *J. Aust. Inst. Agric. Sci.*, **37**, 181–91.
Mott, J. J. (1986). Planned invasions of Australian tropical savannas. In: Groves, R. H., and Burdon, J. J. (Eds.), *Ecology of Biological Invasions*, pp. 89–96. Cambridge University Press, Cambridge.
Nair, N. C., and Henry, A. N. (1983). *Flora of Tamil Nadu Ser. 1 Analysis*, Vol. 1. Botanical Survey of India, Southern Circle, Coimbatore.
National Research Council (1975). *Underexploited Tropical Plants*. National Academy of Science, Washington, DC.
National Research Council (1984). *Amaranth. Modern Prospects for an Ancient Crop*. National Academy Press, Washington, DC. 80 pp.
Ohsawa, M. (1982). Weeds of tea plantations. In: Holzner, W., and Numata, M. (Eds.), *Biology and Ecology of Weeds*, 435–48. Junk, The Hague.
Page, C. N. (1976). The taxonomy and phytogeography of bracken—a review. *Bot. J. Linn. Soc.*, **73**, 1–34.
Polhill, R. M., Raven, P. H., and Stirton, C. H. (1981). Evolution and systematics of the Leguminosae. In: Polhill, R. M., and Raven, P. H. (Eds.), *Advances in Legume Systematics*, pp. 1–26. Royal Botanic Gardens, Kew.
Purseglove, J. W. (1959). History and functions of botanic gardens with special reference to Singapore. *Garden's Bulletin Singapore*, **17**, 125–54.
Ratcliffe, D. A. (1984). Post-medieval and recent changes in British Vegetation: the culmination of human influence. *New Phytologist*, 98, 73–100.
Raven, P. H., and Axelrod, D. E (1978). *Origin and Relationships of the Californian Flora*. Univ. Calif. Publ. Bot. 72.
Raven, P. H., and Polhill, R. M. (1981). Biogeography of the Leguminosae. In: Polhill, R. M., and Raven, O. H. (Eds.), *Advances in Legume Systematics*, pp. 27–34. Royal Botanic Gardens, Kew.
Renvoize, S. A. (1979). The origins of Indian Ocean Island Floras. In: Bramwell, D. (Ed.), *Plants and Islands*, pp. 107–29. Academic Press, London.
Richards, P. W., and Smith, D. (1975). A progress report on *Campylopus introflexus* (Hedw.) and *C. polytrichordis* De Not. in Britain and Ireland. *J. Bryol.*, **8**, 293–8.
Robin, J. M., and Carr, G. W. (1986). Hybridization between introduced and native plants in Victoria, Australia. In: Groves, R. H., and Burdon, J. J. (Eds.) *Ecology of Biological Invasions*, p. 56. Cambridge University Press, Cambridge.
Robinson, R. W., Carr, G. W., and Robin, J. M. (1986). Plants naturalized outside their natural geographical range in Victoria, Australia: dire forboding for the flora. In: Groves, R. H., and Burdon, J. J. (Eds.), *Ecology of Biological Invasions*, p. 57. Cambridge University Press, Cambridge.
Rollins, R. C., and Al-Shehbaz, I. A. (1986). Weeds of South-West Asia in North America with special reference to the Cruciferae. *Proc. Roy. Soc. Edinburgh*, **89B**, 289–99.
Shaughnessy, G. L. (1986). A case study of some woody plant introductions to the Cape Town area (in press).
Smith, P. M. (1986) Native or introduced? Problems in the taxonomy of some widely introduced annual brome grasses. *Proc. R. Soc. Edinburgh, Sect. B*, 273–81.

Smith, R. T., and Taylor, J. A. (1986). *Bracken: Ecology, Land Use and Control Technology*, Parthenon Publishing, Carnforth.

Specht, R. L. (1981). Major vegetation formations in Australia. In: Keast, A. (Ed.), *Ecological Biogeography of Australia*, pp. 165–297. Junk, The Hague.

Stebbins, G. L. (1971). Adaptive radiation of reproductive characters of angiosperms, II: Seeds and seedlings. *Ann. Rev. Ecol. Sys.*, **2**, 237–60.

Stirton, C. H. (1979). Taxonomic problems associated with invasive alien trees and shrubs in South Africa. *Proc. 9th Plenary Meeting AETFAT*, pp. 218–19.

Stone, D. (ed.), (1984). Pre-Columbian Plant Migration. Papers Peabody Museum Archaeology and Ethnology, Vol. 26.

Svenson, R., and Wigren, M. (1986). Observations on the decline of some farmland weeds. *Mem. Soc. Fauna Flora Fennica*, **62**, 63–7.

Toledo, V. (1985). *A Critical Evaluation of the Floristic Knowledge in Latin America and the Caribbean.* The Nature Conservancy, Washington DC.

Tothill, J. C. Mott, J. J., and Gillard, P. (1982). Pasture weeds of the tropics and subtropics with special reference to Australia. In: Holzner, W., and Numata, M. (Eds), *Biology and Ecology of Weeds*, pp. 403–28. Junk, The Hague.

Trabaud, L. (1981). Man and fire: impacts on Mediterranean vegetation. In di Castri, F. Goodall, D. W., and Specht, R. L. (Eds.), *Ecosystems of the World. Mediterranean-type Scrublands*, pp. 523–37. Junk, The Hague.

UNESCO (1979). *Tropical Grassland Ecosystems*, UNESCO, Paris.

Vietmeyer, N. D. (1986). Lesser-known plants of potential use in agriculture and forestry. *Science*, **232**, 1379–84.

Wagner, W. L., Herbst, D. R., and Yee, R. S. N. (1985). Status of the native flowering plants of the Hawaiian islands. In: Stone, C. P., and Scott, J. M. (Eds.), *Hawaii's Terrestrial Ecosystems: Preservation and Management*, pp. 23–74. University of Hawaii, Honolulu.

Webb, D. A. (1985). What are the criteria for presuming native status? *Watsonia*, **15**, 231–6.

Wells, M. J., and Stirton, C. H. (1982). South Africa. In: Holzner, W., and Numata, M. (Eds.), *Biology and Ecology of Weeds*, pp. 339–45. Junk, The Hague.

Wells, M. J., Engelbrecht, V. M., Balsinhas, A. A., and Stirton C. H. (1983). Weed flora of South Africa 2. Power shifts in the veld. *Bothalia*, **14**, 961–5.

Wells, M. J., Poynton, R. J., Balsinhas, A. A. van Hoepen, E., and Abbott, S. K. (1986). The history of introduction of invasive alien plants to Southern Africa, (in press).

Williams, O. B. (1985). Population dynamics of Australian plant communities, with special reference to the invasion of neophytes. In: White, J. (Ed.), *The Population Structure of Vegetation*, pp. 623–35. Junk, The Hague.

Zohary, M. (1962). *Plant life of Palestine*. Reynold Press, New York.

Appendix 2.1. Families, genera and species listed in Holm *et al.* (1979), arranged in descending order of species richness.

Family	No. of genera	No. of species
Angiosperms		
Asteraceae	224	830
Poaceae	166	753
Papilionaceae	87	415
Euphorbiaceae	24	183
Lamiaceae	49	178
Brassicaceae	57	175
Convolvulaceae	14	147
Cyperaceae	18	146
Solanaceae	26	143
Apiaceae	54	142
Rosaceae	24	130
Scrophulariaceae	46	123
Polygonaceae	12	115
Malvaceae	21	111
Mimosaceae	15	99
Rubiaceae	32	97
Amaranthaceae	18	88
Chenopodiaceae	21	82
Caryophyllaceae	24	80
Boraginaceae	27	75
Ranunculaceae	12	74
Verbenaceae	14	67
Acanthaceae	24	59
Onagraceae	8	58
Fagaceae	5	55
Caesalpiniaceae	14	48
Asclepiadaceae	19	46
Commelinaceae	8	42
Cucurbitaceae	17	42
Liliaceae	23	39
Oxalidaceae	2	36
Rhamnaceae	10	34
Lythraceae	6	33
Tiliaceae	5	31
Urticaceae	12	31
Cactaceae	4	30
Orobanchaceae	4	30
Capparidaceae	5	29
Ericaceae	11	29
Juncaceae	2	29
Potamogetonaceae	1	28
Salicaceae	2	28
Saxifragaceae	2	28
Apocynaceae	16	26
Melastomataceae	11	26
Araceae	20	25
Papaveraceae	9	25
Caprifoliaceae	5	23
Geraniaceae	2	23
Alismataceae	4	22
Anacardiaceae	8	22
Hydrocharitaceae	11	22
Moraceae	8	21
Heliotropiaceae	1	20
Iridaceae	10	19
Plantaginaceae	1	19
Ulmaceae	4	19
Myrtaceae	7	17
Oleaceae	5	17
Primulaceae	4	17
Vitaceae	6	17
Bignoniaceae	11	16
Dipsacaceae	5	16
Nymphaeaceae	4	16
Aizoaceae	6	15
Campanulaceae	10	15
Eriocaulaceae	1	15
Gentianaceae	10	15
Hydrophyllaceae	6	15
Zygophyllaceae	6	15
Alliaceae	1	14
Hypericaceae	1	14
Sapindaceae	9	14
Fumariaceae	2	13
Piperaceae	3	13
Portulacaceae	5	13
Sterculiaceae	6	13
Juglandiaceae	1	12
Passifloraceae	2	12
Polygalaceae	2	12
Typhaceae	1	12
Amaryllidaceae	7	11
Betulaceae	4	11
Haloragidaceae	1	11
Lentibulariaceae	1	11
Lobeliaceae	1	11
Nyctaginaceae	3	11
Valerianaceae	4	11

Appendix 2.1. (*Contd.*)

Family	No. of genera	No. of species	Family	No. of genera	No. of species
Berberidaceae	3	10	Orchidaceae	3	4
Loranthaceae	6	10	Santalaceae	3	4
Menispermaceae	8	10	Saururaceae	3	4
Pontederiaceae	4	10	Zingiberaceae	4	4
Rutaceae	7	10	Araliaceae	3	3
Violaceae	3	10	Butomaceae	2	3
Aceraceae	1	9	Ceratophyllaceae	1	3
Lemnaceae	3	9	Elaeagnaceae	2	3
Pedaliaceae	6	9	Hamamelidaceae	2	3
Phytolaccaceae	4	9	Juncaginaceae	1	3
Smilacaceae	1	9	Tamaricaceae	1	3
Sparganiaceae	1	9	Xyridaceae	1	3
Agavaceae	4	8	Aponogetonaceae	1	2
Arecaceae	5	8	Asparagaceae	1	2
Aristolochiaceae	1	8	Calyceraceae	2	2
Balsaminaceae	1	8	Dichapetalaceae	1	2
Combretaceae	2	8	Dioscoreaceae	1	2
Crassulaceae	3	8	Epacridaceae	1	2
Najadaceae	1	8	Eryothroxilaceae	1	2
Sapotaceae	3	8	Frankeniaceae	1	2
Vacciniaceae	1	8	Hydrangeaceae	1	2
Annonaceae	1	7	Icacinaceae	2	2
Callitrichaceae	1	6	Loasaceae	1	2
Cornaceae	1	6	Myrsinaceae	2	2
Ebenaceae	3	6	Nelumbonaceae	1	2
Lauraceae	5	6	Nyssaceae	1	2
Linaceae	1	6	Ochnaceae	1	2
Proteaceae	2	6	Parkeriaceae	1	2
Aquifoliaceae	1	5	Pittosporaceae	2	2
Basellaceae	3	5	Plumbaginaceae	1	2
Bromeliaceae	4	5	Zannichelliaceae	2	2
Cannaceae	1	5	Avicenniaceae	1	1
Cannabaceae	2	5	Barringtoniaceae	1	1
Elatinaceae	2	5	Batidaceae	1	1
Martyniaceae	3	5	Begoniaceae	1	1
Musaceae	2	5	Buddlejaceae	1	1
Myricaceae	2	5	Burseraceae	1	1
Polimoniaceae	3	5	Canellaceae	1	1
Resedaceae	1	5	Caryocaraceae	1	1
Simaroubaceae	5	5	Cassythaceae	1	1
Thymelaeaceae	4	5	Celastraceae	1	1
Meliaceae	4	4	Clusiaceae	1	1
Dilleniaceae	2	4	Cochlospermaceae	1	1
Loganiaceae	4	4	Connaraceae	1	1
Malpighiaceae	4	4	Cyrillaceae	1	1
Marantaceae	4	4	Flacourtiaceae	1	1
Molluginaceae	1	4	Garryaceae	1	1
Myoporaceae	2	4	Gesneriaceae	1	1

Appendix 2.1. (*Contd.*)

Family	No. of genera	No. of species
Haemodoraceae	1	1
Hippuridaceae	1	1
Koeberliniaceae	1	1
Magnoliaceae	1	1
Melianthaceae	1	1
Myristicaceae	1	1
Olacaceae	1	1
Philydraceae	1	1
Platanaceae	1	1
Restionaceae	1	1
Rhizophoraceae	1	1
Ruppiaceae	1	1
Sonneratiaceae	1	1
Styracaceae	1	1
Taccaceae	1	1
Tetragoniaceae	1	1
Trapaceae	1	1
Tropaeolaceae	1	1
Turneraceae	1	1
Xanthorrhoeaceae	1	1
Gymnosperms		
Pinaceae	6	32
Cupressaceae	4	15
Cycadaceae	2	3
Taxaceae	2	3
Ephedraceae	1	2
Taxodiaceae	1	1

Family	No. of genera	No. of species
Ferns, Horsetails and Clubmosses		
Salviniaceae	2	14
Equisetaceae	1	11
Marsileaceae	2	7
Sinopteridaceae	4	7
Thelypteridaceae	3	7
Aspidiaceae	3	6
Dennstaedtiaceae	2	5
Davalliaceae	1	5
Schizaeaceae	1	5
Blechnaceae	3	4
Polypodiaceae	4	4
Selaginellaceae	1	3
Aspleniaceae	2	2
Athyriaceae	1	2
Gleicheniaceae	1	2
Lindsaeaceae	2	2
Osmundaceae	1	2
Pteridaceae	1	2
Cyatheaceae	1	1
Dryopteridaceae	1	1
Gymnogrammaceae	1	1
Ophioglossaceae	1	1
Sphenocleaceae	1	1
Lycopodiaceae	1	1

Appendix 2.2. Genera listed in Holm *et al.* (1979), containing 10 or more species.

Genera		No. of species	Genera		No. of species
Angiosperms					
Cyperus	(Cyperaceae)	81	*Astragalus*	(Papilionaceae)	20
Euphorbia	(Euphorbiaceae)	80	*Indigofera*	(Papilionaceae)	20
Solanum	(Solanaceae)	66	*Medicago*	(Papilionaceae)	20
Polygonum	(Polygonaceae)	62	*Bidens*	(Asteraceae)	20
Panicum	(Poaceae)	57	*Cleome*	(Capparidaceae)	20
Ipomoea	(Convolvulaceae)	57	*Commelina*	(Commelinaceae)	20
Acacia	(Mimosaceae)	53	*Croton*	(Euphorbiaceae)	20
Cuscuta	(Convolvulaceae)	49	*Phyllanthus*	(Euphorbiaceae)	20
Eragrostis	(Poaceae)	48	*Fimbristylis*	(Cyperaceae)	20
Quercus	(Fagaceae)	48	*Heliotropium*	(Heliotropiaceae)	20
Senecio	(Asteraceae)	45	*Hibiscus*	(Malvaceae)	20
Chenopodium	(Chenopodiaceae)	39	*Galium*	(Rubiaceae)	19
Amaranthus	(Amaranthaceae)	37	*Lactuca*	(Asteraceae)	19
Centaurea	(Asteraceae)	35	*Plantago*	(Plantaginaceae)	19
Oxalis	(Oxalidaceae)	34	*Acalypha*	(Euphorbiaceae)	18
Eleocharis	(Cyperaceae)	33	*Asclepias*	(Asclepiadaceae)	18
Rumex	(Polygonaceae)	33	*Aster*	(Asteraceae)	18
Crotalaria	(Papilionaceae)	32	*Lepidium*	(Brassicaceae)	18
Desmodium	(Papilionaceae)	31	*Salix*	(Salicaceae)	18
Carex	(Cyperaceae)	30	*Verbena*	(Verbenaceae)	18
Scirpus	(Cyperaceae)	30	*Brachiaria*	(Poaceae)	17
Rubus	(Rosaceae)	30	*Cirsium*	(Asteraceae)	17
Sida	(Malvaceae)	30	*Xanthium*	(Asteraceae)	17
Salvia	(Lamiaceae)	29	*Baccharis*	(Asteraceae)	16
Cassia	(Caesalpiniaceae)	29	*Carduus*	(Asteraceae)	16
Digitaria	(Poaceae)	28	*Delphinium*	(Ranunculaceae)	16
Ranunculus	(Ranunculaceae)	28	*Eryngium*	(Apiaceae)	16
Juncus	(Juncaceae)	28	*Hydrocotyle*	(Apiaceae)	16
Potamogeton	(Potamogetonaceae)	28	*Ludwigia*	(Onagraceae)	16
Ribes	(Saxifragaceae)	27	*Lupinus*	(Papilionaceae)	16
Trifolium	(Papilionaceae)	26	*Sporobolus*	(Poaceae)	16
Vicia	(Papilionaceae)	26	*Stachys*	(Lamiaceae)	16
Vernonia	(Asteraceae)	25	*Anthemis*	(Asteraceae)	15
Setaria	(Poaceae)	25	*Gnaphalium*	(Asteraceae)	15
Opuntia	(Cactaceae)	25	*Aristidia*	(Poaceae)	15
Orobanche	(Orobanchaceae)	25	*Brassica*	(Brassicaceae)	15
Physalis	(Solanaceae)	23	*Borreria*	(Rubiaceae)	15
Artemisia	(Asteraceae)	22	*Eriocaulon*	(Eriocaulaceae)	15
Lathyrus	(Papilionaceae)	22	*Geranium*	(Geraniaceae)	15
Oenothera	(Onagraceae)	22	*Scleria*	(Cyperaceae)	15
Veronica	(Scrophulariaceae)	22	*Atriplex*	(Chenopodiaceae)	14
Bromus	(Poaceae)	21	*Allium*	(Alliaceae)	14
Eupatorium	(Asteraceae)	21	*Ceanothus*	(Rhamnaceae)	14
Silene	(Caryophyllaceae)	21	*Cenchrus*	(Poaceae)	14

Appendix 2.2. (*Contd.*)

Genera		No. of species	Genera		No. of species
Echinochloa	(Poaceae)	14	*Convolvulus*	(Convolvulaceae)	11
Corchorus	(Tiliaceae)	14	*Hyptis*	(Lamiaceae)	11
Hypericum	(Hypericaceae)	14	*Leucas*	(Lamiaceae)	11
Rhus	(Anacardiaceae)	14	*Lindernia*	(Scrophulariaceae)	11
Sagittaria	(Alismataceae)	14	*Striga*	(Scrophulariaceae)	11
Alternanthera	(Amaranthaceae)	13	*Myriophyllum*	(Haloragidaceae)	11
Erigeron	(Asteraceae)	13	*Nymphaea*	(Nymphaeaceae)	11
Hordeum	(Poaceae)	13	*Lobelia*	(Lobeliaceae)	11
Pennisetum	(Poaceae)	13	*Passiflora*	(Passifloraceae)	11
Linaria	(Scrophulariaceae)	13	*Polygala*	(Polygalaceae)	11
Merremia	(Convolvulaceae)	13	*Prosopsis*	(Mimosaceae)	11
Rosa	(Rosaceae)	13	*Rorippa*	(Brassicaceae)	11
Triumfetta	(Tiliaceae)	13	*Utricularia*	(Lentibulariaceae)	11
Agrostis	(Poaceae)	12	*Avena*	(Poaceae)	10
Chloris	(Poaceae)	12	*Chrysanthemum*	(Asteraceae)	10
Sorghum	(Poaceae)	12	*Cerastium*	(Caryophyllaceae)	10
Arctostaphylos	(Ericaceae)	12	*Daucus*	(Apiaceae)	10
Bacopa	(Scrophulariaceae)	12	*Lippia*	(Verbenaceae)	10
Carya	(Junglandaceae)	12	*Justicia*	(Acanthaceae)	10
Hedyotis	(Rubiaceae)	12	*Piper*	(Piperaceae)	10
Fumaria	(Fumariaceae)	12	*Populus*	(Salicaceae)	10
Mentha	(Lamiaceae)	12	*Prunus*	(Rosaceae)	10
Sisymbrium	(Brassiaceae)	12	*Sesbania*	(Papilionaceae)	10
Typha	(Typhaceae)	12	*Tephrosia*	(Papilionaceae)	10
Abutilon	(Malvaceae)	11	*Gymnosperms*		
Malva	(Malvaceae)	11			
Alopecurus	(Poaceae)	11	*Pinus*	(Pinaceae)	20
Andropogon	(Poaceae)	11	*Juniperus*	(Cupressaceae)	11
Ambrosia	(Asteraceae)	11			
Crepis	(Asteraceae)	11	*Ferns, Horsetails and Clubmosses*		
Solidago	(Asteraceae)	11			
Ammannia	(Lythraceae)	11	*Equisetum*	(Equisetaceae)	11