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Frances M. Johnston and Catherine M. Pickering

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The current status of alien plants in the alpine and subalpine areas of the Australian Alps is assessed in this article. The number of alien species has increased following the region's use by nonindigenous Australians over the last

170 years. One hundred and seventy-five alien plant taxa have been recorded above 1500 m in the Australian Alps. These taxa are mainly perennials from Europe, Asia, and the Americas. They are predominantly associated with disturbance and are categorized here according to the types of human activities with which they are associated. There are roadside or path weeds (78% of species), resort weeds (58%), grazing weeds (25%), and rehabilitation weeds (11%). Just over 20% of the alien taxa have become naturalized in the region. Diversity, distribution, and biology of the species are evaluated along with the threats they pose to the conservation of the region.

Keywords: Alien plants; disturbance; Australian ecosystem; plant diversity; Australian Alps.

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Introduction

The alpine and subalpine areas of southeast mainland Australia, the Australian Alps, contain a significant component of Australia's floral biodiversity and the diversity of alpine floras worldwide (Costin 1989; Good 1992a; Körner 1999). The region is unique in botanical composition, species richness, and internal botanical zonation (Costin 1989). The alpine and subalpine areas above 1500 m in New South Wales alone contain around 377 native plant species, including 31 endemic species (Good 1992a).

The native flora of the Australian Alps is considered to derive from 3 sources: Australian lowland species adapted to alpine conditions, species from other alpine regions, and cosmopolitan species (Barlow 1988). Alien plants are a fourth, more recent source of taxa (Mallen 1986). Some of these species are environmental weeds and pose a serious threat to the ecology of the Australian Alps (Carr et al 1992).

FIGURE 1 Areas above 1000, 1500, and 2000 m in southeastern Australia. (Modified from Green 1998)

Environmental weeds can be a major problem in natural ecosystems (eg, Prieur-Richard and Lavorel 2000). Negative environmental impacts of alien plants include displacement of native species, modification of primary ecosystem functioning, and modification of disturbance regimes and postdisturbance communities (Prieur-Richard and Lavorel 2000). Weed invasions can accelerate the rate of soil erosion, alter other geomorphic processes, alter biogeochemical and hydrological cycles, alter fire regimes, prevent recruitment of native species, and accelerate extinction rates (Hobbs 1989; Mooney and Drake 1989; Carr et al 1992).

For the Australian Alps, as for other conservation areas, it is important to determine the diversity of alien plants present as well as the types of disturbances and other environmental factors with which they are associated. The present article examines the diversity of alien plants recorded in the Australian Alps, the characteristics of these plants, the types of human activities with which they are associated, and the management challenge they pose for conservation organizations.

Methodology

Study area

Alpine and subalpine vegetation in Australia is limited to elevated areas within the southeastern corner of the mainland (the Australian Alps, see Figure 1) and smaller dispersed areas in Tasmania (Green and Osborne 1994). The total area of subalpine and alpine vegetation in mainland Australia above 1500 m is around 2350 km², with 1200 km² in New South Wales (NSW), 150

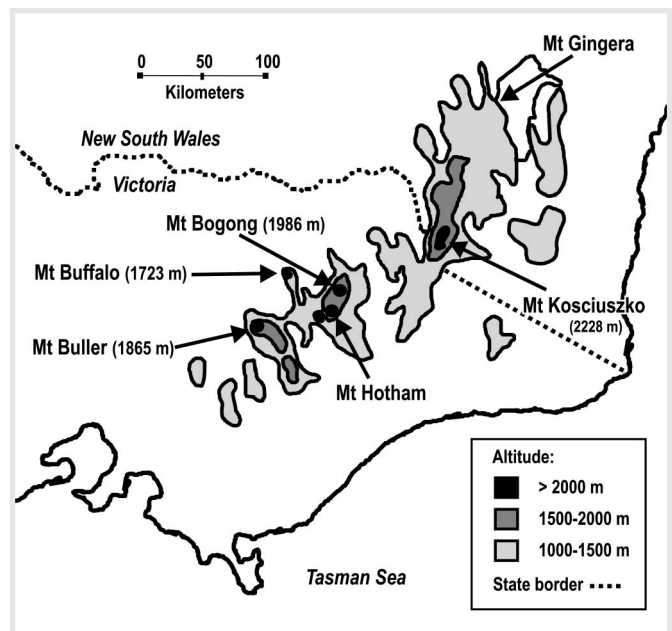


FIGURE 2 The authors inspecting a population of the invasive weed yarrow (*Achillea millefolium*), growing in snow gum woodland. (Photo by Andrew Kirkwood)



km² in the Australian Capital Territory (ACT), and 1000 km² in Victoria (Green and Osborne 1994; see Table 1). Of this, only around 250 km² in NSW (above 1830 m) and 120 km² in Victoria (above 1750 m) is considered to be true alpine (above the treeline; cf Good 1992a; Green and Osborne 1994; Körner 1999).

Subalpine vegetation in Australia starts at the winter snowline (lower boundary of the area that receives snow cover) and reaches to the limit of tree growth (treeline; Costin 1954; Green and Osborne 1994). It is characterized by heaths, grasslands, and snow gum woodland (*Eucalyptus niphophila*; Figure 2; cf Costin 1954; Green and Osborne 1994). The lower boundary for alpine vegetation in Australia, as overseas, is considered to be the treeline (Costin et al 1979; Good 1992a; Green and Osborne 1994; Körner 1999). However, in Australia, the upper limit of alpine vegetation is not a barren rock area or permanent cover of snow and ice (nival zone). Instead, the summit of the highest mountain in Australia (Mt Kosciuszko, 2228 m) sets a relatively modest altitudinal upper limit for alpine vegetation

(Costin 1989; Green and Osborne 1994). Alpine vegetation consists of herbfields, grasslands, bogs, fens, heaths, and small areas of fieldmark (Costin et al 1979; Green and Osborne 1994).

The climate of the subalpine and alpine areas of the Australian Alps is not as severe as in some other alpine regions (Green and Osborne 1994; Körner 1999). Subalpine areas of the Australian Alps are characterized by 1–4 months of snow cover with mean monthly temperatures of 0°C in winter. Annual precipitation varies between 770 and 2000 mm, depending on location. The alpine areas tend to have a harsher climate with minimum temperatures below 0°C for 4–6 months of the year and an average temperature of less than 10°C in the warmest month. Annual precipitation varies between 1780 and 3040 mm, with most of it falling as snow in winter (Green and Osborne 1994). The main growing season for plants is usually restricted to the spring and summer months (Pickering 1993).

Nearly all of the mainland snow country is protected within conservation reserves. The reserves in NSW (Kosciuszko National Park, Brindabella National Park, Scabby Range Nature Reserve, Bimberi Nature Reserve), Victoria (Alpine National Park, Snowy River National Park, Mt Buffalo National Park), and the ACT (Namadgi National Park) are collectively known and managed as the Australian Alps national parks (Good 1992b).

Information sources

Records of alien species occurrences in the alpine and subalpine areas of the Australian Alps in NSW, Victoria, and the ACT were compiled from just over 100 years of published and unpublished vascular plant records (Maiden 1898, 1899; Costin 1954; Thompson and Gray 1981; McDougall 1982; Walsh et al 1984; Mallen-Cooper 1990; Anonymous 1996; Pearson, unpublished data; Duncan 1998; Sainty et al 1998; CSIRO 1999; Ingwersen, unpublished report; McDougall and Appleby 2000). Records of any alien species were entered into a database and the taxonomy revised according to Harden (1993). Where available, location information and available habitat data were included. Information on habitat,

TABLE 1 Number of alien plant families, genera, and species recorded in the Australian Alps above 1500 m (compiled from Maiden (1898, 1899), Costin (1954), Thompson and Gray (1981), McDougall (1982), Walsh et al. (1984), Mallen-Cooper (1990), Anonymous (1996), Pearson (unpublished data), Duncan (1998), Sainty et al. (1998), Ingwersen (unpublished data), McDougall and Appleby (2000), CSIRO (1999)).

Location	Area (km ²)	Family	Genera	Species
New South Wales	1200	41	117	165
Victoria	1000	29	92	117
Australian Capital Territory	150	8	11	10
Total		41	122	175

TABLE 2 Number of alien plant species associated with different types of human disturbance within the Australian Alps (rehab = rehabilitation).

Family	Grazing aliens ^a	Grazing rehab ^b	Naturalized weeds ^c	Roadside/path aliens ^d	Resort aliens ^e	Tourism rehab ^f
Totals	43	19	36	136	102	8
Amaryllidaceae				1		
Apiaceae				1	1	
Apocynaceae				2	1	
Aquifoliaceae	1			1	1	
Asteraceae	8	2	6	16	14	
Boraginaceae	1	2	2	3	2	
Brassicaceae	3	1		8	3	
Callitricheaceae				1	1	
Campanulaceae	1					
Caryophyllaceae	2	1	3	6	5	
Chenopodiaceae	1			6	1	
Euphorbiaceae				1	1	
Fabaceae	4		6	14	7	
Fagaceae				1		
Fumariaceae				1	1	
Gentianaceae			1	1		
Geraniaceae	1			1		
Grossulariaceae	1					
Guttiferaeae				1	1	
Iridaceae				1	2	
Juncaceae			2	4	5	
Labiataeae	1			3	2	
Lamiaceae				2	1	
Liliaceae				2	4	
Malvaceae	2			2	1	
Onagraceae				2	1	
Oxalidaceae	1			1		
Pinaceae				4	1	
Plantaginaceae	1			1	2	
Poaceae	9	10	8	23	18	8
Polygonaceae	3	1	1	4	4	
Primulaceae	1	1		1	1	
Ranunculaceae			1	2	3	
Resedaceae				1		
Rosaceae		1	2	8	10	
Salicaceae				2	1	
Scrophulariaceae	1		4	7	5	
Solaneaceae					1	
Violaceae	1			1	1	

^aCostin (1954).

^bCostin and Wimbush (1963), Bryant (1971), Good (1976).

^cMcDougall (1982), Walsh et al. (1984), Mallen-Cooper (1990).

^dMallen-Cooper (1990), Pearson (unpublished data).

^eMcDougall and Appleby (2000).

^fEnders, personal communication, 2000.

form, dispersal mechanisms, family, origin, environmental tolerances, and flowering period of the species was added from the original references and other texts (Auld and Medd 1992; Bodkin 1992; Harden 1993; Lazarides et al 1997). Estimates of the total and regional diversity of alien species were then obtained from the database. Location data were used to identify the types of human land use that favor particular species.

Results

Diversity and distribution of alien alpine plants

A total of 175 alien vascular plant species have been recorded in the subalpine and alpine zones above 1500 m (Table 1). Using only those surveys conducted in the last 5 years (Pearson, unpublished data; Duncan 1998; Ingwersen, unpublished data; McDougall and Appleby 2000), 140 alien species are present in the Australian Alps. The total number of species and the range of families and genera have increased over the last 100 years. Only 5 families were recorded in the 1890s. Currently, species representing 41 families and 122 genera are recorded for the area (Table 1). The number of species, genera, and families varies among the states. New South Wales, with the largest contiguous alpine and subalpine area, has the largest number of alien species, with 165. Victoria, with a slightly smaller area, has 117 species. Only 10 species were recorded for the small alpine and subalpine area of the ACT, although this may be an underestimate due to undersampling of the area (Table 1). Around half of the alien plants do not extend into the alpine zones at present.

Many alien plants are associated with specific types of land use in the Australian Alps. Based on their location, alien plants are categorized in this study as grazing weeds, rehabilitation weeds, resort weeds, and roadside and path weeds (Table 2); many species are associated with more than one type of land use. There are 136 species of alien plants recorded along roadsides and paths in 1 national park alone (Mallen-Cooper 1990; Pearson, unpublished data). This type of disturbance could account for just under 80% of alien species found in the Australian Alps (Table 2). The next largest group is the resort weeds, with 58% of species found in and around resort buildings and other infrastructure. Without adequate control, roadside and resort weeds can act as sources of propagules for dispersal into surrounding vegetation (Mallen-Cooper 1990). Just over 20% of alien species already appear to be independent of human disturbance providing suitable habitats, having become naturalized aliens (Table 2).

Origin and biology of alien plants

A large number of the alien taxa represent just 4 families: Poaceae (16.1%), Asteraceae (13.2%), Fabaceae

(8.6%), and Rosaceae (6.9%). Many of the Poaceae species were introduced during the early grazing period (9 species; cf Costin 1954) or in revegetation work (10 species; see Table 2). Some species used in rehabilitation work (*Agrostis capillaris*, *Festuca rubra*, *Phleum pratense*, and *Holcus lanatus*) are now considered a threat to native vegetation (Johnston, unpublished report). The greatest number of alien Poaceae were associated with roadsides (23 species) and resorts (18 species). Some Asteraceae species have been deliberately introduced, sometimes in gardens, from where they have escaped into surrounding native vegetation (*Leucanthemum maximum* and *L. vulgare*; cf McDougall and Appleby 2000). Other Asteraceae species are common pasture weeds in Australia and overseas (*Onopordum acanthium*, *Taraxacum officinale*, *Hypochaeris radicata*, and *Achillea millefolium*; cf Lazarides et al 1997) and are found principally along roadsides and resorts in the Australian Alps (Table 2). Fabaceae are a relatively uncommon family in native alpine flora in Australia and overseas (Costin et al 1979; Körner 1999). However, nonnative species of clover (*Trifolium* spp, *Medicago* spp, and *Melilotus albus*) have colonized the Australian Alps. They were widely introduced by early graziers and used for rehabilitation work in the Australian Alps (Johnston, unpublished report). The ecological role and life history of the low-growing clovers with relatively extensive vegetative spread are very different from the native alpine peas, which are all shrubs (Costin et al 1979). The introduced clovers appear to be successful even at high altitude in the Australian Alps. They are found on the highest peaks, with 6 species having become naturalized weeds (Duncan 1998). Most of the Rosaceae are deciduous berry- and fruit-bearing shrubs and trees, such as *Cotoneaster* and *Rubus* species, found in the subalpine (Sainty et al 1998).

The majority of weeds in the Australian Alps originate in Europe and Asia (see Table 3). Slightly more than half of the listed species are perennials (54%), with 20% annuals and the remainder biennials. Ninety percent of the alien species found were herbs, grasses, or rushes, with only 10% being shrubs or trees. Many of the taller plants such as the broom and willows are receiving attention due to the large impact they have on the visual environment (Mallen-Cooper 1990). However, many of the smaller weeds may also pose an environmental threat in the high-altitude areas. These include species, such as *Achillea millefolium*, *Dactylis glomerata*, and *Hypericum perforatum*, that are highly competitive and problem weeds in other national parks (Sainty et al 1998; Coyne, personal communication, 2000).

The alien species in the Australian Alps appear to have a range of dispersal mechanisms. Assuming that the dispersal mechanism characteristic of each species

elsewhere (Auld and Medd 1992; Bodkin 1992; Harden 1993) also applies in the Australian Alps, it would appear that 8.5% of alien species solely spread vegetatively, 59% spread only by seed, while 32.5% spread both vegetatively and by seed dispersal. Seed may be dispersed by animals, both internally and externally, by water, wind, or a combination of these factors (Bodkin 1992). The method of dispersal is dependent on the type of seed and its characteristics. For example, many of the berry-producing weeds rely on birds for dispersal. For weeds found near water, such as the willows and rushes, water is often the primary mechanism for seed dispersal (Sainty et al 1998).

As would be expected, many alien species in the Australian Alps are considered to be frost and drought resistant (47%). It is interesting to note, however, that 11% of the species found in the Alps are considered to be drought and frost tender in other habitats but are still found in areas subject to freezing temperatures in the Australian Alps. For the frost-tender perennials, survival in the snow country may involve reshooting from underground storage organs (*Solanum tuberosum*, *Alstroemeria aurea*, *Achillea millefolium*, and *Ranunculus repens*; cf Auld and Medd 1992; Bodkin 1992; Harden 1993). Other weeds avoid the cold winters by reestablishing each year from the soil seed bank or seed dispersed from other areas, with half of the alien species annuals. The weeds of the alpine zone, however, are not annual. This is consistent with low numbers of annuals found in the native subalpine and alpine floras of Australia and overseas (Costin et al 1979; Pickering 1993; Körner 1999).

Discussion

Kosciuszko National Park: A history of introductions

One of the first records of weeds in the Australian Alps was the result of a survey of the NSW vegetation by Maiden (1889, 1899). Only one species (*Alchemilla xanthochlora*) was recorded as alien in the alpine area (Maiden 1889, 1899), although its status as introduced is doubtful (Costin et al 1979). *Alchemilla xanthochlora*, *Acetosella vulgaris*, *Hypochoeris radicata*, and *Taraxacum officinale* were recorded in the subalpine area, and *Vulpia bromoides*, *Hordeum murinum*, *Lotus corniculatus*, and *Picris hieracioides* (now known as *Helminthotheca echioides*; *Picris hieracioides* noted by Maiden is possibly the native *Picris angustifolia* subsp. *Merxmulleri*) were recorded in the montane zone (Maiden 1889, 1899). Sheep and cattle grazing were already common in much of the Australian Alps at that time, with thousands of cattle and sheep depastured in the region (Johnston, unpublished report).

By the 1950s, weed diversity had increased. Costin (1954) recorded 6 introduced species in the alpine area (*Acetosella vulgaris*, *Hypochoeris radicata*, *Taraxacum offi-*

TABLE 3 Origins of alien species found in the alpine and subalpine areas of the Australian Alps. Based on information for 143 of the 175 alien species recorded in the Australian Alps (compiled from Auld and Medd (1992), Bodkin (1992), Harden (1993), Lazarides et al. (1997).

Origins	% species
Asia only	3.5
Cosmopolitan	1.4
Europe and Asia	17.5
Europe and Mediterranean	2.8
Europe and North America	2.8
Europe only	38.5
Europe, Africa, Mediterranean	2.1
Europe, Asia and Africa	8.4
Europe, Asia, Africa and North America	2.1
Europe, Asia, North America and Mediterranean	0.7
Mediterranean	2.1
North and South America	9.8
Northern Hemisphere	5.6
Other	2.4

nale, *Poa annua*, *P. pratensis*, and *Cerastium fontanum* subsp. *triviale*). A further 38 species were found in the subalpine area and 25 species in the montane zone of the NSW section of the Australian Alps (Table 4, published on the MRD web site as Johnston FM and Pickering CM 2001: www.mrd-journal.org). As a result of serious soil erosion and related impacts of cattle and sheep grazing and associated burning practices, grazing was banned from most of the Australian Alps by the 1950s, although it still occurs in some alpine areas of Victoria (Good 1992a).

To reduce the impacts of erosion on the Kosciuszko summit area, soil conservation work was undertaken in the 1950s in the alpine and subalpine areas of NSW (Johnston 1995). Much of this rehabilitation made use of exotics including *Trifolium arvense*, *T. dubium*, *T. pratense*, *T. repens*, *T. ambiguum*, *T. glomeratum*, *T. hybridum*, *Agrostis capillaris*, *A. stolonifera*, *Dactylis glomerata*, *Festuca rubra*, *Lolium perenne*, *Phleum pratense*, *Poa annua*, *P. pratensis*, and *Avena* species (Costin and Wimbush 1963; Bryant 1971; Good 1976). Natives have replaced alien grasses in rehabilitation work by conservation organizations in much of the Australian Alps (Parr-Smith and Polley 1998).

The realization of the Snowy Mountain Hydroelectric Scheme (1949–1972) had large and, in some cases, irreversible effects on the topography, hydrology, and ecology of native plant and animal communities (Good 1992a). Human settlement associated with the scheme introduced many exotic garden plants such as *Cytisus scoparius* and *Lupinus incanus*. Large-scale plantings of exotic trees including *Pinus* and *Populus* species also occurred (Good 1992a).

Tourism and recreation have been part of the Australian Alps since the 1860s, when the first ski lodge was built at Kiandra, NSW (Good 1992a; Johnston 1995). In the last 30 years, this industry expanded rapidly (Good 1992a; Buckley et al 2000), with the corresponding alteration in soil, hydrology, and ecology of the region (Cousins 1998; Growcock 1999). Associated with the expansion of tourism was the rapid spread of weeds in the areas around resorts (McDougall and Appleby 2000). Some alien species were planted into gardens, including *Lamiastrum gemeobdolen*, *Aquilegia vulgaris*, *Mentha spicata*, *Iris* spp, *Lupinus* spp, *Dianthus barbatus*, *Leucanthemum maximum*, *L. vulgare*, and *Vinca minor* (McDougall and Appleby 2000). Park management agencies also introduced exotic species for more practical purposes, such as vigorously growing species used to rehabilitate ski slopes after the winter season. The NSW National Parks and Wildlife Service Alpine mix used for soil rehabilitation included the exotic *Agrostis capillaris*, *Dactylis glomerata*, *Festuca rubra*, *Lolium perenne*, *Poa pratensis*, *Trifolium pratense*, and *T. repens*. Today, only 1 alien species, *Festuca rubra*, is still used in NSW by park organizations at higher altitudes (Enders, personal communication, 2000).

Surveys conducted in the early 1980s found 200 alien species in the NSW section of the Australian Alps. Twenty-seven of these were recorded in the alpine area and 70 were recorded in both the alpine and subalpine areas (Thompson and Gray 1981; see Table 4, Johnston FM and Pickering, CM 2001, www.mrd-journal.org). In a study examining the distribution of weeds on roadsides and adjacent natural areas in Kosciuszko National Park, 48 species were found in the alpine area, 81 species in the alpine and subalpine areas, and 215 species in the combined alpine, subalpine, and montane areas (Mallen-Cooper 1990). In a 1997 resampling of the same quadrats in Kosciuszko National Park as examined in 1986, 68 species from 19 families were found in all 3 areas, with 46 in the alpine area and 58 in the subalpine area (Pearson, unpublished data).

The flora records for Kosciuszko National Park differ in scale, timing, and methods. Although these differences may contribute to the variation seen in alien plant diversity among the studies (Table 4, Johnston FM and Pickering CM 2001, www.mrd-journal.org), it appears that total weed diversity has increased since the first survey. Activities that are associated with alien plant diversity and abundance such as the construction of roads, trails, and car parks have increased dramatically, particularly during the last 30 years (Buckley et al 2000).

Tourism, climate change, and alien plants

Establishment and spread of weeds in the Australian Alps are enhanced by disturbance associated with the

construction and operation of tourism facilities such as roads, paths, ski runs, buildings, etc (Buckley et al 2000). Over half of the weeds in the high-altitude areas were found around resorts (McDougall and Appleby 2000; Table 2). All these sites can act as foci for the spread of weeds into adjacent natural areas. With summer tourism on the increase (Good 1992a), there may be growing demand for additional facilities that will contribute to the problem (Usher et al 1988; Hodgkinson and Thompson 1997). Developers and conservation organizations need to make informed decisions about weeds and the impacts of disturbance when considering future developments.

Predicted climate change may also result in an increase in distribution and diversity of alien species in the subalpine and alpine areas of the Australian Alps (Good 1998; Buckley et al 2000; Pickering and Armstrong 2000). Decreasing native and alien plant diversity with increasing altitude is characteristic of many alpine and subalpine areas, including the Australian Alps (Costin et al 1979; Mallen-Cooper 1990; Körner 1999). Where climatic conditions are the major limit on the upward expansion of species, the distribution and abundance of alien plants at a given altitude is likely to increase if snow cover declines and average temperatures increase. Such changes are predicted to occur within the next 70 years in the Australian Alps (Whetton 1998; see also evidence reported by Grabherr et al 1994). Ameliorating climatic conditions could interact with disturbance to the habitat, such as that caused by tourism, to amplify the spread of weeds in the Australian Alps.

Evidence to support this comes from experiments on the germination and establishment of alien seed sown into natural plant communities in an alpine area in the Australian Alps. Species of alien plants currently limited to subalpine areas were able to germinate and grow at higher altitudes, particularly following disturbance; however, they were unable to reproduce due to the severity of climatic conditions (Mallen-Cooper 1990). Therefore, changes in climatic conditions along with disturbance are likely to enhance the establishment and spread of these and possibly other weeds.

Conservation implications

In Australia, native plant diversity and abundance is declining while numbers of introduced species are increasing (Humphries et al 1991). Past and current human activities have contributed to this process in conservation reserves (Humphries et al 1991; Low 1999). The introduction of alien species has negative effects on native vegetation, including loss of genetic variation, reduction in distribution and abundance of native plant and animal species, and modification of the environment, including fire regimes, rates of ero-

sion, predation, and hydrology (Hobbs 1989; Mooney and Drake 1989; Carr et al 1992; Low 1999). Therefore, as part of the aim of national park organizations “to preserve and protect the unique or outstanding scenery or natural features” (National Parks and Wildlife Service Act 1974), control of introduced plants has become a high priority.

Current control methods are having limited success, and those employed elsewhere, such as large-scale physical removal or use of broad-spectrum herbicides, are often inappropriate for high-value conservation areas (Anonymous 1996; Sanecki 1999). Given the difficulties in controlling invasions, such as the low success of biological control, the expense of herbicides, and the potential deleterious effects of different control measures, informed management strategies are required.

With limited ecological knowledge of many alien species in high-altitude areas, predicting their effects on native flora largely remains guesswork. The success of a given alien species in the alpine and subalpine environment will depend on its characteristics, its ability to survive in the snow country, and any changes to its

habitat, including disturbance regimes. Therefore, research into the ecology of critical weed species in the Australian Alps should be a major priority for conservation organizations.

The Australian Alps national parks are currently developing a list of priority weed species for research based on the plants’ threat status, distribution in the Australian Alps, impact, and potential for management control. The species considered to constitute major threats are *Cytisus scoparius* and the 3 species of willows, *Salix fragilis*, *S. cinerea*, and *S. nigra*. A further 5 species are considered to be a moderate threat (*Rubus discolor*, *Achillea millefolium*, *Nassella trichotoma*, *Hypericum perforatum*, and *Rosa rubiginosa*; Coyne, personal communication, 2000).

The threat of further plant invasions and the continued spread of those species already present in the Australian Alps appear inevitable, particularly with increased disturbance associated with tourism. Environmental weed management will continue to be difficult and require long-term commitment from all those involved in preserving the Australian Alps (Goodall and Wade 1998; Sun and Walsh 1998).

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