Restoration and Reclamation Review
Student On-Line Journal
Vol.6, No.5, Fall 2000
Department of Horticultural Science
University of Minnesota, St.Paul, MN

Control of commercially important *Pinus* spp. in fynbos

Paul A. Rabie

Introduction

There are at least 111 species in the genus *Pinus* (pines), almost all of which are native to the northern hemisphere where they often are important components of the vegetation (Richardson and Rundel 1998). Many *Pinus* species are economically important sources of timber, pulp, nuts, resin, and other products. Additionally, *Pinus* species often enjoy relatively rapid growth in habitats that are dry, nutrient poor, or otherwise inhospitable to most trees. This combination of traits has resulted in large-scale establishment of pine plantations both within the natural range of pines and well outside of that range, including large regions within the southern hemisphere (Le Maitre 1998). The remarkable adaptability of *Pinus* species and the active dispersal of their propagules by humans have allowed some species of *Pinus* to become invasive weeds in many of the areas where they have been introduced (Richardson and Higgins 1998).

One region in the southern hemisphere that has a long history of pine introductions and a large propensity for pine invasions is the fynbos biome in South Africa (figure 1; Richardson and Higgins 1998). Fynbos composes four-fifths of the Cape Floral Kingdom, the smallest of six floral kingdoms on the planet. It is restricted to the southwestern tip of the Western Cape Province, and most of it experiences a mediterranean climate (cool, wet winters and hot, dry summers) (Cowling and Richardson 1995). It is a fire-adapted system, with a fire return period of 5-40 years, depending on local conditions. Fynbos is a structurally simple vegetation type made up of four basic plant types: proteoid shrubs; ericoid shrubs, restioid herbs (similar to graminoids) and geophytes (bulb plants) (Cowling and Richardson 1995).

Figure 1. Mountain fynbos in the Outeniqua pass with an incipient *Pinus* invasion. Photograph courtesy of Boet Rabie.

Because fynbos has one of the most speciose floras in existence (8600 plant species, 5800 of which are endemic, occur in an area <90,000 km^2), and because the threats from invasive alien species (Macdonald and Richardson 1986) and agricultural and urban development (Rebelo 1992, Richardson *et al.* 1996) are so great, prioritization has been given to the preservation of intact fynbos, and to restoration of fynbos that has been degraded by alien species (e.g. Taylor and Macdonald 1985, Holmes and Richardson 1999), rather than to restoration of fynbos from land that has been entirely transformed (D.M. Richardson, Institute for Plant Conservation, Cape Town, pers. comm.). This strategy is sensible, considering the small area of extant fynbos, the magnitude of the threats to those ecosystems, and the small and shrinking resource base for conservation (Le Maitre *et al.* 1996).

This review will focus on the restoration and maintenance of fynbos infested by the two most important *Pinus* invaders in fynbos: *Pinus radiata* (radiata pine) and *P. pinaster* (cluster pine) (Richardson and Brown 1986). Two additional species, *P. halepensis* (Aleppo pine) and *P. patula* (stone pine), have also been identified as invasive or potentially invasive in fynbos, but their large seed mass prevents them from being as aggressive as *P. radiata* or *P. pinaster* (see below).

Geography and Biology of Pinus spp. Treated in this Review

Pinus radiata has a small native range in north America comprising five areas that span the United States-Mexico border. There are five extant natural populations, covering a total area <6000 ha. Three of these occur on the central California coast; two others are on Guadeloupe Island and Cedros Island, Mexico (Lavery and Mead 1998, and references therein).

P. radiata has proven to be a very successful forestry species, and has been widely planted in many parts of the world. The global extent of *P. radiata* is >4,000,000 ha, much of which occurs in the southern hemisphere. New Zealand, Chile, Australia, Spain and South Africa are (in decreasing order of extent) the most important growers of *P. radiata*, collectively composing >95% of the global *P. radiata* estate (Lavery and Mead 1998, and references therein).

P. pinaster has a presumed native range that covers about 1.3 million ha in the western Mediterranean basin (Morocco, Portugal, Spain, southern France, and southern Italy) (Barbero *et al.* 1998, and references therein). The exact native range of the species is unresolved due to a long history of human dispersal of the species. It has been introduced in Australia, New Zealand, South Africa, Argentina, Chile and the United Kingdom. (Scott 1962 *in* Le Maitre 1998).

With few exceptions, *Pinus* species that have become invasive share many of the biological traits that make them good invaders. Key among these is seed morphology. *P. pinaster* and *P. radiata* both have small winged seeds that are well adapted to long distance dispersal (van Wilgen and Siegfried 1986). *P. radiata* seedlings are capable of establishing >3 km from parent plants in fynbos (Richardson and Brown 1986) and mature trees are capable of self-fertilization (Bannister 1965 *in* Richardson and Brown 1986), allowing lone colonizers to establish new patches. A relatively short juvenile period (with respect to natural fire frequency) is another characteristic that allows *Pinus* spp. to be invasive in fynbos. Most fynbos communities burn at intervals of 10-15 years; *P. radiata* can produce viable seed 9 years after germination in fynbos (Richardson and Brown 1986), and *P. pinaster's* juvenile period is somewhat shorter (Hunter and Douglas 1984 *in* Richardson and Brown 1986). The potential dispersal distances of *Pinus* species and their short juvenile period both increase the likelihood that a burned area will receive *Pinus* propagules in the seed rain. Finally, although seed production is variable from year to year, a short mean interval between large seed crops is another trait that enhances the invasive potential of *Pinus* (Rejmanek and Richardson 1996).

Perhaps most important to the persistence of these species in fynbos is that they are fire resilient. Although adults are not particularly resistant to fire (figure 2), they are serotinous (seeds are retained in cones in the canopy until fire triggers their release), so fire events may kill parent trees but release large numbers of fast-growing propagules onto mineral soil (Richardson and Brown 1986). Post-fire vegetation recovery is slow in fynbos because there is a paucity of grassy or herbaceous vegetation in the understory, and many of the large shrubs are obligate reseeders (fire kills adults). As a result, fast-growing *Pinus* seedlings experience little competition from natives (Johnstone 1986 *in* Agee 1998). Although *Pinus* in fynbos are known to reproduce optimally following fire, seedlings can also establish in fynbos with a post-fire age of <10 years and in senescing vegetation >30 years post-fire (Richardson and Brown 1986, Moll and Trinder-Smith 1992); indeed it seems likely that any given patch of fynbos may have a microsite suitable for *Pinus* germination. The net effect of these biological attributes is that *Pinus* invasions in fynbos can expand at rates that are comparable to *Pinus* invasion rates on recently deglaciated landscapes in the northern hemisphere: several km per generation (Richardson *et al.* 1994).

Figure 2. Partially killed *Pinus* stand approximately 18 months following a fire. Photograph courtesy of Boet Rabie.

Impacts of Pinus spp. on Invaded Fynbos Habitats

Over 79 species of *Pinus* have been introduced to South Africa (Poynton 1979 *in* Richardson and Higgins 1998). *P. pinaster* and *P. radiata* have invaded 30 and 17%, respectively, of the fynbos biome ('invaded' is defined as presence within cells of a ¼ degree grid; references *in* Richardson *et al.* 1992) and 45 and 19% of nature preserves within the fynbos biome ('invaded' is defined as "e 1 mature individual within a 1 km^2 grid cell; Macdonald 1991 *in* Richardson *et al.* 1997). These estimates may be unrealistically high due to the coarse resolution of the grids that were used. But considering the rate at which *Pinus* invasions occur in fynbos (see previous section), they can be considered reasonable estimates of the area that is immediately threatened by *Pinus* invasions.

The greatest concern over *Pinus* invasions in fynbos appears to be caused by the loss of species diversity that accompanies afforestation (Richardson and van Wilgen 1986, Richardson *et al*. 1992, Holmes and Richardson 1999). A study of the changes in diversity following 35 years of afforestation in fynbos near Stellenbosch found that native canopy cover had been reduced from 75% to 20%, number of native species had been reduced from 298 to 126, and mean plant density was reduced from 260 to 78 plants m^{-2} (Richardson and van Wilgen 1986).

A second major concern (and probably the concern that motivates the funding for many fynbos restoration projects) is that afforestation of fynbos greatly reduces water yields from catchments. The threat of reduced water yield motivated most of the early invasive plant management programs in Fynbos (Fenn 1980 *in* Richardson *et al*. 1992) . Empirical and theoretical estimates of water yield reductions following afforestation of fynbos range from 20% (empirical study; Van Wyk 1987 *in* Cowling *et al.* 1997) to 100% (model; Burgers *et al.*1995 *in* Higgins *et al.* 1997). The southwestern Cape of South Africa is a semi-arid environment, and the implications of even a 20% reduction in water supply to Cape Town are substantial; the rapid development of the area will compound the problem (Le Maitre *et al.* 1996).

Pinus invasion also impacts fynbos ecosystem properties and processes. Aboveground biomass in *Pinus* stands can be five times greater than that in uninfested fynbos, producing a much larger fuel load that fynbos vegetation typically produces (van Wilgen 1982). Leaf area index (ratio of total leaf area to total ground area in a stand) is expected to be higher in such stands than in native vegetation, and should affect light transmission to shorter (native) species, rainfall interception, and rates of transpiration (references *in* Versfeld and van Wilgen 1986). Litterfall below *Pinus* canopies also is higher (both by rate and by littermass on the soil surface) in *Pinus* stands than in native fynbos. Because litterfall is a major component of the nutrient cycling process, changes in litterfall rates can have important effects on nutrient cycles by altering the carbon or nutrient quality of litter, and pH of the soil organic matter (Cowling *et al.* 1997). How such changes affect community composition in fynbos is poorly understood. Although researchers have demonstrated nutrient-mediated effects on plant recruitment following fire in an area that had been invaded by nitrogen-fixing *Acacia* species, such effects were not apparent in an area that had been invaded by *Pinus* species (Stock and Allsopp 1992).

Control Techniques for *Pinus* spp. in Fynbos

Prophylactic Options

The considerable recent attention given to the invasibility of plant communities in general (e.g. Trabaud 1991, Hobbs and Huenneke 1992, Richardson and Cowling 1992, Richardson *et al.* 1994, Lavorel *et al.* 1999, Stohlgren *et al.* 1999, Callaway and Ashehoug 2000, Davis *et al.* 2000, Symstad 2000, and many others) implies two practical goals: a) to identify invasible communities so that conservation priorities can be focused there, and b) in the context of restorations, to restore communities in such a way that they have a measure of resistance to invasion. This prophylactic approach to restoration is attractive, but probably will not be useful for *Pinus* species in the fynbos biome. Richardson and Cowling (1992) point out that in fynbos, *Pinus* species invade areas that are not substantially altered by humans, probably because the intense fires that burn through fynbos communities produce conditions that are ideal for germination: exposed mineral soil and a lack of competition (figure 3). Regardless of whether fynbos is generally more invasible than other habitats (see references above), it seems clear that it is invasible by *Pinus*, and no approach to restoration is likely to change that.

Figure 3. Recently burned area of mountain fynbos on the Montague pass. Photograph courtesy of Boet Rabie.

Competitive Control

There is possibly one exception to the general invasibility of fynbos by *Pinus*: lower slopes of mountain fynbos that are dominated by *Protea nitida* (waboom) are unusual in fynbos because they often have an understory of C_4 grasses that may impede the establishment of *Pinus* species (Richardson *et al*. 1994). *Pinus* germination in these habitats may be suppressed by relatively fast recovery of grass species and the development of a canopy following fire. Therefore restoration projects with target communities that include an understory of grass species may be resistant to *Pinus* invasion, and the establishment and maintenance of a continuous cover of grasses may be beneficial. I am not aware of any rigorous investigations of the mechanism or degree of suppression of *Pinus* in fynbos with a graminoid understory. Studies in this area would be desirable: in particular, it might be useful to determine whether there is a net benefit associated with the active promotion of a grass canopy so that restoration activities can be prioritized.

Genetic Control

A second approach to prophylactic control is to genetically engineer cultivated *Pinus* to reduce reproductive output. Genetic modification would be a costly option in terms of research and development, increased labor costs due to the loss of self-seeded trees on plantations, and the need to continually produce infertile or subfertile seedlings. Additionally, there would be a cost in terms of lost revenues from sales of *Pinus* seeds, an enterprise which is fairly lucrative. Genetically engineering *Pinus* is an option that doubtlessly would meet opposition from the forestry industry in South Africa. And the cost may ultimately be too high: benefits would be very slow to arrive and difficult to quantify in economic terms. However the proposition may merit consideration. Richardson *et al.* (1994) pointed out that ‘the largest stands of self-sown pines are invariably near plantations,’ (figure 4) and *Pinus* removal programs are often very expensive (Macdonald *et al.* 1989, van Wilgen *et al*. 1992). A model of the ecological and economic implications of genetically engineered *Pinus* species would be a useful tool to investigate the net cost of genetically modifying *Pinus*. Higgins *et al.* (1997) recently produced a model to investigate the implications of biological control on an economically important *Acacia** (wattle) invader in fynbos; such an approach to *Pinus* seems reasonable. [**Acacia* spp. are an important group of lowland fynbos invaders; see Mehta (this volume) for a discussion of *Acacia saligna* invasion in fynbos.]

Figure 4. ***Pinus*** **plantation near the Outeniqua pass. Photograph courtesy of Boet Rabie.**

Biological Control

Fynbos supports very few native megaherbivores and is poor grazing habitat for domesticated ungulates (Richardson *et al.* 1994). Therefore biological control by grazing, a successful *Pinus* control technique in New Zealand (Crozler and Ledgard 1990), is not a feasible option in fynbos (Richardson *et al* 1994). Pathogens and insect herbivores have the potential to impact *Pinus* populations (de Groot and Turgeon 1988, Harrington and Wingfield 1988), but the importance of *Pinus* to the timber industry precludes their use. Insect granivores may be a compromise option for biological control of *Pinus* in South Africa and have been suggested for use against *P. pinaster* (Neser and Kluge 1986). The research program at the Plant Protection Research Institute in South Africa has recently been expanded to include potential biological control agents for *Pinus* species (van Wilgen *et al.* 2000). Ecological and economic modeling concurrent with feasibility research is desirable.

Restorative Options

Chemical Control

There is very little information regarding the feasibility of chemical control for invasive *Pinus* in fynbos or elsewhere. Donald (1982) investigated the use of paraquat and diquat formulations in fynbos for the control of *P. pinaster* in a series of randomized trials. He tested two modes of application: application of chemical to axe scars, and injection of chemical into holes drilled into the tree trunks. He concluded that dense stands of *P. pinaster* were more economically cleared by chainsaw than with chemicals. New infestations, however, with fewer trees, were more economically killed with chemicals (but note that the economic situation in South Africa is vastly different today than it was in 1982). At the time of publication the most cost-effective treatment was achieved with Reglone (diquat). Best kill rates were achieved by drilling two 9.5 mm holes into the sapwood at an angle of 45° to facilitate retention of the chemical. One ml of diquat was injected into each hole. Richardson *et al*. (1994) pointed out that herbicidal treatment of *Pinus* may be an option in situations where fire is untenable.

Donald's work was motivated by a slump in the market for timber during the 1970's which made it difficult to sell wood from plantation thinnings. At that time it was economically most feasible to 'thin for waste,' so the research was not concerned with the restorative potential of this method of killing *Pinus*. A patch of standing dead trees is a structural anomaly in fynbos that may shade the surface vegetation enough to hamper development of the target fynbos community. If herbicides are used to control adult *Pinus*, it will be necessary to establish at what densities it is appropriate to do so. Perhaps a more serious problem is that standing dead trees will begin to desiccate, probably leading to the release of seed from the serotinous cones at canopy height. It is more desirable that seeds should be released at or near the ground surface where they are less likely to be dispersed by wind (van Wilgen *et al.* 1994).

Although some studies have investigated herbicides that are well suited for use in conifer plantations (i.e. targeted against pteridiophytes and angiosperms; e.g. Freedman *et al.* 1993, Sy *et al.* 1994), I know of no studies that investigate the targeted use of herbicides against conifers.

Fell and Burn Control

Twenty years of *Pinus* control in fynbos has resulted in the development of a relatively effective but expensive mode of control: fell and burn (van Wilgen *et al.* 1992, Richardson *et al.* 1994, van Wilgen *et al.* 1994). The strategy is to cut trees about 18 months before a prescribed burn and leave them on site to allow the serotinous cones to open and release their seeds. Some seeds will be eaten by granivores; others will germinate but should be fire-killed at the time of burning. Fell and burn management of *Pinus* invasions has met with some success: the frequency of *P. pinaster* in 2.6-ha plots in the Cape Peninsula mountains (a 102 km^2 area) was reduced from 82 to 62% between 1960 and 1990 (Moll and Trinder-Smith 1992). *P. pinaster* remains a threat, however, as does *P. radiata* which increased from 10 to 24% frequency during the same period.

The fire prescription for infested fynbos is imperfect, and some of the problems appear to be intractable. Fynbos that is invaded by *Pinus* may have aboveground biomass that is up to five times what is found in native fynbos (Versfeld and van Wilgen 1986), representing a dramatically different fuel load than that produced by native fynbos species. The resulting fire tends to be much hotter than fires in uninvaded fynbos, and can impact the soil physical and biological components dramatically (Breytenbach 1989 *in* van Wilgen *et al.* 1994). Seed banks may be destroyed, and soils can become hydrophobic due to extremely hot fires, increasing overland runoff and erosion (Le Maitre *et al.* 1996). This problem can be compounded if felled trees are stacked into piles, which have the potential to become intense hotspots during a burn. Unnaturally intense fire conditions might be mitigated by avoiding the stacking of fuel materials during the felling process, and by burning under conditions that produce fires of lower intensity, for example, when humidity is high, or with the use of backing burns (burns that move into the wind, rather than with it).

Fire prescriptions call for a 12-15 year fire return period based on the reproductive biology of *Pinus* species: at this interval few trees reach maturity prior to the burn and are felled, and their seedlings are susceptible to fire-kill (Richardson and Brown 1986, van Wilgen *et al.* 1994). This prescription does not work in areas that are invaded by a mixture of *Pinus* and *Acacia*, because *Acacia* reach maturity sooner than *Pinus* and produce abundant seed that are stimulated to germinate by fire; some *Acacia* also resprout following fire (Taylor 1977, Hall 1979, both *in* Trabaud 1991; Richardson *et al.* 1992 *in* van Wilgen 1994).

A 12-15 year fire return interval also presents problems because it is too static. As is the case in many fire-prone landscapes, management through the nineteenth and twentieth centuries reflects the development of ecologists' understanding of the importance of fire (van Wilgen *et al.* 1994). Policy called for the suppression of fire in fynbos until the latter portion of the twentieth century, when the detrimental effects of fire suppression started to become apparent. Fire is now recognized and implemented as an important regenerative process in many ecosystems, including fynbos. The emerging knowledge that a *stochastic* fire regime might be as important over the long term (centuries) as any fire regime is over the short term (decades) has yet to be widely implemented. In the case of fynbos, the fire prescription is driven by the reproductive biology of *Pinus*, the need to prevent uncontrollable wildfires, and the observation that proteoid species appear to maintain viable populations under such a regime (see van Wilgen *et al.* 1994 for a discussion of the circumstances that led to single-species modes of management). The difficulty with a static fire regime is that it will favor some species at the expense of others: such a regime will inevitably lead to the impoverishment of diversity by repeatedly selecting for the same species (references *in* van Wilgen *et al.* 1994).

The goal of *Pinus* management in fynbos for the foreseeable future likely will be control at an acceptable level rather than complete extermination, because the importance of *Pinus* to the timber industry virtually guarantees a constant source of propagules. Thus, there is a real need to develop a more sophisticated fire management system in fynbos that can simultaneously sustain biotic diversity and effect *Pinus* control. Seydack (1992) (summarized *in* van Wilgen *et al.* 1994) presents a large array of options that pay explicit attention to the management of exotic species and the management effort involved.

Research Priorities

Fynbos researchers have produced an impressive body of work concerning invasion biology (Taylor and Macdonald 1985, Richardson and Brown 1986, Richardson and van Wilgen 1986, Macdonald *et al.* 1989, Witkowski 1991, Richardson and Cowling 1992, Musil 1993, Higgins *et al.* 1996, Holmes and Richardson 1999, and many others). However, a review of that literature reveals a surprising paucity of controlled studies that quantify the effects of control and restoration techniques. Evidence appears to be presented largely on the basis of 'conventional wisdom,' and it is likely that after over thirty years of woody invasives management, the protocols that have been developed are generally effective at reducing the abundance of invasive species. However it is equally likely that subtle differences in the application of those techniques will have large effects over the long term, and the only way to monitor the success of ongoing restoration efforts will be to rigorously quantify those effects. Additionally, the relatively recent recognition of the importance of ecosystem function to the maintenance of biotic communities necessitates quantitative studies: it simply is not possible to document nutrient cycling (for example) by casual observations. A final impetus for the rigorous examination of control options is the dwindling resource base for ecosystem management in South Africa (Le Maitre *et al.* 1996). As funding shrinks, it becomes increasingly important to make the best use of available resources.

Conclusion

Government policy for control of invasive *Pinus* in declared water catchment areas within fynbos stipulates burning at 12-15 year intervals (references *in* van Wilgen *et al.* 1994), and land managers' experience suggests that felling *Pinus* about 18 months prior to prescribed burns is a good way to effect control. At present, these represent the best management practices for control of invasive *Pinus* in fynbos. More research is needed to establish techniques that effect control in the context of a more stochastic fire regime, and to determine the relative effects of seasonality of burns on the maintenance of biotic diversity and on *Pinus* control. [Presently, burns are conducted in late summer or early autumn, based largely on the response of proteoid species to this regime (van Wilgen *et al.* 1994)].

Fynbos is the world's most diverse floral kingdom, and current research clearly demonstrates that the vast plant diversity there is threatened (van Wilgen *et al.* 1992). Although *Pinus* invasions are not the only component of this threat, they are a major threat, and their control will be one in a series of steps that is necessary if the fynbos floral kingdom is to be preserved.

Literature Cited

Agee, J. K. 1998. Fire and pine ecosystems. Pages 193-218 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge.

Barbero, M., R. Loisel, P. Quezel, D. M. Richardson, and F. Romane. 1998. Pines of the mediterranean basin. Pages 153-170 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge.

Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521-523.

Cowling, R. M., and D. M. Richardson. 1995. Fynbos. South Africa's unique floral kingdom. Fernwood Press, Cape Town. 156 pages.

Cowling, R. M., D. M. Richardson, and P. J. Mustart. 1997. Fynbos. Pages 99-130 *in* R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. Vegetation of southern Africa. Cambridge University Press, Cambridge, England.

Crozler, E. R., and N. J. Ledgard. 1990. Palatability of wilding conifers and control by simulated sheep browsing. FRI Bulletin - New Zealand Ministry of Forestry, Forest Research Institute 155:139-143.

de Groot, P., and J. J. Turgeon. 1998. Insect-pine interactions. Pages 381-404 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528-534.

Donald, D. G. M. 1982. The control of *Pinus pinaster* in the fynbos biome. South African Forestry Journal 123:3-7.

Freedman, B., R. Morash, and D. Mackinnon. 1993. Short-term changes in vegetation after the silvicultural spraying of glyphosate herbicide onto regenerating clearcuts in Nova Scotia, Canada. Canadian Journal of Forest Research 23:2300-2311.

Harrington, T. C., and M. J. Wingfield. 1998. Diseases and the ecology of indigenous and exotic pines. Pages 381-404 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge.

Higgins, S. I., M. J. Morris, E. J. Azorin, and R. M. Cowling. 1997. A dynamic ecological-economic model as a tool for conflict resolution in an invasive-alien-plant, biological control and native-plant scenario. Ecological Economics 22:141-154.

Higgins, S. I., D. M. Richardson, and R. M. Cowling. 1996. Modeling invasive plant spread: the role of plant-environment interactions and model structure. Ecology 77:2043-2054.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324-337.

Holmes, P. M., and D. M. Richardson. 1999. Protocols for restoration based on recruitment dynamics, community structure, and ecosystem function: Perspectives from South African fynbos. Restoration Ecology 7:215-230.

Lavery, P. B., and D. J. Mead. 1998. *Pinus radiata*: a narrow endemic from North America takes on the world. Pages 432-449 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge.

Lavorel, S., A.H. Prieur-Richard, and K. Grigulis. 1999. Invasibility and diversity of plant communities: from patterns to processes. Diversity and Distributions 5:41-49.

Le Maitre, D. C. 1998. Pines in cultivation: a global view. Pages 407-431 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge.

Le Maitre, D., B. W. van Wilgen, R. A. Chapman, and D. H. McKelly. 1996. Invasive plants and water resources in the western Cape Province, South Africa: modeling the consequences of a lack of management. Journal of Applied Ecology 33:161-172.

Macdonald, I. A. W., D. L. Clark, and H. C. Taylor. 1989. The alien flora of the Cape of Good Hope Nature Reserve. South African Journal of Botany 55:56-75.

Macdonald, I. A. W., and D. M. Richardson. 1986. Alien species in terrestrial ecosystems of the fynbos biome. Pages 77-91 *in* I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Oxford University Press, Stellenbosch, South Africa.

Moll, E. J., and T. Trinder-Smith. 1992. Invasion and control of alien woody plants on the Cape Peninsula Mountains, South Africa - 30 years on. Biological Conservation 60:135-143.

Musil, C. F. 1993. Effect of invasive Australian acacias on the regeneration, growth and nutrient chemistry of South African lowland fynbos. Journal of Applied Ecology 30:361-372.

Neser, S., and R. L. Kluge. 1986. The importance of seed-attacking agents in the biological control of invasive alien plants. Pages 285-293 *in* I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Oxford University Press, Stellenbosch, South Africa.

Rebelo, A. G. 1992. Preservation of biotic diversity. Pages 309-344 *in* R. M. Cowling, editor. The ecology of fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 71:1655-1661.

Richardson, D. M., and P. J. Brown. 1986. Invasion of mesic mountain fynbos by *Pinus* radiata. South African Journal of Botany 52:529-536.

Richardson, D. M., and R. M. Cowling. 1992. Why is mountain fynbos invasible and which species invade? Pages 161-181 *in* B. W. v. Wilgen, D. M. Richardson, F. J. Kruger, and H. J. van. Hensbergen, editors. Fire in South African mountain fynbos. Springer-Verlag, Berlin.

Richardson, D. M., R. M. Cowling, and B. B. Lamont. 1996. Non-linearities, synergisms and plant extinctions in South African fynbos and Australian kwongan. Biodiversity and Conservation 5:1035-1046.

Richardson, D. M., and S. I. Higgins. 1998. Pines as invaders in the southern hemisphere. Pages 450-473 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge.

Richardson, D. M., I. A. W. Macdonald, J. H. Hoffmann, and L. Henderson. 1997. Alien plant invasions. Pages 535-570 *in* R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. Vegetation of southern Africa. Cambridge University Press, Cambridge, England.

Richardson, D. M., I. A. W. Macdonald, P. M. Holmes, and R. M. Cowling. 1992. Plant and animal invasions. Pages 270-308 *in* R. M. Cowling, editor. The ecology of fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town.

Richardson, D. M., and P. W. Rundel. 1998. Ecology and biogeography of *Pinus*. Pages 3-46 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus*. Cambridge University Press.

Richardson, D. M., and B. W. van Wilgen. 1986. Effects of thirty-five years of afforestation with *Pinus* radiata on the composition of mesic mountain fynbos near Stellenbosch. South African Journal of Botany 52:309-315.

Richardson, D. M., P. A. Williams, and R. M. Hobbs. 1994. Pine invasions in the southern hemisphere: determinants of spread and invadability. Journal of Biogeography 21:511-527.

Scholes, M. C., and T. E. Nowicki. 1998. Effects of pines on soil properties and processes. Pages 341-353 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge.

Stock, W. D., and N. Allsopp. 1992. Functional perspective of ecosystems. Pages 241-249 *in* R. M. Cowling, editor. The ecology of fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town.

Stohlgren, T. J., L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, Y. Son, D. Binkley, G. W. Chong, and M. A. Kalkhan. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69:25-46.

Sy, M., R. Jobidon, and H. Margolis. 1994. Differential tolerance of coniferous species to the microbially produced herbicide bialaphos. I. Morphological and growth effects. Canadian Journal of Forest Research 24:2191-2198.

Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81:99-10.

Taylor, H. C., and S. A. Macdonald. 1985. Invasive alien woody plants in the Cape of Good Hope Nature Reserve. I . Results of a first survey in 1966. South African Journal of Botany 51:14-20.

Trabaud, L. 1991. Is fire an agent favouring plant invasions? Pages 179-190 *in* R. H. Groves, editor. Biogeography of mediterranean invasions. Cambridge University Press, Cambridge.

van Wilgen, B. W. 1982. Some effects of post-fire age on the above-ground biomass of fynbos (macchia) vegetation in South Africa. Journal of Ecology 70:217-225.

van Wilgen, B. W., W. J. Bond, and D. M. Richardson. 1992. Ecosystem management. Pages 345-371 *in* R. M. Cowling, editor. The ecology of fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town.

van Wilgen, B. W., D. M. Richardson, and A. H. W. Seydack. 1994. Managing fynbos for biodiversity: constraints and options in a fire-prone environment. South African Journal of Science 90:322-320.

van Wilgen, B. W., and W. R. Siegfried. 1986. Seed dispersal properties of three pine species as a determinant of invasive potential. South African Journal of Botany 52:546-548.

van Wilgen, B. W., T. Willems, F. Van der Heyden, H. G. Zimmermann, and D. Magadlela. 2000. Big returns from small organisms: developing a strategy for the biological control of invasive alien plants in South Africa. South African Journal of Science 96:148-152.

Witkowski, E. T. F. 1991. Growth and competition between seedlings of *Protea repens* (L.) L. and the alien invasive, *Acacia saligna* (Labill.) Wendl. in relation to nutrient availability. Functional Ecology 5:101-110.

Versfeld, D. B., and B. W. van Wilgen. 1986. Impact of woody aliens on ecosystem properties. Pages 239-246 *in* I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Oxford University Press, Stellenbosch, South Africa.