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Plant invasions – the role of mutualisms

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ABSTRACT

Many introduced plant species rely on mutualisms in their new habitats to overcome barriers to establishment and to become naturalized and, in some cases, invasive. Mutualisms involving animal-mediated pollination and seed dispersal, and symbioses between plant roots and microbiota often facilitate invasions. The spread of many alien plants, particularly woody ones, depends on pollinator mutualisms. Most alien plants are well served by generalist pollinators (insects and birds), and pollinator limitation does not appear to be a major barrier for the spread of introduced plants (special conditions relating to *Ficus* and orchids are described). Seeds of many of the most notorious plant invaders are dispersed by animals, mainly birds and mammals. Our review supports the view that tightly coevolved, plant-vertebrate seed dispersal systems are extremely rare. Vertebrate-dispersed plants are generally not limited reproductively by the lack of dispersers. Most mycorrhizal plants form associations with arbuscular mycorrhizal fungi which, because of their low specificity, do not seem to play a major role in facilitating or hindering plant invasions (except possibly on remote islands such as the Galapagos which are poor in arbuscular mycorrhizal fungi). The lack of symbionts has, however, been a major barrier for many ectomycorrhizal plants, notably for *Pinus* spp. in parts of the southern hemisphere. The roles of nitrogen-fixing associations between legumes and rhizobia and between actinorhizal plants and *Frankia* spp. in promoting or hindering invasions have been virtually ignored in the invasions literature. Symbionts required to induce nitrogen fixation in many plants are extremely widespread, but intentional introductions of symbionts have altered the invasibility of many, if not most, systems. Some of the world's worst invasive alien species only invaded after the introduction of symbionts. Mutualisms in the new environment sometimes re-unite the same species that form partnerships in the native range of the plant. Very often, however, different species are involved, emphasizing the diffuse nature of many (most) mutualisms. Mutualisms in new habitats usually duplicate functions or strategies that exist in the natural range of the plant. Occasionally, mutualisms forge totally novel combinations, with profound implications for the behaviour of the introduced plant in the new environment (examples are seed dispersal mutualisms involving wind-dispersed pines and cockatoos in Australia; and mycorrhizal associations involving plant roots and fungi). Many ecosystems are becoming more susceptible to invasion by introduced plants because: (a) they contain an increasing array of potential mutualistic partners (e.g. generalist frugivores and pollinators, mycorrhizal fungi with wide host ranges, rhizobia strains with infectivity across genera); and (b) conditions conducive for the establishment of various alien/alien synergisms are becoming more abundant. Incorporating perspectives on mutualisms in screening protocols will improve (but not perfect) our ability to predict whether a given plant species could invade a particular habitat.

Key words: biological invasions, global change, invasibility, mycorrhiza, nitrogen fixation, pollination, prediction, risk assessment, seed dispersal.

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CONTENTS

I. INTRODUCTION

Many plant species introduced by humans to areas outside their natural ranges (hereafter 'alien plants') establish self-perpetuating populations (i.e. they become 'naturalized'). Some of these species spread from sites of introduction, become integrated into native communities and disrupt their functioning. In many cases, invasive alien species suppress or eliminate native species, causing a loss of biodiversity.

Good progress has been made in the last two decades in the study of plant invasions (e.g. see Drake *et al.*, 1989; D'Antonio & Vitousek, 1992; Pyšek *et al.*, 1995; Rejmánek, 1996*a*; Williamson, 1996 for recent reviews). Important advances in our understanding of invasions have come from careful studies of single invasion events, comparative studies (contrasting the behaviour of the same species under different conditions, or different species in the same area), and, most recently, from modelling studies (e.g. Higgins & Richardson, 1998). Despite the progress, invasions are still irritatingly idiosyncratic; there are exceptions to every generalization that ecologists have described. Many interacting factors influence the composition, abundance and diversity of species at different scales. It is therefore not surprising that predicting the fate of introduced species is complicated.

Various physical and biotic features act, at least potentially, as 'filters' or 'barriers' to invasion (Kruger, Richardson & Van Wilgen, 1986). The success of many invaders can also be ascribed, at least partly, to the beneficial effects of various abiotic features in the target systems. Many invasions, therefore, rely on inherent properties of the invaded system for their success. Features of the prevailing disturbance regime often provide opportunities for establishment, for example by causing the release of seeds from serotinous cones, triggering germination, reducing competition and herbivory, and providing pulses of resources that allow the potential invader to establish. Flowing water and wind are often very important vectors of dispersal for propagules of incipient invaders. These factors, together with the complex historical and cultural considerations that

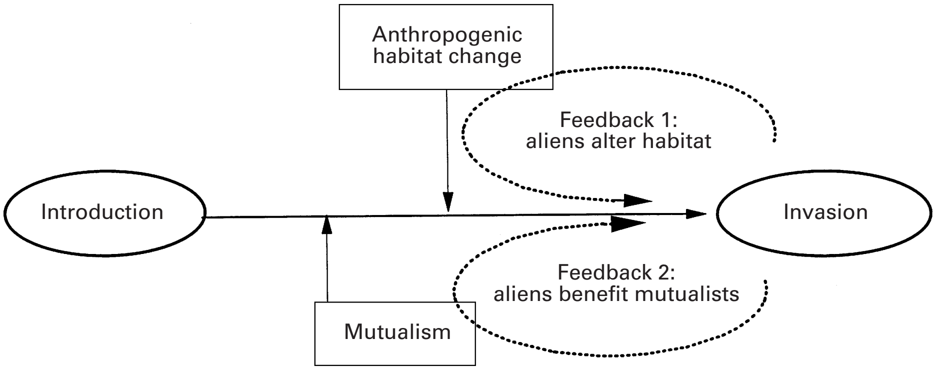


Fig. 1. General model of invasion of alien plants facilitated by mutualisms (including pollination, seed dispersal and nutrient acquisition), and by anthropogenic changes to indigenous vegetation, disturbance regimes, and nutrient cycling in natural habitats. Note that successful invasions are often self-enforcing in that they further alter habitats and processes and benefit their own mutualists.

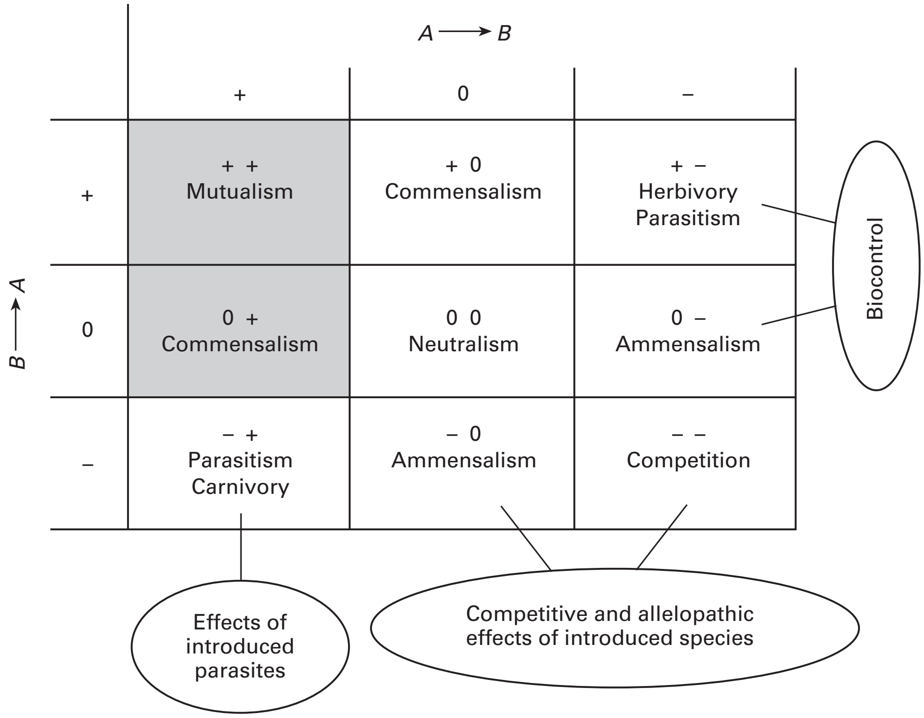
have influenced the movement of humans between regions and their activities within regions, have shaped the distinctive invasive alien floras of different areas. By invoking a combination of these factors, one can often 'explain' the composition of a given invasive alien flora, or rationalize the success of a particular organism in a given system.

Several recent papers have presented protocols for screening new introductions for their potential invasiveness (Tucker & Richardson, 1995; Reichard & Hamilton, 1997), or explanations for the differential success of related taxa as invaders (e.g. Richardson, Cowling & Le Maitre, 1990 for *Banksia* and *Pinus*). Such predictions or explanations are based on factors such as: geographic origin and bioclimatic matches; climatic and latitudinal range; taxonomic relationships; past performance after introductions to other regions; assessments of the likely tolerance of an organism to features of the prevailing disturbance regime; and assessments of many aspects of reproductive biology and general ecology (see Bingelli, 1996; Reichard & Hamilton, 1997; Rejmánek, 1998, for overviews). The importance of unanticipated positive interactions is highlighted when one assesses instances where such techniques yield erroneous results (i.e. success as an invader when failure is predicted), for example for some *Pinus* species in the southern hemisphere (Richardson *et al.*, 1990; Richardson & Higgins, 1998).

One reason for errors in predicting the outcome of introductions is the failure of most screening protocols or evaluations to consider the potential role of positive interactions. Invasion events very often depend on, or are at least greatly enhanced by, the establishment of mutualisms between the alien organism and other organisms (native or themselves introduced) already established in the system. Models such as that shown in Fig. 1 are implied in many general accounts of invasions, but there is no clear framework for determining the importance of various types of mutualisms in facilitating or preventing invasions.

There are many possible interactions between an invading species and other biota (Fig. 2). Invasion ecology has traditionally emphasized biotic interactions that affect the alien species negatively, notably through competition/amensalism and herbivory; factors considered to be the major components of 'ecological resistance' of communities to invasion (e.g. *sensu* Elton, 1958). Another issue that has enjoyed considerable attention is the control of alien plants by herbivory and pathogens (+ − interactions in Fig. 2). This bias in favour of negative interactions is also evident in ecology in general (Kareiva & Bertness, 1997), although recently much more attention is being given to the role of positive interactions in promoting coexistence (e.g. Bertness & Callaway, 1994; Callaway & Walker, 1997).

The fact that introduced plants can establish facultative mutualistic relations soon after introduction did not escape the attention of Charles Darwin who observed: 'Within two years after planting [the non-native] *Berberis dulcis* a bush very unlike the common barberry…its flowers were visited by bees, visits indispensable, I believe, to its fertilization, and its fruit was devoured by the Robin, which would disseminate its seed' (Stauffer, 1975, p. 344). Another pertinent observation by Darwin, cited by Bennett (1873), was the finding that the alien *Impatiens capensis* was visited by native bumblebees in England. Notwithstanding such early



B → A \ A → B	+	0	–
+	+ + Mutualism	+ 0 Commensalism	+ – Herbivory Parasitism
0	0 + Commensalism	0 0 Neutralism	0 – Ammensalism
–	– + Parasitism Carnivory	– 0 Ammensalism	– – Competition

Fig. 2. Possible interactions between introduced plant species (A) and other organisms (B); the latter may be native or introduced. Signs in the body of the table show the type of interaction (+, positive; −, negative; 0, neutral). The first sign indicates the effect of A on B; the second shows the effect of B on A. Interactions in shaded cells are the focus of this paper.

records, positive interactions have not been afforded the attention they deserve in the invasion literature. Because of the need to gain a predictive understanding of invasions it is appropriate to assess the level of understanding of the importance of positive interactions and to propose a conceptual framework for gaining further insights.

By definition, all alien plants have benefited through human-aided dispersal to a new region, and very often also through intensive propagation and dissemination within the new region. In this review we ignore mutualisms directly involving humans. Rather, we focus on instances where alien plants have depended on the establishment of mutualisms with other organisms to reproduce and spread in their new environment. We have also not addressed 'mutualisms' in which the alien plant benefits from disturbance caused by animals which benefit from increased food availability of highly productive aliens (e.g. Schiffman, 1994). The role of disturbance in initiating and sustaining invasions has been well described recently (e.g. Hobbs & Huenneke, 1992). Rather, we concentrate on mutualisms involving animal-mediated pollination and seed dispersal, and symbioses between plant roots and microbiota that are very often implicated in the establishment and spread of alien plant species in new environments. In our combined experience with plant invasions in many parts of the world, these are the most important categories of mutualisms that have mediated the performance of introduced plants. Our aim is to provide a framework for understanding the importance of mutualisms in plant invasion ecology. We also re-evaluate the tendency to focus on negative interactions when considering community invasibility, and examine whether there is any way of incorporating the understanding of the role of mutualisms into improved protocols for predicting invasiveness. Most of the evidence presented here was gleaned from studies that did not address these issues directly, and some of our inferences may be considered speculative. Bearing in mind the vastness of the topic, we have tried to rationalize our choice of examples and their relative contributions to our arguments as thoroughly as possible.

II. ANIMAL-MEDIATED POLLINATION

Approximately 80% of flowering plants are facultative or obligate out-crossers (Brown, 1990) and many of these depend on animals for pollination. Most animal-pollinated plants are served by several to many species, often of widely diverse taxonomic origin. Pollination by a single species is very rare, although *Ficus*, *Yucca* and orchids are notable exceptions (references in Bond, 1994). The movement of plants to habitats new to them, usually without their normal pollinators, offers the opportunity to test many crucial issues in pollination ecology (e.g. those raised by Waser *et al.*, 1996). Surprisingly, very few studies have addressed these issues explicitly.

(1) The incidence of animal-mediated pollination in alien floras

Baker (1965, 1974), in his early attempts at characterizing 'ideal weeds', included self-compatibility and unspecialized pollination requirements as features that should lead to greater invasiveness. Unfortunately, very little quantitative information is available on the breeding biology and pollination requirements of most invasive alien plants. Notable cases of highly successful aliens that are almost entirely autogamous (self-fertilizing) include: e.g. garlic mustard (*Alliaria petiolla*) in North America (Cavers, Heagy & Kokron, 1979); cheatgrass (*Bromus tectorum*) in North America (Upadhyaya, Turkington & McIlvride, 1986); Hottentot fig (*Carpobrotus edulis*) in California (Vilà, Weber & D'Antonio, 1998); *Hypericum perforatum* in North America (Crompton *et al.*, 1988); crystalline iceplant (*Mesembryanthemum crystallinum*) in California (N. Vivrette, unpublished data). There are, however, also notable alien invaders that are obligate outcrossers; North American examples include *Centaurea diffusa* and *C. maculosa* (Harrod & Taylor, 1995), and purple loosestrife, *Lythrum salicaria* (Levin, 1970; Mal *et al.*, 1992).

Very little has been published on the relative importance of different pollination syndromes in invasive alien floras. Published accounts of the 'weeds' of Canada (*Canadian Journal of Plant Sciences*; 1980–1998) show that approximately two-thirds of the species listed were facultatively self-fertile. Most of these were agricultural weeds growing in highly disturbed settings where opportunities for cross-pollination may be limited. By contrast, a survey of the invasive alien woody plants in North America (Reichard, 1994) revealed that 56% of successful species are apparently outcrossing. Carr (1993), describing the invasive alien flora of Victoria, Australia, states that many species are insect-pollinated and that a wide range of native (predominately Hymenoptera, Lepidoptera and Diptera), alien (notably honeybees; *Apis mellifera*), or recent immigrant (especially the ubiquitous *Syrphis* spp.) insects are implicated. Thus, many introduced plant species, particularly woody ones, require pollinator mutualisms to become invasive.

Woodell (1979) showed that many of the plant species introduced to Aldabra Island were pollinated by a native sunbird and a native beetle. In Victoria, Australia, a very large proportion of the insect-pollinated environmental weeds of Old World origin are pollinated by alien honeybees which are abundant throughout the state (introduced approximately 150 years ago). Plants that are pollinated by hummingbirds (Trochilidae) and sunbirds (Nectarinidae) in their natural ranges are well served by native Australian nectarivores, primarily the honeyeaters (Meliphagidae). These plants include species from such diverse groups and origins as *Aloe* (Liliaceae; from South Africa); *Cestrum* (Solanaceae; from South America) and *Hakea* and *Grevillea* (Proteaceae; from other parts of Australia). The Victorian example shows that many alien plant species are extremely well served by pollinators with which they have no 'experience' (see Herrera, 1996, pp. 70–71, for supporting evidence).

(2) Evidence of pollinator-limited seed set in native and alien plants

The extent to which individual plant species are limited by the absence (or shortage) of pollinators is an issue that has stimulated much research. Surprisingly, little detailed work has been done on introduced plants. Rather, research has focused on pollinator limitation in self-incompatible or facultatively outcrossing plant populations in their native ranges. Pollinator limitation to seed set was found in 42% of 99 pollen supplementation studies reviewed by Young & Young (1992), and many more studies have demonstrated pollinator limitation to seed set in native species. Very few experimental studies have addressed pollinator limitation to seed production in introduced non-crop plant species (but see Stanton, 1987; Parker, 1997). Well-documented cases of severe pollen limitation in introduced species are the failure of red clover (*Trifolium pratense*) to set seed in New Zealand before bumblebees were introduced (Hopkins, 1914) and the failure of *Ficus carica* (Condit, 1947) and *Melilotus* (Faegri & van der Pijl, 1966) to set seed in North America.

Predicting under what conditions pollinators might limit the spread of an introduced plant is not simple. Parker (1997) found that invasions of Scotch broom (*Cytisus scoparius*) in western Washington, U.S.A., can be strongly limited by pollinator activity, but that limitation varied among sites. This species, an obligate out-crosser, has acquired both native and introduced pollinators in its new range. Parker (1997) suggests that pollinator limitation exists because pollinators are more attracted to simultaneously flowering native species than to the broom. Pollen limitation to seed set was lowest in urban sites where there were greater numbers of native bumblebees visiting the flowers and fewer species of native species that flowered at the same time as *C. scoparius*.

In contrast to Parker's (1997) finding of pollinator limitation, Stanton (1987), studying *Raphanus sativus* in California, U.S.A., and Levin (1970), working on *Lythrum salicaria* in the central U.S.A., found that these self-incompatible alien herbs were not pollen limited because both native bees and introduced honeybees were abundant, attentive, and could promote seed set in these species. Indeed, Levin (1970) found that *L. salicaria* was more attractive to both native and introduced generalist pollinators than native *L. alatum* flowering simultaneously in the same habitat. He attributed this difference to the bigger flowers of the alien.

Introduced honeybees are often considered to be poor pollinators (Westerkamp, 1991), but their abundance over a wide range of habitats should increase the likelihood that outcrossing aliens will have at least some visitors. Willson & Burley (1983) suggested that the presence of introduced honeybees has reduced the likelihood of pollinator limitation for any outcrossing plant species in many parts of North America. Furthermore, many pollinating insects can readily learn to respond to plant reward cues, even when they are exposed to plant species with which they did not evolve. For example, Weiss & Lamont (1997) found that native insect species could discriminate and respond to floral colour phases in both native and alien plants. These colour phases served to direct visitors towards flowers that had not yet been pollinated. This responsiveness of pollinators to 'new' host plants further supports the idea that pollinator mutualisms can emerge quickly.

(3) Invasion of plants with specialized animal pollinators

It is logical to predict that plants with specialized pollination syndromes are less likely to be pollinated in foreign environments than plants without specialized requirements. Certainly, it is unlikely that plants offering specialized rewards to endemic insects would spread in areas where such specialist pollinators are absent. For example, the genus *Diascia* in Namaqualand, South Africa, is visited by specialized bees that remove oil from spurs in the lower petals using modified front legs (Steiner & Whitehead, 1990). Orchids, a large, diverse family known for their highly specialized pollination syndromes, have been widely cultivated, yet very few species have become invasive (Daehler, 1998; Pyšek, 1998). We can only guess that part of the limitation on spread is the lack of suitable pollinators. Some orchids mimic female wasps and are pollinated by deceived males of the same species (Dressler, 1981). It is very unlikely that plants with such tight mutualisms could find suitable pollinators outside their natural ranges and we know of no cases where such species have invaded. There are, however, many records of alien plants thriving in the absence of animals thought to be the dominant pollinator in their natural ranges and acquiring types of pollinators that are completely new to them. For example, *Fuschia magellanica* is pollinated by the green-backed firecrown hummingbird (*Sephanoides galeritus*) in its native range in South America, but is pollinated solely by generalist insects in Britain (Valentine, 1977).

The invasion ecology of *Ficus* species introduced to Florida in the USA and New Zealand is informative. Only three of 60 *Ficus* species introduced to Florida have become invasive, and they did so only after the accidental introduction of their specific wasp pollinators (Ramirez & Montero, 1988; McKey & Kauffman, 1991; Nadel, Frank & Knight, 1992). Although Florida has native figs, native fig wasps have not moved onto the introduced fig species (Kjellberg & Valdeyron, 1990). Ramirez & Montero (1988) predicted that the pollinator of *F. microcarpa*. *Parapristina verticillata*, would spread rapidly south from Florida, Honduras, and the Mexican State of Morelos, where the wasp probably established in the early 1980s (*F. microcarpa* is planted abundantly in all the tropical and subtropical countries in this region). In New Zealand (which has no native figs), *F. macrophylla* and *F. rubiginosa* were cultivated for many years without setting seed. Both species acquired their pollinating wasps recently, apparently by long-distance dispersal by wind from their natural range in eastern Australia (Gardner & Early, 1996). In Africa, *Ficus lutea* planted outside its native range was successfully pollinated by fig wasp species that were not its normal pollinator (Ware & Compton, 1992). Ware and Compton (1992) observed that figs of *F. lutea* stayed receptive for an unnaturally long time (presumably due to the lack of pollination), which facilitated incidental colonization by alien pollinators. Recent evidence (e.g. Anstett, Michaloud & Kjellberg, 1995) shows that this is more general in the genus than was previously thought. Also, fig wasps seem to travel greater distances than was previously thought (Nason, Herre & Hamrick, 1998). Both these findings suggest that *Ficus* is not as unique in its dependence on pollinators as is sometimes argued. Nonetheless, figs represent the most widely studied case of pollinator-mediated limitation of invasion.

(4) Implications for invasions

Only a tiny proportion of potential invaders among introduced plant species have been known to be prevented from spreading because of the absence of pollinators. It appears relatively easy for introduced plants to attract suitable pollinators in their introduced range. Even some plants thought to have highly specialized pollination requirements can thrive in the presence of generalist pollinators (see the *Fuchsia magellanica* example above). *Ficus* and orchids may be exceptions (but see above). Pollinator specificity tends to be much greater in tropical than temperate plant species (Bawa, 1990); it may therefore be that pollinator limitation as a barrier to invasion will only be common for tropical species introduced to temperate zones.

Many generalist pollinators have expanded their ranges in recent times. Concern has been expressed that such invasions have disrupted native pollination systems (references in Waser *et al.*, 1996). Very little has been published about the potential impacts of invasions by such super-generalists as *Apis mellifera* on the pollination ecology of invasive alien plants (for a recent review see Butz-Huryn, 1997). A recent study (Barthell *et al.*, in press) suggests that *A. mellifera* facilitates invasion by yellow starthistle (Centaurea solstitialis) in some Californian ecosystems by significantly increasing seed set compared to that achieved by native pollinators alone. The increased abundance of *A. mellifera* may be exacerbating the problem of alien plant invasions in other systems as well. Although Butz-Huryn (1997) claims that honeybees probably contribute little to the success of most weeds (see also Butz-Huryn & Moller, 1995), several researchers we consulted felt that this conclusion is premature. Further work is clearly required.

III. SEED DISPERSAL BY ANIMALS

The ability of the propagules of alien plant species to disperse and invade natural habitats in a new region is greatly enhanced by adaptations for transport in or on animals and other moving objects. Animals may have the added advantage of moving seeds to sites that are nutrient-enriched, disturbed or otherwise ideal for germination and seedling establishment. Animals most often disperse seeds by eating or caching food plants, collecting material for nest construction, or inadvertently transporting adhesive propagules on their fur, feathers, feet or beaks. Of the 199 'representative invasive species' listed by Cronk & Fuller (1995), 25% are known to be dispersed by birds, 14% by mammals and 1% by ants (45% have no obvious adaptations for animal dispersal; dispersal modes for 25% of species are unknown). Although comparable data for native floras are not available, the data show that many invasive alien plants are dispersed by animals. Representative examples of different categories of dispersal of alien plants by animals are given in Table 1.

Carr (1993) reports that approximately 100 species (8%) of the naturalized flora of Victoria, Australia have fleshy fruits adapted for dispersal by birds and mammals. Known dispersers include an alien blackbird, foxes and livestock plus native species such as birds (emus, silver gulls, blackfaced cuckooshrikes, little and red wattlebirds, mistletoe birds, silvereyes, pied currawongs and ravens), mammals (kangaroos, grey-headed flying foxes, European foxes) and reptiles (Cunningham's skink). The situation in Victoria, similar to that in many other parts of the world, shows that alien plants with fleshy fruits benefit from mutualisms involving a wide range of animals with no previous experience of dispersing their seeds. Below we provide further details of these mutualisms.

(1) Mechanisms of alien seed dispersal by animals

Frugivorous and omnivorous birds have facilitated the spread of fleshy-fruited and arillate alien plants from points of introduction into natural ecosystems throughout the world (e.g. Dean, Holmes & Weiss, 1986; Carr, 1993; Williams & Karl, 1996; Sallabanks, 1993). Primarily bird-dispersed plants (those with showy black, blue or red fleshy fruits) constitute 27% of Cronk & Fuller's (1995) list of 199 environmental weeds; this is clearly a very general (and diffuse) mutualism.

The success of fleshy-fruited plants as invaders in regions where frugivorous birds are available may be partially dependent on the relative availability of indigenous and alien fruits. For example, in the Montpellier region of France where there are 65 native taxa with fleshy fruits, none of the 19 alien fleshy-fruited shrubs has become invasive. Debussche & Isenmann (1990) suggest that this failure to invade, despite the abundance of suitable dispersers, may be because of competition for dispersal from the many indigenous fleshy-fruited species. This situation contrasts with others where species bearing fleshy-fruits are uncommon (on nutrient-poor soils in Australia and South Africa, dunes in California, U.S.A.), rare in the landscape because of habitat destruction (Queensland and New South Wales in Australia), or where fleshy fruits are seasonally scarce. Invasions of fleshy-fruited plants into nutrient-poor habitats appear to be facilitated by both nutrient enrichment (Amarell, 1997; Auge & Brandl, 1997) and the increases in frugivorous birds that are associated with growth of urban and suburban areas (Debussche & Isenmann, 1990). Habitat loss, such as the reduction of subtropical rainforest in New South Wales, is implicated in the spread of alien *Cinnamomum camphora* and *Ligustrum lucidum* fruits by frugivorous birds that are now dependent on these garden ornamentals in winter (Hackett, 1996, 1997). Sallabanks (1993) has demonstrated that the invasive alien *Crataegus monogyna* produced larger displays of higher quality fruit than its native congener and that this contributed to its rapid spread in western Oregon.

The successful invasion of European fleshy-fruited species such as *Rubus* spp. into Europeanized Australia has been further facilitated by another seed disperser, the alien European red fox (Brunner, Harris & Amor, 1976). This sort of alien/alien synergism has precipitated the ecologically damaging invasion of Hawaiian forests by the fleshy-fruited tree, *Myrica faya* (La Rosa, Smith & Gardner, 1985; Woodward *et al.*, 1990). Likewise, the alien blackbird (*Turdus merula*) is an important disperser for many serious environmental weeds in Victoria including *Chrysanthemoides monilifera* (Asteraceae), *Ligustrum lucidum* (Oleaceae), *Myrsiphyllum asparagoides* (Liliaceae), *Pyracantha coccinea* (Rosaceae) and *Schinus molle* (Anacardiaceae) (Carr, 1993). All these species are also alien to the blackbirds natural range.

Mammals, particularly bats and primates, disperse plants that use aroma rather than colour to advertise ripe fruits (van der Pijl, 1982). Strongly scented fruits such as *Psidium cattleianum* attract both native and alien mammals wherever they are introduced. Omnivores, including canids, bears, and pigs include fruit in their diet and disperse a wide range of plant species (Stiles, 1989) including many aliens. Even herbivores consume fleshy fruits. For example, cattle take fallen guavas (*Psidium guajava*; Somarriba, 1986) and *Ziziphus mauritanica* fruits (Grice, 1996), and hares and deer feed on *Carpobrotus edulis* fruits which are borne close to the ground (D'Antonio, 1990). In the latter case, *C. edulis* provides ripe fruit during a period of the year when other food is scarce and in habitats in which no native species bear fleshy fruit. In all these cases, dispersal accelerates invasion.

The widespread transport by large herbivores of small-seeded grasses and forbs (including Aizoaceae, Amaranthaceae, Chenopodiaceae, Fabaceae and Portulacaceae) is seldom considered a form of mutualism. However, Janzen (1984) recognized the role of herbivores in the long-distance dispersal of small hard seeds ingested with herbage. He pointed out that for such grasses and forbs 'leaves are the fruit'. This applies to most awnless grasses and many other herbaceous plants considered to have no dispersal mutualism with animals. Domesticated and wild herbivores carry thousands of viable seeds of weedy species in their guts, dispersing them *via* dung into natural vegetation (Malo & Suárez, 1995). In this way, introduced sheep and cattle moving between planted pastures and natural vegetation have spread the African grass *Eragrostic lehmanniana* in the U.S.A. (Anable, McClaren & Ruyle, 1992; Fredrickson *et al.*, 1997), and the European grasses *Holcus lanatus* and *Poa annua* onto islands of the Tristan da Cunha group in the South Atlantic (Wace, 1967), and leguminous forbs into the tropical grasslands of Australia (Gardener, McIvor & Jansen, 1993). Nitrophilous pasture weeds such as *Amaranthus* spp., *Chenopodium murale* and *Urtica urens* are similarly dispersed in herbivore dung after incidental consumption of seed with herbage. Seeds of Australian saltbushes (*Atriplex lindleyi* and *A. semibaccata*) germinate from dung of sheep, native antelope, ostriches and tortoises (Milton, 1992; Milton *et al.*, 1995; S. J. Milton, unpublished data).

Where they have been introduced to northern and southern Africa, *Atriplex* spp. invade the most heavily grazed areas (Le Floc'h, Le Houerou & Mathez, 1990). Large mammals that feed on protein-rich dry pods of woody legumes are particularly successful dispersers of woody weeds in savannas. For example, African *Acacia nilotica*, which has carbohydrate-rich pods attractive to large African herbivores that disperse its hard seeds, is spread in Australia by non-native cattle (Carter & Cowan, 1993). American *Prosopis* spp. are similarly dispersed by domestic sheep and cattle in Australia, southern Africa and the Americas (Meadly, 1965; Brown & Archer, 1987; Harding & Bate, 1991).

Vertebrates can also disperse plant propagules by intentionally caching collected seeds away from parent plants (Nel, 1967; Kollmann & Schill, 1996), or by using seed-bearing stems as their nest material (Dean, Milton & Siegfried, 1990). Seed predators can be important dispersers, when some of the seeds they store or scatter hoard for future use germinate before they are recovered (Smith, 1975). Such dispersal events are not strictly mutualistic but are influential in mediating invasive behaviour and are thus applicable here. Many other animals also disperse seeds indirectly. Dean & Milton (1988) described the widespread occurrence of seed dispersal by raptors. Many carnivorous mammals also disperse seeds (e.g. feral cats, by preying on seed-ingesting lizards in the Canary Islands; Nogales, Medina & Valido, 1996).

Ants are by far the most important invertebrate dispersers of seeds. Insectivorous ants are attracted to seeds that bear elaiosomes (oily food bodies derived from funicles). The ants collect seeds that fall to the ground, carry them to their nests and, after consuming the elaiosome, discard the seeds in their underground nests. Myrmecochory results in seed burial, often in unshaded, nutrient-enriched sites where seeds are protected from predators and fire, and where post-fire establishment is favoured (Bond & Stock, 1989). In South African fynbos and Australian kwongan, adaptation for ant dispersal is most frequent in fire-adapted vegetation types on nutrient-poor soils (Bond & Slingsby, 1983). The existence of such ant-plant mutualisms in fynbos has facilitated invasions of Australian *Acacia saligna* (Holmes, 1990*a*, *b*). Although dispersal in water, in soil moved by humans, and by birds (Knight & Macdonald, 1991) has been much more important in increasing the range of this alien species (Richardson *et al.*, 1992), ants are important in short-distance dispersal and because they bury the seeds, providing protection from predators and fire. In the western U.S.A., leafy spurge (*Euphorbia esula* L.), a serious rangeland weed, bears elaiosomes and has been found to be dispersed by *Formica* ants which appear both to bury seed and to discard seed on mounds after removal of the elaiosome (Pemberton, 1988). The extent to which this has contributed to the success of this plant is not known, but *E. esula* individuals are common on or near nest sites and ants may facilitate the formation of foci of small populations over the landscape. This in turn may speed the invasion process (Moody & Mack, 1988).

Collection of seeds by harvester ants is not a true mutualism as the target seeds are not specialized for dispersal by such ants. Nevertheless, these seed predators may contribute to the success of alien plants. Harvester ants, such as *Pogonomyrmex* species in arid regions of the U.S.A. and *Messor* species in southern Europe, Israel and South Africa, collect the most abundant seeds available and transport them over distances of 50–100 m to their nests (Milton & Dean, 1993), where they maintain stores of viable seeds for later consumption (Ofer, 1980; Dean & Yeaton, 1992). When the ant nests are disturbed by predators, the viable seeds are released onto the organically enriched soils of the nest mound (Dean & Yeaton, 1993*a*). In this way, harvester ants are facilitating invasions of alien plants, including Australian *Atriplex* spp. and European *Bromus* spp. into relatively undisturbed South African rangelands (Dean & Yeaton, 1993*b*).

(2) Other dispersal mutualisms

In the vast majority of cases we reviewed, seed dispersal mutualisms that establish in alien habitats closely approximate associations that exist in the natural range of introduced plants. New types of associations are also emerging. For example, several species of wind-dispersed pine (*Pinus* spp.) native to North America and the Mediterranean Basin are dispersed by cockatoos in Australia (Richardson & Higgins, 1998, pp. 461–462; Table 1). Although the birds destroy most of the seeds, some survive to establish isolated foci in habitats (eucalypt forests) that they would otherwise not have been able to invade. *Pinus pinea* from Europe is dispersed by the alien squirrel *Sciurus carolinensis* in South African fynbos (Richardson *et al.*, 1990); this mutualism accounts for the (modest) success of this pine as an invader in the region. Another novel pine-mammal mutualism (albeit less profound in terms of invasion dynamics) exists in South Africa, where baboons

Table 1. *Examples of different categories of seed-dispersal mutualisms implicated in alien plant invasions. The list is by no means exhaustive, but aims to give a wide range of examples representing many plant groups, geographic regions, and types of animal dispersers; many of these examples are discussed in the text*

ORNITHOCHORY

Alien plants dispersed by generalist *native* birds

Lantana camara is dispersed by at least 15 native bird species in Hong Kong, principally *Pycnonotus jocosus*, *P. sinensis* and *Zosterops japonica* (Corlett, 1998*a*; R. T. Corlett, unpublished data).

Ligustrum spp. dispersed by several native bird species in Argentina (Montaldo, 1993)

Mahonia aquifolium (North American) by *Turdus merula* in Central Germany (Auge & Brandl, 1997).

Maesopsis eminii in East Usambara forests, Tanzania, is dispersed by native hornbills (Binggeli & Hamilton, 1993).

Myrica faya dispersed by native thrushes in Hawaii (La Rosa *et al*., 1985).

Opuntia ficus indica (central American) by *Corvus capensis* and *C. alba* in South Africa (Milton & Dean, 1987).

Pinus elliottii (a wind-dispersed pine) is dispersed into native forests in Queensland, Australia, by glossy black cockatoos (*Calyptorhynchus lathami*). Although these birds destroy most seeds, some survive to establish isolated foci. Similar 'new' mutualisms involving *P. radiata* in South Australia and *P. pinaster* in Western Australia have also been described (Richardson & Higgins, 1998).

Pittosporum undulatum dispersed by several native frugivorous birds in Jamaica (Goodland & Healey, 1996).

Rosa multiflora dispersed by mockingbird (*Mimus polyglottos*) in North America (Stiles, 1989; White & Stiles, 1992).

Schinus teribinthifolius dispersed by silvereyes (*Zosterops lateralis*) in Australia (Panetta & McKee, 1997) and by American robins (*Turdus migratorius*) in North America (Ewel, 1986).

Solanum mauritianum dispersed by Rameron pigeons (*Columba arquatrix*) in South Africa (Oatley, 1984).

There are many other examples in the literature. Many alien plant species dispersed by native birds in forest remnants in Nelson, New Zealand (Williams & Karl, 1996).

Alien plants dispersed by generalist *alien* birds

Acacia cyclops dispersed by European starlings (*Sturnus vulgaris*) and other (native and alien) birds in South Africa (Glyphis *et al*., 1981).

Cinnamomum zeylanicum dispersed by alien mynahs (*Acridotheres tristis*) in the Seychelles (Fleischmann, 1997).

Lantana camara dispersed by alien birds in Hawaii (Smith, 1985).

Myrica faya is dispersed by *Zosterops japonica* (Vitousek & Walker, 1989) and *Carpodacus mexicanus* (La Rosa *et al*., 1985) in Hawaii.

Schefflera actinophylla is dispersed by parrots in Florida, U.S.A. (D. Gordon, personal communication).

There are numerous other examples in the literature. For example, many alien plant species (19 species listed) are dispersed by European blackbirds (*Turdus merula*) in Victoria, Australia (Carr, 1993), and New Zealand (Williams & Karl, 1996).

OTHER VERTEBRATE-MEDIATED SEED DISPERSAL

Alien plants dispersed by generalist *native* mammals

Atriplex lindleyi (Australia) is dispersed by Kudu (*Tragelaphus strepciseros*) in the South Africa karoo (Milton *et al*., 1995).

Carpobrotus edulis in California coastal habitats is dispersed by brush rabbits, jack rabbits and mule deer (D'Antonio, 1990); *C. chilensis* and *C. edulis* × *chilensis* hybrids by native deer and rabbits (Vilà & D'Antonio, 1998).

Cecropia peltata, *Muntingia calabura* (also dispersed by birds) and *Psidium guajava* are dispersed by the native fruit bat *Cynopterus brachyotis* in Singapore (Phua & Corlett, 1989).

Pinus koraiensis, introduced to Hokkaido, Japan, is dispersed by the native squirrel *Sciurus vulgaris orientis* (Hayashida, 1989).

Prosopis chilensis dispersed by bonnet macaques and chitals in India (Balasubramanian & Bole, 1993).

Alien plants dispersed by generalist *alien* mammals

Several species dispersed by *Macaca fascicularis* on Mauritius (Sussman & Tattersall, 1986).

Pinus pinea (Richardson *et al*., 1990) and *Quercus robur* (Knight, 1985) dispersed by the alien squirrel *Sciurus carolinensis* in the Western Cape, South Africa.

Myrica faya, *Passiflora mollissima* and *Psidium guajava* are dispersed by feral pigs in Hawaii (Smith, 1985).

Table 1 (*cont.*)

Alien plants dispersed by generalist *native* reptiles

Chrysanthemoides monilifera, *Lycium ferocissimum* and *Schinus molle* are dispersed by Cunningham's skink in Victoria (Carr, 1993).

Schizmus barbatus (European) and *Atriplex semibaccata* (Australia) dispersed by *Geochelone pardalis* in the Karoo (Milton, 1992).

Alien plants dispersed by *native* invertebrates

Atriplex lindley (Australia) and *Bromus* spp. by *Messor capensis* in the Karoo (Milton & Dean, 1993).

Acacia cyclops and *A. saligna* dispersed over short distances (2–3 m) by native *Anoplolepis* and *Pheidole* spp. in the Western Cape, South Africa. Although the distance of dispersal is short, the fact that seeds are buried seems important in ensuring escape from rodent predation (Holmes, 1990*a*), and thus in facilitating the development of dense stands (Holmes, 1990*b*).

Cytisus scoparius dispersed by native ants in California (Bossard, 1991).

Euphorbia esula dispersed by *Formica obscuripes* in Montana, U.S.A. (Pemberton, 1988).

Spread of the non-native species *Grevillea rosmarinifolia* and *Viola ordorata* is facilitated by the native ant *Iridomyrmex purpureus* in Australia (Smith, 1989).

(*Papio ursinus*; a species from a lineage with no history of association with *Pinus*) disperse seeds of *P. pinaster* over short distances while feeding on cones (Dean *et al.*, 1986). Another example is the dispersal of *Prosopis chilensis* seeds by bonnet macaques and chitals in India (Balasubramanian & Bole, 1993).

(3) Implications for invasions

Our findings support the view that vertebrate-dispersed plants have converged into generalized dispersal syndromes regardless of phylogenetic and geographical origins. This is shown by the rapidity with which mutualistic seed-dispersal interactions establish. Increasing specificity of dispersal agents is associated with increasing seed size for birds (Herrera, 1984; Martin, 1985) and some mammal faunas (e.g. Janzen & Martin, 1982), thus species with small-seeded fruits are likely to have more potential dispersers than those with large-seeded fruits (Wheelwright, 1985; Corlett, 1998*b*). These species should therefore be less likely to fail as invaders due to the absence of suitable dispersers when compared to large-seeded introduced species. Besides making plants acceptable to a wide range of dispersers, small-seededness also means more seeds, increasing the probability that dispersers will carry some seeds (enough to initiate invasions) over large distances. A comparison of seed size of fleshy-fruited plants in gaps *versus* edges of natural forest in central Europe indicates that production of many small seeds rather than fewer large seeds increases a plant's probability of reaching scattered or distant patches of suitable habitat (Kollmann, 1997).

The size of fruiting display is an important component of fruit removal/dispersal for animal-dispersed plants. For introduced species, at least two studies have shown that the more invasive of two congeners produced larger fruit displays and had higher fruit removal rates than their less-invasive relatives (e.g. Sallabanks, 1993; Vilà & D'Antonio, 1998). The assessment of overall fruit display might thus aid in assessing invasion potential.

Although some fleshy-fruited plants with small seeds are avoided by generalist dispersers (e.g. *Melia azederach* and *Nandina domestica* introduced to California, U.S.A., are never dispersed; M. Rejmánek, personal observation), this syndrome is well-represented in invasive alien floras and has value in screening. Plants with fleshy fruits containing small seeds should always be considered high-risk introductions.

With respect to the new types of mutualisms, such as the pine-cockatoo association in Australia – could these have been predicted *a priori*? The answer is probably yes, but not without a very good understanding of the ecology of both partners. The great number of introduced species and possible mutualists suggests to us that setting limits for 'acceptable risk' with respect to seed dispersal, without prohibiting every introduction, is not practical. Fortunately, such novel dispersal events are not common and do not initiate the most widespread and damaging invasions (although they may result in the aliens colonizing habitats within their adventive range that would otherwise not have been available). For practical purposes, we can propose no generalizations to account for such novel mutualisms in screening tools.

IV. MYCORRHIZAL FUNGI

Mutualistic interactions between fungi and plant roots are common in the plant kingdom. Most common of these are the arbuscular mycorrhizas (Trappe, 1987) formed by fungi in the Glomales (Zygomycotina) (Morton, 1988) which associate with a diverse array of higher plants (60% of higher plants are estimated to form these mycorrhizas; Trappe, 1987). The other common mycorrhizas (ectomycorrhizas, ericoid and orchid mycorrhizas) include members of both the Basidiomycotina and Ascomycotina as fungal partners (Fitter & Moyersoen, 1996; Straker, 1996). Several gymnosperm and angiosperm taxa form ectomycorrhizas, whereas the ericoid and orchid mycorrhizas are restricted to the Ericales and Orchidales. Arbutoid mycorrhizas are confined to a few taxa in the Ericales. The fungal partners in mycorrhizas usually supply nutrients to plants in exchange for photosynthetic carbon, and may also offer protection against pathogens, toxins and drought stress (Read, 1986).

Arbuscular mycorrhizas are by far the most common form of mycorrhiza in all undisturbed terrestrial ecosystems and among all types of rooted plants. Levels of specificity among host plants and fungal species are fairly low, and many species of arbuscular mycorrhizal fungi have a cosmopolitan distribution (based on morphological, rather than physiological, criteria; Morton & Bentivenga, 1994). However, plant responses to mycorrhizas are influenced by the genotype of both partners and by various environmental factors (Bever *et al.*, 1996; Johnson, Graham & Smith, 1997; Streitwolf-Engel *et al.*, 1997). Consequently, the interaction between an introduced plant and resident fungi may take diverse forms, which may promote or inhibit the plant.

Ectomycorrhizas are generally, although not exclusively, formed by trees. The conifers of the northern forests are ectomycorrhizal, as are most trees in temperate deciduous forests (Read, 1991). Although some common species in tropical and subtropical forests and woodlands are ectomycorrhizal, most tree species in these systems are arbuscular mycorrhizal (Janos, 1987; Högberg, 1992). Among ectomycorrhizas, specificity among the fungal and plant partners can vary from fungi which are restricted to single host plants to widespread fungi forming ectomycorrhizas with several plant species. Ericoid mycorrhizas have a broad distribution but are restricted to nutrient-poor soils. Although edaphic specialisations have given rise to different strains of ericoid mycorrhizal fungi, specificity of the fungal symbionts has yet to be resolved (Straker, 1996). Non-mycorrhizal plants are usually a small component of undisturbed ecosystems; they usually have a ruderal life cycle and are common only immediately after disturbance (Trappe, 1987).

(1) The mycorrhizal status of invasive alien plants

Koske, Gemma & Flynn (1992) relate the high level of arbuscular mycorrhizal mycotrophy among invasive alien plant taxa in Hawaii to the high incidence of arbuscular mycorrhizas in the native flora. This pattern seems to apply at a global scale, since the majority of the 199 'representative invasive species' listed by Cronk & Fuller (1995) probably form arbuscular mycorrhizas. Approximately 7% of species on this list are ectomycorrhizal, 1% are ericoid mycorrhizal, and 10% are non-mycorrhizal.

The cosmopolitan distribution of most arbuscular mycorrhizal fungi (and their low host-specificity) means that most invading plants can form mycorrhizas. Alien plants are therefore, *ipso facto*, most likely to be arbuscular mycorrhizal but this by itself is unlikely to confer any particular competitive advantage over native arbuscular mycorrhizal plants unless the invaders can utilize these mycorrhizas in an unusual way. For example, Marler, Zabinski & Callaway (1997) have found that Asian knapweed (*Centaurea maculosa*) plants, when invading native prairies in North America, are able to tap into the mycorrhizal networks connecting native plant roots and use these connections to their benefit. When *Festuca idahoensis* is grown with mycorrhizal *C. maculosa* its growth is reduced and growth of *C. maculosa* is enhanced even though the growth of both species does not respond to mycorrhizas in the absence of the other species (Marler, Zabinski & Callaway, 1999). Although the mechanism for this interaction between plants and mycorrhizas is unknown, it suggests that *C. maculosa* may parasitise or damage adjacent neighbours through mycorrhizal connections. Other studies using isotope tracers have demonstrated carbon and nutrient sharing among neighbouring plants due to interconnections created by arbuscular mycorrhizal fungi (Chiariello, Hickman & Mooney, 1982; Watkins *et al.*, 1996). In a microcosm study, Grime *et al.* (1987) showed that arbuscular mycorrhizas enhanced the diversity of grassland mixes by raising the status of subordinate

Table 2. *Estimates of the prevalence of mycorrhizal types‡ among major environmental weeds in southern Africa and the fynbos biome, and in the native flora of the fynbos biome*

Mycorrhizal type	Invasive alien species in southern Africa* (%)	Invasive alien species in the fynbos biome* (%)	Indigenous species in fynbos biome† (%)
Arbuscular mycorrhizas	61	35	62
Ectomycorrhizas	24	48	0
Ericoid mycorrhizas	0	0	8
Orchid mycorrhizas	0	0	2
Non-mycorrhizal	10	13	23
Unknown	5	4	4

* Richardson *et al.* (1997).

† Allsopp & Stock (1993).

‡ The most important environmental weeds in southern Africa (terrestrial species only) were categorized according to mycorrhizal groups using information in the literature. Where no information on the mycorrhizal status of a species could be found, we inferred its status from the plant's taxonomic position (noting that more than one type of mycorrhiza is formed in some taxa; Newman & Reddell, 1987).

species relative to canopy dominants. Similarly, establishment of alien seedlings may be facilitated if these plants can benefit from rapidly becoming colonised from an existing mycorrhizal fungal network supported by the natural vegetation.

The carbon costs of supporting mycorrhizas can be quite high (Harley & Smith, 1983; Douds, Johnson & Koch, 1988). Because of this, non-mycorrhizal species might be expected to be prominent among alien plants. Indeed, Pyšek (1998) includes the Brassicaceae and Chenopodiaceae (both non-mycorrhizal), in his list of six 'best invader' plant families. However, non-mycorrhizal plants are invasive mainly in disturbed environments where low mycorrhizal propagule numbers disadvantage mycorrhizal species (Reeves *et al.*, 1979; Miller, 1987). They are often rapidly replaced during succession by plants which are dependent on mycorrhizas (Miller, 1987). Exceptions to this are likely, however, in arid environments where non-mycorrhizal or facultatively mycorrhizal invaders may persist because they reduce the mycorrhizal infectivity of the soil by not supporting growth and reproduction of the mycorrhizal fungi in an environment where mycorrhizal propagules are inherently low (Berliner, Mitchell & Allsopp, 1989; Jacobson, 1997; N. Allsopp, unpublished data). Stands of alien *Atriplex* spp. in South African karoo and invasive *Brassica* spp. in North America may represent examples of persistent invasions of non-mycorrhizal plants. Another exception to the concept of non-mycorrhizal species as weedy, early-successional invaders is that of Australian Proteaceae which invade South African fynbos (*Hakea* spp.), and *Grevillea banksii* and especially *G. robusta* which invade in Hawaii.

(2) Case study: southern Africa

To establish whether correlations exist between the mycorrhizal status of native floras and that of invasive alien floras, we examined these floras for southern Africa, and specifically the fynbos biome. The proportions of mycorrhizas among the most important environmental weeds in southern Africa (Table 2) are fairly typical of many terrestrial ecosystems in that most species are arbuscular mycorrhizal (*cf.* Högberg, 1982; Harley & Harley, 1987; Brundrett & Kendrick, 1988; Brundrett & Abbott, 1991; Allsopp & Stock, 1993). Arbuscular mycorrhizas are not necessarily responsible for the success of the invaders, but they do not represent a major barrier to invasion. Only the presence of ectomycorrhizal species among the invasive aliens is unusual since there are no reports of indigenous species forming ectomycorrhizas in South Africa (Stock *et al.*, 1997). Also conspicuous is the absence of alien plants that form ericoid mycorrhizas. Since the Cape Floristic Region is the centre of speciation in the Ericaceae, we would have expected that alien species requiring ericoid mycorrhizal symbionts would find the region easy to invade.

There are distinct differences as well as similarities between the mycorrhizal status of native and invasive alien plants in fynbos. Most of the alien herbs invading lowland fynbos (Vlok, 1988), and major weeds such as the nitrogen-fixing *Acacia saligna* form arbuscular mycorrhizas. Nonetheless, arbuscular mycorrhizas are under-represented among the invasive aliens. Fynbos has very poor soils and a diversity of nutrient-acquisition systems in its native flora (Allsopp & Stock, 1993). Many introduced plants cannot cope with the extremely poor soils and the arbuscular mycorrhizal association does not necessarily confer any (or sufficient) benefit to potential invaders under these conditions. Indeed, the absence of mycorrhizal dependence seems to be an advantage for some native species in this environment (e.g. cluster-root forming Proteaceae and Restionaceae). Alien species with this strategy (e.g. *Hakea* spp.) have invaded fynbos. New nutrient-acquisition systems in the form of ectomycorrhizas (largely pines) may confer advantage to some aliens in this environment (see below).

(3) Invaders that rely on unique mycorrhizal associations

Although most invading plants have mycorrhizal systems that are already present in the target habitat, there are some interesting examples of plants which invade habitats which (initially) lack the required mycorrhizal symbionts. Ectomycorrhizal species have invaded some southern hemisphere systems where there are very few or no native ectomycorrhizal species. In South Africa, there are no reported native ectomycorrhizal species, while in New Zealand only *Kunzea*, *Leptospermum* (both Myrtaceae) and *Nothofagus* (Fagaceae) form ectomycorrhizas. Establishment of *Pinus* spp. was retarded in many parts of the southern hemisphere by the lack of suitable mycorrhizal fungi (e.g. Poynton, 1979). Introduced pines have therefore invaded a wide range of systems in both countries by forming ectomycorrhizas with introduced mycorrhizal fungi (Richardson, Williams & Hobbs, 1994; Read, 1998). In New Zealand, there is no evidence of native ectomycorrhizal fungi forming associations with pines (P. Johnston, personal communication). Initial mycorrhizal colonization of pine roots in these new environments has to be *via* spores (Davis, Grace & Harrell, 1996; Read, 1998). It appears that pine trees introduced with soil provide this inoculum. In most parts of the southern hemisphere, pines existed in plantations for many years before invading indigenous vegetation (Richardson *et al.*, 1994; Richardson & Higgins, 1998). Read (1998) suggested that a factor contributing to these lags is that compatible mycorrhizal inoculum, in the form of airborne spores, needed time to accumulate in the soil before pines could establish and proliferate. He reasons that the initial establishment of ectomycorrhizas from spores is slow, but once dense tree populations are established, seedlings can become ectomycorrhizal very rapidly though infection from the established fungal network. Richardson *et al.* (1994) suggested that dense pine stands are now so widespread in the southern hemisphere that inoculum limitation no longer retards invasion.

Two alien orchid species (*Arundina graminifolia* and *Spathoglottis plicata*) are widespread and abundant invaders in Hawaii (Wester, 1992) where there are no native orchids. Koske *et al.* (1992) confirm that these species form orchid mycorrhizas in Hawaii. It is unknown whether these orchids form mycorrhizas with introduced fungi, or whether there were compatible, free-living fungi present in Hawaii that could form orchid mycorrhizas.

(4) Invasions facilitated through pre-adaptation to local mycorrhizal fungi

While invaders with mycorrhizal associations that are quite different from those of the natives may have access to resources that native species cannot tap, invaders that are similar to natives may face fewer barriers to entering a system (Koske *et al.*, 1992). Invasion of the Galapagos Islands by the obligately arbuscular mycorrhizal *Psidium guajava* may only be possible because arbuscular mycorrhizas are already present on the islands (Schmidt & Scow, 1986). The success of certain nutrient-acquisition systems in the native flora of an area, including ericoid mycorrhizas and cluster roots, may mean that alien species with the same adaptations are pre-adapted to flourish in these habitats. Earlier in this section we discussed why being arbuscular mycorrhizal was unlikely to confer any specific pre-adaptation to a new environment since so many species have these generalized associations. We will, however, speculate on how facultatively mycorrhizal species may be advantaged in some circumstances.

(*a*) *Ericoid mycorrhizas*

Several members of the Ericales from the northern hemisphere and South Africa have invaded a variety of habitats on soils of low to moderate fertility in Australia and New Zealand. Taxa of the Epacridaceae which are ericoid mycorrhizal (Hutton, Dixon & Sivasithamparam, 1994) form part of the native flora of these invaded environments. It is likely that invasive species such as *Calluna vulgaris*, *Erica arborera*, *E. baccans*, *E. caffra*, *E. lusitanica* (Wardle, 1991; Lazarides, Cowley & Hohnen, 1997), which are obligately mutualistic with ericoid mycorrhizal fungi, relied on indigenous ericoid mycorrhizal species to establish and invade. Possessing a similar nutrient-acquisition system to some indigenous species apparently allows these plants to exploit the nutrient-poor soils.

The establishment of these species in Australia and New Zealand suggests that the specificity of ericoid mycorrhizas is quite broad. If this ability to form mycorrhizas with indigenous ericoid fungi is widespread among the Ericales, then the lack of suitable mycorrhizal symbionts may not be a barrier to alien Ericales in Australia, New Zealand and South Africa.

(b) Facultative arbuscular mycorrhizal species

Some alien plants may be favoured by their facultative arbuscular mycorrhizal status. They can establish as non-mycorrhizal plants when mycorrhizal inoculum is low, such as following major soil disturbance, but their continued survival usually depends on being able to out-compete indigenous mycorrhizal species if mycorrhizal inoculum levels recover. Persistence of alien *Bromus tectorum* in American sagebrush steppe has been attributed to its facultatively mycorrhizal condition (Goodwin, 1992). When grown without competition, *Bromus tectorum* grows best when non-mycorrhizal and will establish successfully in disturbed sagebrush. However, when grown in competition with wheatgrass, it grows better if it is mycorrhizal. Although both species benefit from mycorrhizas, Goodwin (1992) proposes that this flexibility in response to mycorrhizas allows *Bromus tectorum* to persist in sagebrush steppe. C. M. D'Antonio & T. Schuur (unpublished data) found that the aggressive African grass, *Melinis minutiflora*, was facultatively mycorrhizal in Hawaiian soils where it is a very successful invader whereas native species in the same habitats were always mycorrhizal. Further experimental work on the relative abilities of highly successful *versus* less successful aliens to reduce their mycorrhizal colonization levels under nutrient-rich or less competitive conditions might prove revealing.

(5) Future dangers associated with mycorrhizal mutualisms

There has been considerable intentional intercontinental movement of soil containing mycorrhizas. This, and their lack of specificity and potential for long-distance transport in air (Allen & MacMahon, 1985), water currents (Koske & Gemma, 1990) and by animal vectors (Warner, Allen & MacMahon, 1987), has resulted in a fairly cosmopolitan distribution of mycorrhizal fungi. Despite this, evidence points to the importance of interactions between plant species and edaphic environments in maintaining somewhat distinct fungal communities (Johnson, Tilman & Wedin, 1992; Bever *et al.*, 1996). Whether or not this matters to invaders is unknown.

Exploitation of mycorrhizas is seen as a way of developing more sustainable agriculture, where fertiliser requirements can be lowered due to the positive influence of mycorrhizas on plant nutrition. While some research focuses on agricultural practices which nurture indigenous mycorrhizas (Dodd *et al.*, 1990), introducing 'improved' mycorrhizal populations is another alternative. This involves developing hardy mycorrhizal strains that tolerate a wide range of edaphic and other environmental conditions and elicit high growth responses from a broad range of plants. In these inocula, there may be highly competitive strains which could invade natural habitats, making them more vulnerable to invasion by plants which are particularly favoured by these species.

The selection of super-strains of ectomycorrhizal fungi could threaten indigenous flora and fungi. For example, strains of *Pisolithus tinctorus* which can cope with extremely harsh or toxic soil conditions are being selected for their ability to enhance growth in plantations and on mine dumps. If these super-strains are released (or escape) into natural systems they may enhance the competitiveness of introduced trees that are currently not invasive (or only weakly so). Rare and ecologically sensitive ecosystems such as serpentine communities and saline wetlands, and nutrient-poor sites in general, may be particularly vulnerable to the introduction of mycorrhizas with broad environmental tolerances. Before improved strains of mycorrhizas are introduced we recommend screening of their capacity to become naturalised in indigenous vegetation and their capacity to facilitate invasion by non-native plants.

V. SYMBIOSES BETWEEN PLANTS AND NITROGEN-FIXING BACTERIA

There are two main symbiotic nitrogen-fixation systems: those involving symbioses between legumes and Proteobacteria (e.g. *Bradyrhizobium* spp. and *Rhizobium* spp.), and those between actinorhizal plants and actinomycetes (e.g. *Frankia* spp.). Both systems, which fix atmospheric nitrogen at approximately the same efficiency, are implicated in the invasive spread of alien plants but their roles in facilitating or hindering invasions have been virtually ignored in the growing literature on plant invasions.

(1) Invasion of nitrogen-fixing legumes: the role of symbionts

Among the legumes (Fabaceae), of which approximately 18000 species have been described, the occurrence of nodulation varies considerably among subfamilies. De Faria *et al.* (1989) examined 3395 species for nodulation (approximately 20% of legume species and 57% of genera); they found that most species of subfamilies Papilionoideae (97%) and Mimosoideae (90%) are nitrogen fixers. However, only 23% of subfamily Caesalpinioideae in their sample were found to nodulate.

Legumes are hugely important as sources of food for humans and livestock, fibre, fuel wood and in various types of agroforestry. Many species have great value as ornamentals or other amenity plants. Partly because of their widespread use by humans, many of the world's most problematic environmental weeds are nitrogen-fixing legumes (notably species in the genera *Acacia*, *Albizia*, *Cytisus*, *Genista*, *Leucaena*, *Lupinus*, *Mimosa*, *Paraserianthes*, *Parkinsonia*, *Prosopis*, *Robinia*, *Sesbania*, *Spartium* and *Ulex*).

There are many cases of introduced woody legumes nodulating abundantly (and presumably also invading) without rhizobium inoculation when introduced to new habitats (Allen & Allen, 1981). De Faria *et al.* (1989) document this for Australian *Acacia* spp., *Cytisus* spp., *Leucaena* spp. and *Robinia* spp. in Brazil. The lack of nodulation after introduction appears to be the exception rather than the rule with woody legumes. This suggests that either effective rhizobia for woody species are widely distributed between continents, and/or that many legume trees can be nodulated by a wide range of strains of rhizobia. There is ample support for the latter contention. For example, Halliday & Somasegaran (1983) document successful nodulation by the *Rhizobium* strain TAL 1145 on *Acacia farnesiana*, *Calliandra calothyrsus*, *Gliricidia sepium*, several species of *Leucaena*, *Mimosa invisa*, *M. pudica* and *Sesbania grandiflora*. There are, however, isolated cases of legumes failing to nodulate following introduction. Halliday & Somasegaran (1983) note that *Leucaena leucocephala* failed when introduced to Australia and eastern Colombia until inoculated with effective *Rhizobium* strains. In a study of seven sites on Jamaica, Zimpfer, Smyth & Dawson (1997) found rhizobia able to nodulate *L. leucocephala* at only one site.

(2) Invasion of actinorhizal plants: the role of symbionts

At least 194 plant species in 24 genera are nodulated by actinomycetes in the genus *Frankia* (Frankiaceae). These 'actinorhizal' plants are woody, dicotyledonous angiosperms in the Betulaceae, Casuarinaceae, Coriariaceae, Datiscaceae, Elaeagnaceae, Myricaceae, Rhamnaceae and Rosaceae (Benson & Silvester, 1993). They are typically early-successional plants on nutrient-poor sites. Many species are widely used in afforestation (including agroforestry) and agriculture (Dawson, 1986), restoration and for a wide range of amenity purposes, and thus are widely cultivated outside their natural ranges. At least the following actinorhizal species are important invaders of natural systems: *Casuarina equisetifolia*, *Elaeagmus angustifolia*, *E. umbellata*, *E. pungens* and *Myrica faya* (Cronk & Fuller, 1995).

Frankia strains exhibit various degrees of host specificity, and much work still needs to be done before we have sound rule for predicting specificity (Benson & Silvester, 1993). It is, however, clear that, as with legumes, there are differences between actinorhizal taxa in their ability to form associations with local (not intentionally introduced) microsymbionts.

Although *Alnus* species (alders) are not major invaders, species such as *A. glutinosa* are listed in some regional weed lists (e.g. for Connecticut and Tennessee, U.S.A.; see also Daehler, 1998). Alders are nodulated wherever they are transplanted throughout the world, including places where they have no natural presence (e.g. in New Zealand; Clawson *et al.*, 1997). Thus, it seems that alder *Frankia* are rather cosmopolitan.

Casuarina species, native to Australasia, are not infected with as broad a selection of *Frankia* as *Alnus*. They are nodulated in Florida, U.S.A., parts of North Africa (but not central Sudan; Miettinen, Karsisto & Musa, 1992), and the Pacific rim, but *not* in New Zealand or California, U.S.A. In Florida (and probably in other areas where *Casuarina* thrives outside its natural range), they are nodulated by a *Frankia* strain that is found almost exclusively outside of Australia and which was probably dispersed along with translocated seedlings beginning in the eighteenth century (J. O. Dawson, personal communication). This *Frankia* strain accumulates under established stands, but is undetectable using baiting techniques elsewhere in soils outside the native range. For example, Zimpfer *et al.* (1997), found no

C. cunninghamiana-infective *Frankia* in any of the soils they sampled in Jamaica.

Elaeagnus umbellata (autumn olive; Oleaceae), an actinorhizal tree from Asia, is widely grown in the eastern and central U.S.A. for ornamental purposes, wildlife promotion, land reclamation, and has been used experimentally as a nurse plant for the valuable timber crop *Juglans nigra* (Paschke, Dawson & David, 1989). Native birds disperse its seeds, and this species (especially the USDA selection 'Cardinal') is now highly invasive in Illinois, U.S.A. This species nodulates readily with apparently indigenous soil *Frankia* (Paschke & Dawson, 1994) (there are no native *Elaeagnus* in this region). In the western U.S.A. (where *E. commutata* is native), the alien *E. angustifolia* invades riparian habitats. It is likely that the alien species relies on native *Frankia* strains, but this has not been studied.

For *Myrica*, the spectrum of *Frankia* that inhabits nodules varies with species. For example, *M. gale* in the north-east U.S.A. is infected by only one strain of *Frankia* whereas *M. pensylvanica*, with an overlapping range, associates with many *Frankia* strains (D. R. Benson, unpublished data). Walker *et al.* (1986) speculated that *M. faya* relied on an introduced symbiont to establish and become highly invasive in Hawaii. The *Frankia* was thought to have been introduced because the symbiosis is apparently absent from the native flora (P. M. Vitousek, personal communication). However, *Myrica* is known to be a 'promiscuous' host, and some types of *Frankia* are apparently saprophytic and not obligate symbionts (Paschke & Dawson, 1992; Burleigh & Dawson, 1994). Hence, they are widespread in soils, even in soils lacking hosts (J. O. Dawson, personal communication). Whether the *Frankia* infecting *Myrica* on Hawaii is native or introduced remains to be determined. Whether or not the *Frankia* is native, simultaneous dispersal of *M. faya* seeds and *Frankia* by native and alien birds clearly facilitates establishment and spread of the former (Burleigh & Dawson, 1994).

(3) Implications for invasions

Our review suggests that symbionts required to induce nitrogen fixation in introduced species are extremely widespread. Much work remains to be done on the ecology, biogeography and taxonomy of the symbionts, but currently available evidence suggests that intentional introductions of symbionts have clearly altered the invasibility of many, if not most, systems. The agroforestry literature abounds with references to support this contention. Whenever nodulation of an economically important woody legume has failed, introduction of effective rhizobial strains has followed quickly. Some strains, notably TAL 1145, have been widely introduced throughout the tropics. For example, The Oxford Forestry Institute regularly distributed a mixture of rhizobia (up to six strains, including TAL 1145, packed in sterile peat medium) along with its seed lots (Hughes, 1998, pp. 94–95). Similarly, 10 (out of approximately 100) suppliers in the 1997 edition of the International Centre for Research on Agroforestry (ICRAF)'s Tree Seed Suppliers Directory, supply *Rhizobium*, *Bradyrhizobium* or *Frankia* strains routinely with seed. Once introduced, inoculum spreads rapidly, notably in bird faeces (Paschke & Dawson, 1993; Burleigh & Dawson, 1995 for *Frankia*). Several recent studies have revealed the presence of *Frankia* in soils of tropical areas that lack host plants. Major advances in the understanding of the distribution and ecology of these symbionts are needed.

Other human endeavours related to nitrogen fixation also have potential to affect invasions. Cereals and other non-legumes usually require heavy applications of nitrogen fertilizer. It is reasoned that if these species could be genetically manipulated to form effective symbiotic or associative nitrogen-fixing systems, this would decrease or remove our major dependence on fertilizer nitrogen. The transformation of plants and micro-organisms through molecular genetics promises the development of new symbiotic and associative biological nitrogen-fixation systems. This could result in plant species that do not invade at present becoming invasive in certain situations.

VI. DISCUSSION

Alien plants very often require symbionts or mutualistic partners to overcome barriers to establishment in foreign environments. Mutualisms that facilitate invasions occur at all the main phases of the life-cycle of invading plants. In most cases, these appear to be readily acquired. While much of the invasion literature has focused on identifying factors aiding resistance of communities to invasion, evidence for resistance has been difficult to acquire. We surmise that the easy acquisition of mutualistic symbionts is an important reason for so many ecosystems being susceptible to invasion by alien plants. In some cases, mutualisms between alien plants and other organisms that facilitate spread involve the same species as are involved in the natural range of the species concerned, constituting the reunion of separated partners. It is not surprising that once (albeit often after a time lag) the original function is restored, population growth and hence invasion occurs. In many other cases, mutualisms involve the pairing of taxa that evolved in isolation. These mutualisms reinvent processes found in the natural range of the invading species.

Most introduced plants arrive without the pollinators that serve them in their natural range, but thrive in the presence of generalist pollinators (native or introduced). There are very few well-documented cases of alien plants failing to set seed because of the absence of pollinators. Highly specialized pollinator/plant relationships such as fig/wasp associations (e.g. Nadel *et al*., 1992) are exceptions. Generalist pollinators abound in natural ecosystems and they readily visit introduced plants [e.g. Donovan & Macfarlane (1984) state that introduced bumblebees visit 400 introduced plant species in New Zealand]. Pollinator limitation is not a major barrier for the spread of most alien plants. Plants of temperate areas often have very diverse pollinator faunas and are thus sufficiently buffered against pollinator failure (Bond, 1994).

Many species of fleshy-fruited plants (mainly trees and shrubs) have invaded with the aid of generalized local frugivores. This supports the well-established notion that tightly coevolved, plant-vertebrate seed-dispersal systems are extremely rare (if indeed any exist; Wheelright & Orians, 1982; Herrera, 1985; Jordano, 1995). In other words, plants that rely on vertebrate animals for dispersal are not, as a rule, limited reproductively by the lack of seed dispersers. Indeed, even native tree species thought to have highly specialized dispersers that are now extinct, survive through acquired mutualisms (Bond, 1994). Generalist frugivores that disperse seed sufficiently widely to launch landscape-transforming invasions are widespread and abundant in many systems (e.g. Table 1). These are usually birds or mammals that disperse small, fleshy fruits of woody shrubs and trees. There are also many opportunities for less reliable dispersal; these include indirect dispersal such as through predation of frugivorous by carnivorous animals, omnivory by carnivores (e.g. foxes often eat fruit and can move seeds great distances; Ortiz, Arista & Talavera, 1995), or through the forging of opportunistic associations with resident animals (e.g. pines and cockatoos in Australia). Ants are important for some invading plants, but mainly in carrying seeds to safe sites, rather than dispersing seeds over sufficient distances to facilitate widespread invasions.

Arbuscular mycorrhizas were implicated in the colonization of land by early plants and their role in aiding plants in nutrient acquisition should not be underestimated. Evidence reviewed here shows that mycorrhizal symbioses are also very important factors governing the human-orchestrated reshuffling of the world's flora. Like pollination and dispersal mutualisms, relatively few plants engaged in mycorrhizal associations have highly specialized fungal associates. However, several of these have become aggressive invaders of ecosystems in which they have been plants. In nutrient-poor environments, such as those typically invaded in Australia, Hawaii, New Zealand and South Africa, invading plants must possess traits which enable them to obtain sufficient nutrition. These traits include well-provisioned seeds, root adaptations for nutrient acquisition, and the ability to grow under low-nutrient conditions. Pre-adaptation to a low-nutrient environment through the possession of a nutrient-acquisition system typical of such environments (e.g. cluster roots or ericoid mycorrhizas) or novel modes of nutrient acquisition (e.g. ectomycorrhizas) appears to offer solutions to the problem of establishing in poor soils. In the case of pines, invasion is the result of introduction and gradual build-up of the necessary symbiont. It seems likely that human-mediated movement of plants and soils is now so widespread that it is only a matter of time before fungal spore populations reach sufficiently high levels to allow ectomycorrhizal trees or shrubs to spread everywhere in otherwise compatible environments. Ectomycorrhizal spores can remain dormant in soil far from their hosts for long periods (T. D. Bruns, personal communication). This suggests that changes to ecosystems (including enhanced invasibility) where ectomycorrhizas have been introduced will persist long after current invaders are removed.

Of the four main categories of mutualisms addressed in this review, those involving symbioses between plants and nitrogen-fixing bacteria have received the least attention in the invasion literature. Many of the world's most notorious wildland weeds are nitrogen-fixing trees and shrubs (e.g. Australia acacias in South Africa, brooms and gorse in California, U.S.A., and New Zealand, *Myrica faya* and *Prosopis pallida* in Hawaii, *Mimosa pigra* in Australia). Despite the importance of this group of plants as invaders, we know almost nothing about the role of nitrogen fixation in promoting or limiting invasion rates for most species. Most of these species are not obligate nitrogen fixers, so their success as invaders suggests that either suitable nitrogen-fixing partners are readily available in a wide range of ecosystems and specificity is low, or that nitrogen fixation is not particularly critical to the success of these species. More research is required to understand the ease of acquiring these symbiotic relationships, their contribution to invasion success and the role of these acquisitions in explaining lags between a species introduction and its widespread occurrence in the landscape. Further insights that are entirely pertinent to invasions could be gleaned from the literature on plant introductions for afforestation and restoration (e.g. Handel, 1997; Wunderle, 1997; Martin-Laurent, 1998). This is particularly important because the literature in these fields is much more explicit concerning reasons for failures of translocated plants (whereas the invasion literature generally focuses on reasons for successes).

Besides the categories of mutualisms we have reviewed here, there are others that could promote invasions but about which we know little. For example, in the last decade there has been growing interest in the role of leaf fungal endophytes in conferring an advantage to plants in the presence of herbivores (e.g. Clay, 1996). As with arbuscular mycorrhizal fungi, these associations appear to be widespread in the plant kingdom. Yet the specificity of associations, and the nature of the associations (mutualistic? pathogenic?) are poorly known, as is their role in invasion.

(1) Mutualisms and community invasibility

Mainstream plant ecology over the past 50 years has focused on the role of competition in structuring plant assemblages. Arguments about community invasibility have largely reflected this bias, and invasibility has been thought to be negatively correlated with species richness, and positively correlated with the number of 'empty niches'. Many authors (starting with Darwin) have argued that species more distantly related to the native species at a site should be more successful as invaders than species closely related to natives, presumably because the former are likely to be different in their resource utilization and therefore more easily escape competition with native species (Simberloff, 1986; Moulton & Pimm, 1987; Rejmánek, 1998). While there is some evidence to support this idea, its relevance to a given site will depend on the balance between the long-term effects of competitive *versus* facultative interactions in determining community composition. Species that are somewhat similar to native species should rapidly garner the services of potential mutualists including pollinators, dispersers and mycorrhizal fungi. Many authors have also recently addressed the role of species diversity in influencing invasibility. The premise that more diverse communities should be less prone to invasion (e.g. Elton, 1958) reflects the bias in favour of competition as the most prevalent force structuring communities and the assumption that the strength of competition increases with increasing species richness. Yet, if invasions are facilitated by a diverse array of pollinators, dispersers, fungi and bacteria, and disturbance or climatic variability creates windows of opportunity when competition is minimized, then we should expect invasibility to be positively correlated with native species richness. Several recent studies have suggested that systems in which native species are more diverse are also those in which invaders are diverse (e.g. Rejmánek, 1996*b*; Stohlgren *et al.*, 1999).

Only recently have ecologists recognized that facilitative interactions are extremely common in natural communities and are at work even when competition is occurring (e.g. Bertness & Callaway, 1994; Callaway & Walker, 1997). It is clear from our review that facilitative interactions involving alien species are widespread and important in accelerating the invasion of natural communities by non-native species. We suggest that a paradigm shift is needed in invasion ecology, away from a focus on competition or biotic resistance controlling invasion to one in which competition is viewed as a temporally and spatially variable process against a backdrop of diverse facilitative interactions.

(2) Are communities becoming easier to invade?

Recent studies evaluating the success of bird and insect introductions suggest that propagule supply is critical in determining invasion success (e.g. Hopper & Rausch, 1993; Duncan, 1997). Two of the types of mutualisms we reviewed here, pollination and dispersal, are important determinants of propagule supply for plants. Because these mutualisms appear so easy to acquire, propagule spread of insect-pollinated, fleshy-fruited plants with small seeds should be expected almost wherever such species are introduced. The prevalence of alien insects (notably honeybees and bumblebees) and birds may accelerate this problem. Many introduced fleshy-

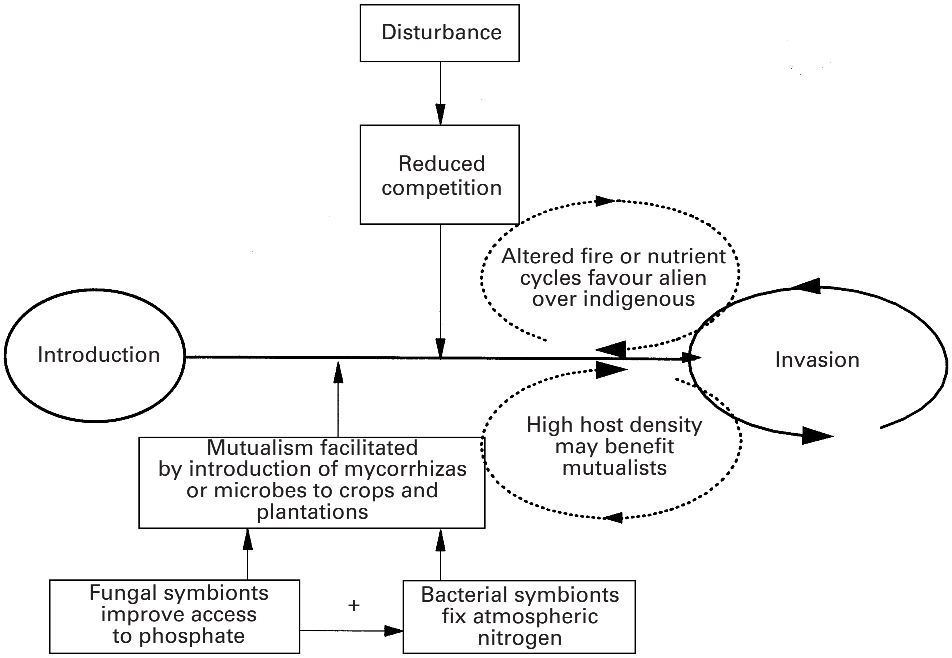


Fig. 3. Establishment (and, increasingly, invasion) of plants introduced for timber or food production is often facilitated by introductions of mutualists such as mycorrhizal fungi and microbes. *Acacia*, *Casuarina* and *Pinus* species have clearly benefitted from the intentional introduction of mutualists. Some species, such as *A. saligna*, benefit from a combination of bacterial and fungal symbionts. Natural communities disturbed by erosion, alteration of fire regimes, trampling or harvesting, are particularly susceptible to invasion. Once alien species have invaded a community, they reinforce habitat change by further altering fire regimes (e.g. *Hakea* and *Pinus*), by accelerating nutrient cycling (*Acacia*, *Prosopis*), or altering soil acidity and nutrient availability. Invasions of plants with nutrient-acquisition mutualisms are likely to benefit their mutualists, thus facilitating further invasive spread.

fruited plant species are grown in urban gardens and hedgerows, where they attract dispersers that later migrate out of urban areas (e.g. Green, 1984; Lenz, 1990). Consequently we must expect an increasing flow of propagules from cities and gardens into the remaining fragments of our wildland ecosystems. More invasions will surely result.

The other types of mutualisms we reviewed here, those involving plant roots, will affect the success of species after seed production and dispersal have occurred. In the case of arbuscular mycorrhizal fungi, the generalized nature of arbuscular mycorrhizal associations ensures that alien plant species will encounter mutualists they might need to acquire soil nutrients or survive in the face of a variety of stresses. Indeed, we need to understand more about how aliens might tap into mycorrhizal networks to invade 'undisturbed' (mature) communities or use established mycorrhizal connections to parasitize plant neighbours (see Marler *et al.*, 1997). In the case of strong specialization, as with ectomycorrhizas, the need for a fungal partner can restrict spread. As we continue to move soil and microbes around the world, establish forest plantations of alien trees and tamper with the genetics of mycorrhizal fungi, the likelihood that suitable fungal partners will be found by establishing propagules is most likely accelerating for many species, even those that are currently not invasive. The problem is exacerbated by increasing disturbance levels in many systems (Fig. 3). Also, once symbionts such as *Frankia* spp. are present in a region, they are dispersed rapidly by the local biota.

We have focused mainly on classic mutualisms (+ + interactions in Fig. 2), but facilitative interactions go beyond these mutualisms and include a wide variety of interactions and synergisms. The role of alien/alien synergisms in facilitating invasions is now being recognized and there are many examples where an established invader facilitates the establishment of later invaders not only through direct mutualisms but also through alteration of disturbance regimes or resource supply rates. For example, nitrogen-rich litter under the alien nitrogen-fixing tree *Myrica faya* promotes earthworm invasion in Hawaiian forests (Aplet, 1990) and may facilitate the establishment of other alien plants such as *Psidium cattleianum* (Wall & Moore, 1999, p. 113). Similarly, soil disturbance activities of feral pigs promote invasion of Hawaiian forests by introduced plants (e.g. Huenneke & Vitousek, 1990; Aplet, Anderson & Stone, 1991), and physical activity by the introduced water buffalo in Australia leads to the large-scale invasion of parts of tropical Australia by *Mimosa pigra* (Lonsdale & Braithwaite, 1988). D'Antonio & Dudley (1993) refer to these alien-alien facilitations as 'invader complexes' and Simberloff & von Holle (1999) suggest the term 'invasional meltdown' for the process by which alien species facilitate one another, leading to an acceleration in both invasion and impact. We believe that such complexes are widespread and that, coupled with our continued movement of species around the world and other anthropogenic disruptions of ecosystem functioning, ecosystems are becoming increasingly easy to invade.

(3) Incorporating mutualisms into predictions

Can the evidence reviewed here be incorporated in protocols for predicting invasiveness? We believe that some of it can. Major efforts have been made in the last two decades to find species traits that correlate with 'invasiveness'. Rejmánek (1996*a*) proposed a model for predicting invasiveness in woody species. Characters related to seed production and dispersal (seed size) are important elements of invasiveness in his model. In terms of mutualistic interactions, seed production and dispersal involve pollination and frugivory. However, because most introduced plants do not face pollination barriers we believe that knowledge of pollination biology will not provide much insight into whether or not a species will become invasive. Indeed, even Parker's (1997) demonstration of pollinator limitation of seed set in Scotch broom in Washington state, is of limited practical value: in spite of pollinator limitation, broom is abundant and expanding throughout the study region. One lesson repeatedly learned from biological weed control and Leslie-matrix type models is that production of seeds has to be reduced by at least 60% to make weed populations decrease in size (e.g. Hoffmann, 1990; Shea & Kelly, 1998). Therefore, unless pollination problems approach this level, they are unlikely to prevent invasions. Also, even if seed set is lower in the alien range, some important alien invaders have other avenues for regeneration (e.g. through clonal propagation in *Eichhornia crassipes*; Barrett, 1980).

By contrast, incorporation of dispersal syndromes into screening criteria is essential. If species are not wind-dispersed but are invasive it is often largely because of vertebrate seed dispersal. For example, the species that were not correctly classified as 'low risk' species in Tucker & Richardson's (1995) attempt to screen woody plants for their invasiveness in South African fynbos were vertebrate dispersed. In Rejmánek's (1996*a*) model, increasing seed size must be associated with vertebrate seed movement in order for a species to become invasive. With the exception of a few fleshy-fruited species that are probably not dispersed because of 'unfavourable' chemistry (e.g. *Nandina domestica* in California, U.S.A.), we believe that it will be relatively easy to match fruit characteristics with potential dispersers in assessing invasion potential. In addition to incorporating plant characteristics that might promote seed dispersal by animals into screening protocols for plants, animals being considered for importation or release could also be screened for their potential to disperse alien plant seeds.

Like pollination mutualisms, knowledge of the general mycorrhizal status of a species may not help to refine our ability to predict invasiveness. However, where invaders have specialized associations that might confer a unique advantage for obtaining resources in potential habitats or have unique abilities to use mycorrhizal connections (e.g. *Centaurea maculosa* in Montana prairies), *a priori* identification of these traits might help avert destructive invasions. Thus, consideration of specialized or unique mycorrhizal affiliations should be included in screening. More research is needed to further illuminate the prevalence of such relationships.

Mutualistic relations enable plants to cross some abiotic or biotic barriers and they contribute to 'non-linearities and synergisms' that make invasions difficult to predict (Richardson, Cowling & Lamont, 1996). Further knowledge on this topic will provide a refinement of various general 'rules' that are starting to emerge in invasion ecology. Furthermore, the possibility exists that mutualisms involving introduced species are having a direct detrimental effect on native species. Such effects might arise in many ways and if we are to predict both the success and impact of non-native species then we must include an understanding of mutualisms in our research efforts.

Janzen (1985) wrote: 'Mutualisms have been thought to death; what we need are solid descriptions of how organisms actually interact, experiments with what happens when a potential mutualist is removed'. Amazingly, the superb opportunities for gaining new insights on mutualisms afforded by the movement of species to new habitats have been virtually ignored by biologists (*cf.* Bronstein, 1994). Given the increasing importance of alien plant invasions worldwide, and the important role that mutualisms play in facilitating these invasions, much more work is urgently required.

VII. CONCLUSIONS

(1) Establishment and spread of introduced plants very often depends on, or is at least greatly enhanced by, the establishment of mutualisms with organisms already resident in the new environment. These mutualisms may re-unite the same taxa that form partnerships in the native range of the plant, but some forge totally novel combinations.

(2) Only very few potential invaders are prevented from spreading because of the absence or shortage of pollinators. Even some plants thought to have highly specialized pollination requirements have thrived in the presence of generalist pollinators (*Ficus* spp. and orchids are interesting exceptions).

(3) The rapid establishment of seed-dispersal mutualisms between introduced plants and vertebrates (especially birds and mammals), emphasizes the diffuse nature of these mutualisms. Plants with small-seeded fleshy fruits are dispersed by a very diverse assemblage of native and alien animals. Ants disperse some alien plants over short distances, but not far enough to generate widespread invasions – their main role in facilitating invasions is in transporting seeds to safe sites.

(4) Most mycorrhizal plants form associations with arbuscular mycorrhizal fungi. Because of their low specificity, these fungi do not seem to play a major role in mediating plant invasions, except perhaps on some remote islands which are poor in arbuscular mycorrhizal fungi. For many ectomycorrhizal plants, notably for *Pinus* spp. in the southern hemisphere, the lack of symbionts was a major barrier to establishment and invasion before the build-up of inoculum through human activity.

(5) Symbionts required to induce nitrogen fixation in many plant species are extremely widespread, but there are big differences among plant genera with respect to the specificity of symbionts required for nodulation. Most legumes can be nodulated by a wide range of strains of rhizobia but some alien legumes do fail to establish until appropriate rhizobia are introduced. For actinorhizal plants, there is a much greater variability with regard to the specificity of actinomycetes required to induce nodulation (e.g. introduced *Casuarina* spp. are more often limited by the absence of appropriate *Frankia* than are alien *Alnus* spp.). For both legumes and actinorhizal plants, human-mediated distribution of symbionts has undoubtedly made many environments more open to invasions.

(6) Positive interactions are more important in plant invasions than is generally acknowledged. Assembled evidence suggests that a paradigm shift is required in invasion ecology, away from a focus on competition or biotic resistance controlling invasion to one in which competition acts as a temporally and spatially variable process against a backdrop of diverse facilitative interactions.

(7) Evidence from diverse sources clearly shows that most ecosystems are becoming easier to invade. One important reason for this is that potential partners required to establish pollination, seed-dispersal, mycorrhizal and plant-bacteria mutualisms have been spread around the world by humans. Together with other changes such as altered disturbance and nutrient regimes, these are facilitating alien plant invasions worldwide.

(8) Insights gained from this survey of the role of mutualisms in alien plant invasions can be incorporated into screening protocols which could help to reduce the incidence of future invasions.

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