Sleeper weeds – a useful concept?

A.C. Grice[A,C] and **N. Ainsworth**[B,C]
[A] CSIRO Sustainable Ecosystems, Private Bag PO, Aitkenvale, Queensland 4814, Australia.
[B] Victorian Department of Natural Resources and Environment, Keith Turnbull Research Institute, PO Box 48, Frankston, Victoria 3199, Australia.
[C] Co-operative Research Centre for Australian Weed Management.

Summary

The term 'sleeper' is widely and often somewhat loosely applied in weed science to describe introduced species that remain relatively scarce and/or scattered for a considerable period after they have become naturalized, with the implication that some species will subsequently become more highly invasive. We argue that the 'sleeper weed' concept actually encompasses a variety of ecological phenomena. We propose that individual weed species that could be regarded as 'sleepers' can be ascribed to one of six general classes that relate to either the characteristics of the species, the characteristics of the environment in which it has become naturalized, or to the perceptions of the observer. While the current concept of 'sleeper weeds' may help raise awareness of future weed risks, a more refined analysis would help focus attention on situations where the risks are most likely to be realized and identify times, places and mechanisms whereby this may occur.

Introduction

Plant invasions pose major threats to natural ecosystems in many parts of the world and, in many regions, exotic plant species make up a substantial proportion of the flora. Considerable effort has been directed at describing and understanding invasion processes and a terminology has arisen to support this effort. One term that, at least in Australia, is now widely used in discussions of plant invasions is 'sleeper' or 'sleeper weed'. It was coined by Groves (1999) to refer to 'invasive plants that have naturalized in a region but not yet increased their population size exponentially'. This definition can be taken to include a large number of species that have not yet become serious weeds even though they have become naturalized. Importantly, the term has come to be most commonly, and somewhat loosely, applied to species that remain relatively scarce and/or scattered for a considerable period after they have become naturalized. Our aim here is to re-examine the concept of 'sleeper weeds'. Is it a valuable one in relation to our understanding and management of weeds and what ecological phenomena does it encompass? We advocate six categories that could facilitate a more discerning use of the concept of the 'sleeper weed'.

There are an estimated 1500–2000 naturalized plant species in Australia, making up 10–15% of the vascular flora (Humphries *et al.* 1991). These species have been progressively introduced from the time of European occupation with the number of species in mainland Australian states increasing at least linearly up to the present (Specht 1981), and possibly more rapidly in recent decades (Groves and Hosking 1998).

Knowledge of the spatial and temporal patterns of weed invasions is important as a basis for managing them. This has prompted efforts to describe the histories of particular plant invasions (e.g. *Nassella trichotoma* (Nees) Arech. (serrated tussock) (Auld and Coote 1981), *Opuntia aurantiaca* Lindley (tiger pear) and *Parthenium hysterophorus* L. (parthenium) (Auld *et al.* 1982), *Mimosa pigra* L. (giant sensitive plant) (Lonsdale 1992, Lonsdale *et al.* 1995)). Temporal patterns of invasion have been described in terms of a series of general phases (Hobbs and Humphries 1995) (Figure 1). Within this general framework there is scope for considerable variation. For example, introduction may occur as a single event or multiple events that could occur more or less simultaneously or be spread over time. Likewise naturalization, wherein a species establishes self-replacing populations (Richardson *et al.* 2000), may occur at one or more locations and times. Thereafter, the rates of increase in the number and size of infestations will be determined by the interactions between the intrinsic demographic characteristics of the plant and the environment that it is invading. Here we use the term 'invasive' to refer to a plant that is spreading to areas that are 'distant from sites of introduction', regardless of whether its presence has any detrimental effect beyond the simple presence of a non-native species (Richardson *et al.* 2000).

Although most species have not been studied in detail, variation in the time-course of plant invasions into Australia is obvious. Perhaps most simply, species differ in terms of the date of introduction. Many of the species that are now major weeds in Australia were introduced during the early to mid-1800s. These include *Xanthium occidentale* Bertol. (Noogoora burr) and *X. spinosum* L. (Bathurst burr) (Hocking and Liddle 1995), *Echium plantagineum* L. (Paterson's curse) (Piggin and Sheppard 1995), *Emex australis* Steinh. (spiny emex) (Gilbey *et al.* 1998) and *Rubus fruticosus* L. (blackberry) (Amor *et al.* 1998). Important weeds have also emerged, however, from subsequent introductions through the second half of the nineteenth century (e.g. *Carthamus lanatus* L. in the 1860s (Peirce 1995), *Mimosa pigra* in 1891 (Lonsdale *et al.* 1995), *Eichhornia crassipes* (Mart.) Solms-Laubach (water hyacinth) in 1894 (Wright and Purcell 1995), *Acacia nilotica* (Benth.) Brenan (prickly acacia) in the 1890s (Mackey 1998), *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth in 1895 (van Klinken and Campbell 2001), *Cryptostegia grandiflora* Roxb. ex R.Br. (rubber vine) in the late 1800s (Tomley 1998)) and the first half of the twentieth century (e.g. *Nassella trichotoma* in the early 1900s (Campbell and Vere 1995), *Senecio madagascariensis* Poiret (fireweed) in 1918 (Sindel *et al.* 1998), *Prosopis* spp. in the 1920s (van Klinken and Campbell 2001), and *Alternanthera phileroxoides* (Mart.) Griseb. (alligator weed) in the 1940s (Julien 1995)). Among the most recently introduced plants that have already become recognized as important

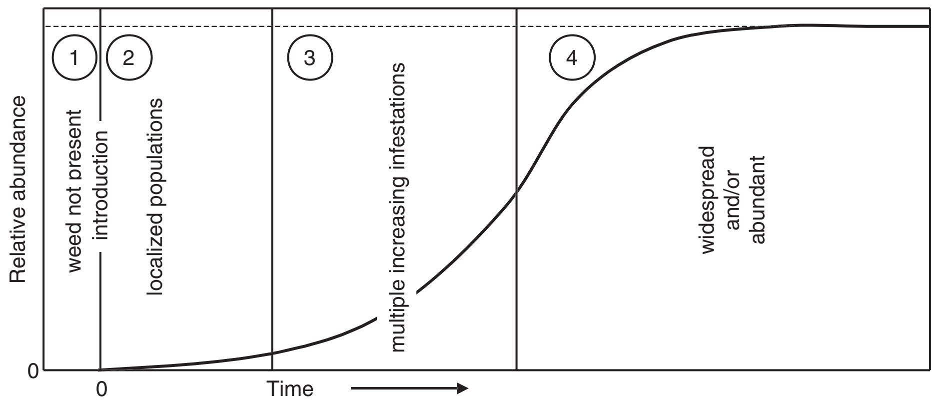

Figure 1. Four generalized phases of a plant invasion (after Hobbs and Humphries 1995).

weeds in Australia are *Carduus nutans* L. (nodding thistle) that was reported in 1950 (Popay and Medd 1995), *Salvinia molesta* D.S.Mitchell in 1952 (Room and Julien 1995), *Parthenium hysterophorus* in 1955 (Navie *et al*. 1998) and *Cabomba caroliniana* A. Gray (cabomba) in 1967 (Mackey and Swarbrick 1998).

Exotic species have apparently varied greatly in the time they have taken to become naturalized or attain the status of being significant weeds. It is often difficult to determine when naturalization of a species occurred. In some cases, naturalization occurred within relatively few years of introduction. This appears to have been the case, for example, with *P. hysterophorus* in Australia, where a 1958 introduction was rapidly spreading by the mid-1970s (Navie *et al.* 1998). In other species the stage of rapid spread was not reached for several decades. This may have been the case with *Mimosa pigra* that was introduced around Darwin sometime between 1870 and 1890 but remained a minor weed and geographically restricted until the 1970s (Lonsdale *et al.* 1995). However, it is not clear from this history when naturalization actually occurred.

Groves (1999) maintained that, 'Most naturalized plant species increase initially only to a limited extent, after which they show no further apparent population increase in their new habitat for many years. Only after an extended period of time does the rate of population growth for such species increase…' There are few quantitative data in evidence of this, though it is in this 'extended period' that species could be said to be in a 'sleeper' phase. In terms of the generalized phases of plant invasion, such species would be in the post-naturalization phase in which there is a small number of relatively restricted populations (phase 2 of Figure 1). Factors mentioned by Groves which might influence the time between naturalization and rapid population increase (and thus influence sleeper status) were; favourability of arrival site, biological attributes enabling persistence, time from naturalization and re-location of a naturalized plant to a more suitable site. The last of these was identified as especially important.

Mack *et al.* (2000) described lag phases as a characteristic of the early stages of many invasions. They attributed lag phases to a limited capacity to detect change in small populations, slow growth in initially restricted populations, poor adaptation to a new environment, and/or the susceptibility of small populations to stochastic events. Similarly, Binggeli (2000) pointed to lag phases in the early stages of invasion by woody species, wherein either naturalization is delayed after first introduction or the 'species exhibits a limited population growth'. He speculated that lag phases could result from 'genetic adaptations' although there are few data available to support this explanation for woody species. 'Abiotic factors' (e.g. physical barriers to spread; lack of critical disturbance) and 'biotic factors' (e.g. absence of pollinators; age to first flowering of long-lived species) could also result in lag phases in the invasion process.

Only a relatively small proportion of the 2000 or so exotic species naturalized in Australia are currently recognized as major weeds. In other words, most of the total impact of weeds in Australia is apparently attributable to a relatively small proportion of naturalized exotic species. At any time and place, a large proportion of naturalized species may be relatively restricted or uncommon, a phenomenon that has been described using the so-called 'tens rule' (one out of ten species passes through each of the successive stages; 'imported', 'found in the wild', 'self sustaining populations', 'pest status'; Williamson and Fitter 1996). Many factors could no doubt contribute such a situation but the validity of the 'rule' has been questioned and it has been argued that there may be many already-naturalized species that have not yet realized their full potential as weeds (e.g. Low 2002). This is certainly apparent in relation to the 70 or so species that were nominated as Weeds of National Significance and for which current and potential distributions were compared by bioclimatic analysis (Thorp and Lynch 2000). As presently used, 'sleeper weed' is an inclusive term for any naturalized species that, at present, is not obviously increasing or spreading rapidly. Logically such a species can cease to be a sleeper weed only by becoming extinct or by becoming invasive. Undoubtedly many species that are labelled 'sleepers' will become invasive in the future, whilst others may never do so. Understanding the ecological basis of the apparently soporific state of many naturalized plants may assist early recognition of circumstances in which invasive behaviour could commence. Such improved understanding could provide scope for their more effective management in line with the 'early intervention' principle of weed management (Grice 2000).

The ecology of sleepers

What then might be the ecological status of species that could be described as 'sleepers'? What ecological forces are involved? We advocate that individual weeds that could be regarded as 'sleepers' could be ascribed to one of six general classes. These classes relate to either the characteristics of the species, to the characteristics of the environment in which it has become naturalized, or to the perceptions of the observer.

1. Restricted by a narrow genetic base poorly adapted to the local environment

The population growth of an introduced plant may be limited because the genotype(s) introduced, although persisting long enough to be considered a self-sustaining population, are not sufficiently well suited to local conditions to permit rapid population growth. This constraint may decrease over time in sexually reproducing species if continuing selection produces genotypes that are better adapted to those conditions. Alternatively, other genotypes that are pre-adapted to local conditions may be introduced, so that there is an appearance of a lag phase between naturalization and rapid invasion, but in fact, invasion by the later introduction may have commenced immediately. A delay could also occur if better-adapted genotypes arise from eventual interbreeding of naturalized populations that originate from different areas of the species' home range. There are certainly cases in which species in an introduced range have limited genetic variability compared with the same species in its native range (e.g. Barrett and Richardson 1986). Recent advances in molecular techniques have given rise to much improved understanding of the origins of weed populations and their breeding biology. Populations of *Bromus tectorum* L. (cheatgrass) in North America have been found to originate from only a small proportion of the native range of the species (Novak and Mack 2001) and those authors suggest that the adventive (casual) status of the species in some regions of North America may result from introduced material having a genotype that is not well suited to the local conditions.

2. Restricted by limited suitable habitat

A naturalized plant may not be invasive because there is only a small area of suitable habitat available near the site of introduction. If this habitat is permanently scarce over the whole of the region into which the plant is introduced then it will remain very limited in distribution, although conceivably it could have severe impacts within this limited habitat. Conversion from sleeper to invasive could occur when a rare dispersal event (e.g. by flood waters) enables the species to move to larger/less isolated areas of suitable habitat. Probability of dispersal by different means is certainly not always constant over time. For example, frugivorous birds may change their feeding behaviour as a new food source becomes more abundant, or if a preferred food source becomes suddenly scarce, and this could lead to the dispersal of some plants increasing relatively abruptly at some time after naturalization. Invasive behaviour could also commence if changes to management of adjacent land increase the availability of suitable habitat.

3. Restricted by limited opportunities for recruitment

A naturalized plant may be restricted because it is growing in an environment in which opportunities for recruitment are episodic. When appropriate conditions for recruitment do arise, rapid population growth may occur. A species in such a situation is likely to increase in abundance in a step-wise fashion, each step corresponding to a major recruitment event. Possible Australian examples of this pattern include *A. nilotica* in western Queensland (Brown and Carter 1998), and *Tamarix aphylla* (L.) Karst. (athel pine) in the Northern Territory (Fuller 1993). In the early stages of such a process, the species will exhibit the characteristics of a sleeper, that is, although it is naturalized, its population is relatively stable. However the rate of invasion does not actually increase over time, the true rate merely becomes more apparent when more recruitment events have occurred. *Hypericum perforatum* L. (St. John's wort) behaves rather in this manner; established plants can survive for years and achieve some vegetative spread whilst also producing large numbers of long-lived seeds. Establishment of substantial numbers of seedlings however requires conditions that occur as infrequently as once in seven years (Briese 1997).

4. Restricted by a low intrinsic population growth rate.

A higher intrinsic rate of increase has the potential to produce more rapid invasion. Biological characteristics that contribute to a high intrinsic rate of increase include a short juvenile (non-reproductive) phase and a high reproductive output (Baker 1965). A naturalized plant species that has a low rate of population increase will tend not to attract attention as a weed because it takes longer to pass through each of the generalized phases of invasion. In fact, a species could be increasing exponentially but at such a low rate that it is perceived to be stable. Despite a slow rate of increase, a species could eventually become widespread and have considerable impacts, especially if the difficulty of achieving control of established infestations compensates for the slowness of their spread.

There are probably numerous species that conform to this pattern. They may be present for many years or even decades, with populations increasing and ranges expanding only slowly. *Tamarindus indica* L. (tamarind) is an example. Macassan traders apparently introduced it to Australia in the 17th and 18th centuries (Brock 1993). The species is long-lived, slow-growing and has an extended juvenile period. It has spread only slowly along the northern Australian coastline with most populations close to old Macassan camps (Specht and Mountford 1958). When restriction of invasion rate is entirely due to intrinsically slow reproductive rate there can be no sudden increase in rate of spread, although there may in some circumstances be a perception of such an increase.

5. Restricted by the absence of mutualists

A species may be restricted in its rate of spread or population increase by the absence of a mutualist species with which it co-occurs in its native range (Richardson *et al.* 2000). Mutualisms could involve pollination, dispersal or symbiotic associations between plant roots and micro-organisms. Parker (1997) showed that growth of some populations of the invasive shrub *Cytisus scoparius* (Scotch broom) in the western USA, are limited by the availability of insect pollinators. The spread of *Acacia nilotica* is facilitated by cattle-aided dispersal (Radford *et al.* 2001). Richardson *et al.* (2000) point to the importance of symbiotic associations with micro-organisms, especially nitrogen-fixing bacteria, as a factor in plant invasion. The absence of essential mutualisms is at least potentially capable of inducing a 'sleeper' phase during an invasion.

6. Species that are wrongly perceived to be not invasive

A plant species may be spreading rapidly in a new region but this may be unrecognized due to lack of interest or experience in identifying it on the part of local land managers (Binggeli 2000), so that it appears to meet the definition of a sleeper weed. If increased attention is given to the species, for example by its inclusion in a new publication or training course, then many 'new' populations will be located and this may be misinterpreted as a recent dramatic increase in the rate of spread. Plants that are highly visible (e.g. pines invading heathland), are less likely to increase unnoticed than inconspicuous species. Invasion histories may be reconstructed for some woody plants by establishing the age of the oldest plants in each infestation, but there are many species for which it is not possible to determine whether the species' population increased suddenly or perception suddenly changed. Continuation of a rate of spread above the historical average rate would support the 'sudden increase' view, although this may often be complicated by intensive control efforts following from the enhanced interest in the plant.

Relevance to research and management

Conceivably, any introduced plant that becomes naturalized may suffer one of a number of fates. The naturalized population could dwindle to extinction; the species could persist but as a small and restricted population; it could become common and widespread but have relatively minor impacts; or it could become abundant and widespread and have major consequences for land use and/or the structure, function and composition of native plant and animal communities. An ability to predict the fate of naturalized species, including potential impacts and patterns of spread, while they are in the early stages of invasion, would be a valuable tool for making decisions about where weed management resources should be directed.

Some naturalized species rapidly move to a phase where they are abundant and widespread, such that trends become apparent soon after introduction. These species do not pass through an obvious 'sleeper' phase, and their future can often be adequately predicted early in the invasion process. Others, however, do pass through what might be regarded as a sleeper phase and remain relatively restricted, in terms of distribution and population size, for extended periods of time. It is for these species that a predictive capacity would be valuable. Groves (1999) used a combination of known weediness overseas and a high probability of successful eradication to identify sleeper weeds with a high priority for immediate action. Control of species meeting these criteria would be highly cost-effective in avoiding future weed problems. Misdirection of effort to species that in fact would not have proved to be major problems could mean some resources are expended unnecessarily. However, the resources consumed on such 'false alarms' can be justified, given the relatively low cost of managing species in the early stages of invasion rather than when they become widespread. A more important consideration is the possibility that species with no history of weediness overseas may be overlooked. It is within this group of species that it would be especially useful to investigate the reality of apparent sleeper behaviour, and the reasons for it, if it is occurring.

The term 'sleeper' has become quite widely used, particularly in Australia. Many species have been labelled sleepers but often there is no attempt to justify that labelling. Usually, use of the term does not recognize the variety of quite different phenomena that it potentially encompasses. For example, Randall (2001) presents a list of 958 species that have been introduced into Australia as garden plants and have become naturalized, actually identified to be weeds or are considered weeds elsewhere in the world. Almost 400 of these are classed as sleepers but this classification is not of much value without an explanation of how each decision has been made or an understanding of the underlying ecological processes.

A better understanding is required of the variety of phenomena conceivably covered by the term 'sleeper'. Although we have been able to suggest species or situations as examples of the six classes that we have defined, those classes are essentially hypothetical. It would be useful to confirm that the classes are real, to quantitatively describe examples of each, and to gather information on the frequency with which each of them occurs. This task will be not be easy because it will depend on studying events and entities that are uncommon.

Further it would be valuable to develop approaches for allocating species perceived as sleepers to more definitive classes on the basis of the ecological forces that constrain them. This would identify, at least in general terms, the circumstances under which those constraints may be removed. For any species, it would be necessary to identify any environmental changes or events that may trigger expansion of its population or range.

Accounts of the historical spread of various weeds in Australia often mention events that apparently produced sudden large increases in distribution or population size (e.g. Fuller 1993) including drought, floods and altered land management. The amount of support for these explanations varies, but is often no more than local opinion. There is a general lack of well-documented histories of introduction and spread that might provide good examples of the various sleeper weed phenomena (Groves 1999). Factors leading to rapid increase in a few species can probably already be assigned to the classes suggested here. For example, the increase in populations of *A. nilotica* in western Queensland, Australia, has been dependent on a shift from sheep to cattle as the predominant livestock (Brown and Carter 1998). This could be considered as a case of sleeper behaviour due to restricted suitable habitat (class 2) being ended when suitable habitat was increased by human intervention. In this case, suitable habitat could be described in terms of the absence of sheep (that consume seeds) and the presence of cattle (that are dispersal agents).

Under the classification given, many 'sleepers' are probably not actually inactive. Small population size or limited range cannot be taken to imply that populations are stable, that ranges are not expanding or that other important changes are not taking place. Rather, important demographic or distributional developments may be occurring but not detected because they take place slowly or episodically or because they are not seen as being significant. It seems inappropriate to apply the term 'sleeper' to such cases. Detection of small changes in the early stages of invasion is likely to be difficult, but it would facilitate implementation of an important principle of weed management, that of early intervention in the invasion process (Grice 2000). Where suitable action is taken very early in the invasion process, it may even be possible to eradicate a weed, although there are few cases where eradication is a realistic option (e.g., *Kochia scoparia* Schrad. in Western Australia (Dodd and Moore 1993, Dodd 1996, Dodd and Randall 2002) and *Helenium amarum* (Rafin) H.L. and *Eupatorium serotinum* Michx. in south-eastern Queensland (Tomley and Panetta 2002)).

Conclusion

The current value of the concept of 'sleeper weeds' lies in raising awareness of the fact that there are many naturalized plants that have not yet become abundant, or widespread, or had a major impact on land use or natural ecosystems. It points to the possibility that there are many potential weeds already naturalized that could one day present major problems. However, the term may also be misunderstood to mean that all weeds pass through a sleeper phase, that there is a universal cause for such behaviour, or that the term represents a single ecological phenomenon. In reality a wide variety of ecological phenomena are probably involved. There would be great value in distinguishing the various factors that can cause naturalized plants to go through (or appear to go through) an inactive phase and then later become rapidly invasive. A more refined terminology would reflect these distinctions. This would allow attention to be given to situations where the potential threats are most likely to be realized and to identify times, places and mechanisms where this may occur.

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References

Amor, R.L., Richardson, R.G., Pritchard, G.H. and Bruzzese, E. (1998). *Rubus fruticosus* L. agg. *In* 'The biology of Australian weeds', Volume 2, eds F.D. Panetta, R.H. Groves and R.C.H. Shepherd, pp. 225-46. (R.G. and F.J. Richardson, Melbourne).

Auld, B.A. and Coote, B.G. (1981). Prediction of pasture invasion by *Nassella trichotoma* (Gramineae) in south east Australia. *Protection Ecology* 3, 271-7.

Auld, B.A., Hosking, J. and McFadyen, R.E. (1982). Analysis of the spread of tiger pear and parthenium weed in Australia. *Australian Weeds* 2, 56-60.

Baker, H.G. (1965). Characteristics and modes of origin of weeds. *In* 'The genetics of colonising species', eds H.G. Baker and G.L. Stebbins, pp. 147-69. (Academic Press, New York).

Barrett, S.C.H. and Richardson, B.J. (1986). Genetic attributes of invading species. *In* 'Ecology of biological invasions: an Australian perspective', eds R.H. Groves and J.J. Burdon, pp. 21-33. (Canberra: Australian Academy of Science).

Binggeli, P. (2000). Time-lags between introduction, establishment and rapid spread of introduced environmental weeds. Proceedings Third International Weed Science Conference. Manuscript No. 8., CD-ROM. (International Weed Science Society, Oxford, USA).

Brock, J. (1993). 'Native plants of Northern Australia'. (Reed, Chatswood, Australia).

Brown, J.R. and Carter, J. (1998). Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* 13, 93-102.

Campbell, M.H. and Vere, D.T. (1998). *Nassella trichotoma*. *In* 'The biology of Australian weeds', Volume 1, eds R.H. Groves, R.C.H. Shepherd and R.G. Richardson, pp. 189-202. (R.G. and F.J. Richardson, Melbourne).

Dodd, J. (1996). Comparison of the eradication programs for kochia (*Kochia scoparia* (L.) Schrad.) and skeleton weed (*Chondrilla juncea*) in Western Australia. Proceedings of the 11th Australian Weeds Conference, pp. 82-4. (Weed Science Society of Victoria, Melbourne, Victoria).

Dodd, J. and Moore, J.H. (1993). Introduction and status of *Kochia scoparia* in Western Australia. Proceedings of the 10th Australian and 14th Asian-Pacific Weed Conference, eds J.T. Swarbrick, C.W.L. Henderson, R.J. Jettner, L. Streit, S.R. Walker, Volume II, pp. 496-500. (The Weed Science Society of Queensland, Brisbane, Queensland).

Dodd, J. and Randall, R. (2002). Eradication of kochia (*Bassia scoparia* (L.) A.J. Scott, Chenopodiaceae) in Australia. Proceedings of the 13th Australian Weeds Conference, eds H. Spafford Jacob, J. Dodd and J.H. Moore, pp. 300-303. (Plant Protection Society of WA, Perth, Western Australia).

Fuller, M.R. (1993). The invasion and control of *Tamarix aphylla* on the Finke River, Central Australia. Proceedings of the 10th Australian and 14th Asian-Pacific Weed Conference, eds J.T. Swarbrick, C.W.L. Henderson, R.J. Jettner, L. Streit, S.R. Walker, Volume II, pp. 44-46. (Weed Society of Queensland, Brisbane, Australia).

Gilbey, D.J., Weiss, P.W. and Shepherd, R.C.H. (1998). *Emex australis* Steinh. *In* 'The biology of Australian weeds', Volume 2, eds F.D. Panetta, R.H. Groves and R.C.H. Shepherd, pp. 89-105. (R.G. and F.J. Richardson, Melbourne).

Grice, A.C. (2000). Weed management in Australian rangelands. *In* 'Australian weed management systems', ed. B.M. Sindel, pp. 429-58. (R.G. and F.J. Richardson, Melbourne, Victoria).

Groves, R. (1999). Sleeper weeds. Proceedings of the 12th Australian Weeds Conference, pp. 632-636. (Tasmanian Weeds Society, Hobart, Tasmania).

Groves, R.H. and Hosking, J.R. (1998). Recent incursions of weeds to Australia 1971–1995. Technical Series No. 3. Cooperative Research Centre for Weed Management Systems, Australia.

Hobbs, R.J. and Humphries, S.E. (1995). An integrated approach to the ecology and management of plant invasions. *Conservation Biology* 9, 761-70.

Humphries, S.E., Groves, R.H. and Mitchell, D.S. (1991). Plant invasions of Australian ecosystems: a status review and management directions. Kowari 2, 1-116.

Hocking, P.J. and Liddle, M.J. (1995). *Xanthium occcidentale* Bertol. complex and *X. spinosum* L. *In* 'The biology of Australian weeds', Volume 1, eds R.H. Groves, R.C.H. Shepherd and R.G. Richardson, pp. 241-302. (R.G. and F.J. Richardson, Melbourne).

Julien, M.H. (1995). *Alternanathera philoxeroides* (Mart.) Griseb. *In* 'The biology of Australian weeds', Volume 1, eds R.H. Groves, R.C.H. Shepherd and R.G. Richardson, pp. 1-12. (R.G. and F.J. Richardson, Melbourne, Victoria).

Lonsdale, W.M. (1992). The biology of *Mimosa pigra*. *In* 'A guide to the management of *Mimosa pigra*', ed. K.L.S. Harley, pp. 8-32. (CSIRO, Canberra).

Lonsdale, W.M., Miller, I.L. and Forno, I.W. (1995). *Mimosa pigra* L. *In* 'The biology of Australian weeds', Volume 1, eds R.H. Groves, R.C.H. Shepherd and R.G. Richardson, pp. 169-88. (R.G. and F.J. Richardson, Melbourne, Victoria).

Low, T. (2002). Why are there so few weeds? Proceedings of the 13th Australian Weeds Conference, eds H. Spafford Jacob, J. Dodd and J.H. Moore, pp. 1-6. (Plant Protection Society of WA, Perth, Western Australia).

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. and Bazzaz, F.A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10, 689-710.

Mackey, A.P. (1998). *Acacia nilotica* ssp. *indica* (Benth.) Brenan. *In* 'The biology of Australian weeds', Volume 2., eds F.D. Panetta, R.H. Groves and R.C.H. Shepherd, 1-18. (R.G. and F.J. Richardson, Melbourne, Victoria).

Mackey, A.P. and Swarbrick, J.T. (1998). *Cabomba caroliniana* A.Gray. *In* 'The biology of Australian weeds', Volume 2, eds F.D. Panetta, R.H. Groves and R.C.H. Shepherd, pp. 19-36. (R.G. and F.J. Richardson, Melbourne, Victoria).

Navie, S.C., McFadyen, R.E., Panetta, F.D. and Adkins, S.W. (1998). *Parthenium hysterophorus* L. *In* 'The biology of Australian weeds', Volume 2., eds F.D. Panetta, R.H. Groves and R.C.H. Shepherd, pp. 157-76. (R.G. and F.J. Richardson, Melbourne, Victoria).

Novak, S.J. and Mack, R.N. (2001). Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (cheatgrass). *Bioscience* 51, 114-21.

Parker, I.M. (1997). Pollinator limitation of a *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. *Ecology* 78, 1457-70.

Parsons, W.T. and Cuthbertson, E.G. (1992). 'Noxious weeds of Australia'. (Inkata Press, Melbourne).

Peirce, J.R. (1995). *Carthamus lanatus* L. *In* 'The biology of Australian weeds'. Volume 1, eds R.H. Groves, R.C.H. Shepherd and R.G. Richardson, pp. 51-66. (R.G. and F.J. Richardson, Melbourne, Victoria).

Piggin, C.M. and Sheppard, A.W. (1995). *Echium plantagineum* L. *In* 'The biology of Australian weeds', Volume 1, eds R.H. Groves, R.C.H. Shepherd and R.G. Richardson, pp. 87-110. (R.G. and F.J. Richardson, Melbourne, Victoria).

Popay, A.I. and Medd, R.W. (1995). *Carduus nutans* L. spp. *nutans*. *In* 'The biology of Australian weeds', Volume 1, eds. R.H. Groves, R.C.H. Shepherd and R.G. Richardson, pp. 29-49. (R.G. and F.J. Richardson, Melbourne, Victoria).

Radford, I.J., Nicholas, D.M., Brown, J.R. and Kriticos, D.J. (2001). Paddock-scale patterns of seed production and dispersal in the invasive shrub *Acacia nilotica* (Mimosaceae) in northern Australian rangelands. *Austral Ecology* 26, 338-48.

Randall, R. (2001). Garden thugs, a national list of invasive and potentially invasive garden plants. *Plant Protection Quarterly* 16, 138-71.

Richardson, D.M., Allsopp, N. D'Antonia, C.M., Milton, S.J. and Rejmànek, M. (2000). Plant invasions – the role of mutualisms. *Biological Reviews* 75, 65-93.

Richardson, D.M., Pyek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D. and West, C.J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6, 93-107.

Room, P.M. and Julien, M.H. (1995). *Salvinia molesta* D.S. Mitchell. *In* 'The biology of Australian weeds', Volume 1, eds R.H. Groves, R.C.H. Shepherd and R.G. Richardson, pp. 217-30. (R.G. and F.J. Richardson, Melbourne, Victoria).

Sindel, B.M., Radford, I.J., Holtkamp, R.H. and Michael, P.W. (1998). *Senecio madagascariensis* . *In* 'The biology of Australian weeds', Volume 2, eds F.D. Panetta, R.H. Groves and R.C.H. Shepherd, pp. 247-67. (R.G. and F.J. Richardson, Melbourne, Victoria).

Specht, R.L. (1981). Major vegetation formations in Australia. *In* 'Ecological biogeography of Australia', ed. A. Keast, pp. 163-298. (W. Junk, The Hague).

Specht, R.L. and Mountford, C.P. (1958). 'Records of the American-Australian scientific expedition to Arnhem Land. 3. Botany and plant ecology'. (University Press, Melbourne, Victoria).

Thorp, J.R. and Lynch, R. (2000). The determination of weeds of national significance. Launceston: National Weeds Strategy Executive Committee. ISBN 0 642 44913 9.

Tomley, A.J. (1998). *Cryptostegia grandiflora* Roxb. ex R.Br. *In* 'The biology of Australian weeds', Volume 2, eds. F.D. Panetta, R.H. Groves and R.C.H. Shepherd, pp. 63-76. (R.G. and F.J. Richardson, Melbourne, Victoria).

Tomley, A.J. and Panetta, F.D. (2002) Eradication of the exotic weeds *Helenium amarum* (Rafin) H.L. and *Eupatorium serotinum* Michx. from south-eastern Queensland. Proceedings of the 13th Australian Weeds Conference, eds H. Spafford Jacob, J. Dodd and J.H. Moore, pp. 293-6. (Plant Protection Society of WA, Perth, Western Australia).

van Klinken, R.D. and Campbell, S.D. (2001). The biology of Australian weeds. 37. *Prosopis* L. species. *Plant Protection Quarterly* 16, 2-20.

Williams, M. and Fitter, A. (1996). The varying success of invaders. *Ecology* 77, 1661-6.

Wright, A.D. and Purcell, M.F. (1995). *Eichhornia crassipes* (Mart.) Solms-Laubach. *In* 'The biology of Australian weeds', Volume 1, eds R.H. Groves, R.C.H. Shepherd and R.G. Richardson, pp. 111-21. (R.G. and F.J. Richardson, Melbourne, Victoria).