The ecology and invasion history of hawkweeds (*Hieracium* species) in Australia

N.S.G. Williams and **K.D. Holland**
Australian Research Centre for Urban Ecology, Royal Botanic Gardens Melbourne, c/o School of Botany, The University of Melbourne, Victoria 3010, Australia. Email: nsw@unimelb.edu.au

Abstract
Hawkweeds (*Hieracium* spp.) are perennial herbs that are serious environmental and agricultural weeds in many temperate and subalpine areas of the world. In Australia, they are recognized as a significant threat and their importation is now prohibited. However, four *Hieracium* species are already naturalized. It is believed that populations of *H. pilosella* may no longer persist, while efforts to control *H. aurantiacum*, *H. praealtum* and *H. murorum* are continuing. This paper reviews the invasion history of known infestations in Australia, as well as the general biology and ecology of invasive hawkweeds.

Introduction
Hawkweeds are perennial herbs of the large northern hemisphere genus *Hieracium* (Asteraceae). They show enormous phenotypic variability, resulting in many subspecies, varieties and forms (Mráz and Szelag 2004, Zidorn *et al.* 2002). Consequently, the taxonomy of the group and number of species is debated (Coskunçelebi 2003). This is thought to be due to frequent hybridization events during the evolution of the group (Mráz and Szelag 2005). Over 9000 *Hieracium* species have been proposed or recognized (Strother 1997), some of which are serious environmental and agricultural weeds.

Once established, some hawkweeds spread rapidly by stolons and rhizomes, forming dense mats of plants that outcompete other species, lowering biodiversity and reducing forage value of pastures (Rinella and Shelley 2002). They are of concern in many countries due to their invasiveness and impact. In New Zealand, *Hieracium* spp. dominate the vegetation on more than 500 000 ha of the South Island, threatening viability of the pastoral industry and conservation values of native tussock grasslands (Duncan *et al.* 1997). At least ten hawkweed species are naturalized in New Zealand (Webb *et al.* 1988) after arriving in the mid-1800s in contaminated grass seed and being planted by acclimatization societies (Trewick *et al.* 2004). Eleven species are naturalized in the United States (Rinella and Shelley 2002). Hawkweeds have also invaded Japan, Canada and Patagonia (Svavarsdottir *et al.* 1999, Wilson and Callihan 1999).

Four *Hieracium* spp. are naturalized in Australia, and pose a substantial threat to agriculture and the environment. Quarantine regulations now prohibit importation of hawkweeds into Australia (National Heritage Trust 2003, NSW Department of Primary Industries 2005) and they are listed as noxious weeds in Victoria, New South Wales and Tasmania (National Heritage Trust 2003). Despite this, they are still sometimes sold to gardeners (Blood 2004, Morgan 2000) and may be found in wildflower seed mixes (National Heritage Trust 2003).

Climatic modelling suggests hawkweeds could spread across large areas of the high rainfall regions of mainland south-eastern Australia and Tasmania. For example, approximately 270 000 km^2 of land is considered potentially at risk from *H. aurantiacum* (Cunningham *et al.* 2003). Potential production losses in grazing areas are conservatively estimated at $74 million (Brinkley and Bomford 2002). However, *Hieracium* spp. have also been identified as 'sleeper weeds' (Brinkley and Bomford 2002). Sleeper weeds pose a serious threat but are currently in the early stages of establishment and have a limited distribution. Early eradication may therefore be highly cost effective (Brinkley and Bomford 2002).

This paper reviews the biology and ecology of invasive *Hieracium* spp. and documents the invasion history of known naturalized species in Australia. By doing so, we hope to raise awareness of invasive hawkweeds and provide weed managers with information that may assist control and eradication of infestations. Records of *Hieracium* spp. were obtained from herbaria in Melbourne, Sydney, Canberra, Hobart, Perth and Adelaide. Further data and detailed invasion histories of *Hieracium* spp. in Australia were obtained through discussions with weed experts and land managers in state government departments and agencies around Australia. Information on the ecology of invasive *Hieracium* spp. was obtained through searches of the scientific literature, internet resources, and discussion with Australian and international experts.

Hieracium species in Australia
Four *Hieracium* spp. have been found naturalized in Australia: *H aurantiacum*, *H. praealtum*, *H. pilosella* and *H. murorum*. The morphology of each species is briefly described below and the available information on their invasion history in Australia provided. Detailed species descriptions can be found in Webb *et al.* (1988).

The genus *Hieracium* is commonly split into two groups: the stoloniferous species (i.e., possessing 'runners'), known as the *Pilosella* group, and a larger group of non-stoloniferous species (*Hieracium sensu stricto*), which includes *H. murorum* (Makepeace 1985a, Webb *et al.* 1988). *Pilosella* contains approximately seventy species, and includes most of the hawkweeds that are considered weeds worldwide (Makepeace 1985a), including *H. aurantiacum*, *H. pilosella* and *H. praealtum* (Webb *et al.* 1988).

Hieracium aurantiacum L. (orange hawkweed)
Hieracium aurantiacum has a basal rosette of leaves and a single stem 15–40 cm tall. Plants produce bright, red-orange flowerheads in clusters of 5–15 heads at the top of the stem (Webb *et al.* 1988). In Australia, *H. aurantiacum* flowers from January to March, making plants most conspicuous at this time (National Heritage Trust 2003). The species is also known as *Pilosella aurantiaca* (L.) F.W.Schultz & Sch.Bip. (Blood 2001, Webb *et al.* 1988), and is native to mountains of northern and central Europe (Morgan 2000, Webb *et al.* 1988) where it occurs primarily in meadows and hillsides (Wilson and Callihan 1999). In Australia, *H. aurantiacum* subsp. *carpathicola* Nägeli & Peter has been found naturalized in Tasmania, Victoria and New South Wales, and has been collected from a garden in Perth.

Tasmania
The largest populations of *H. aurantiacum* in Australia occur in Tasmania, scattered throughout the Central Highlands and Southern Midlands (Figure 1). The species is thought to have initially escaped from gardens in towns associated with hydroelectricity schemes (Andrew Crane personal communication). The largest infestation is in the Hobart suburb Fern Tree, on the foothills of Mt. Wellington, where it established before 1963 (National Heritage Trust 2003). Mapping shows the population expanded down-slope due to seed dispersal via wind and watercourses, and is now spread over 500 ha. It is thought that slashing roadsides also spreads the species, including to one site at Snug, 20 km from the nearest known population (National Heritage Trust 2003) and other populations at Mt. Arrowsmith and Derwent Bridge that are thought to have come from nearby road maintenance depots. Recently, concern has been expressed that seed and plant parts may be dispersed by mountain bike riding, which is a popular recreation activity on Mt. Wellington

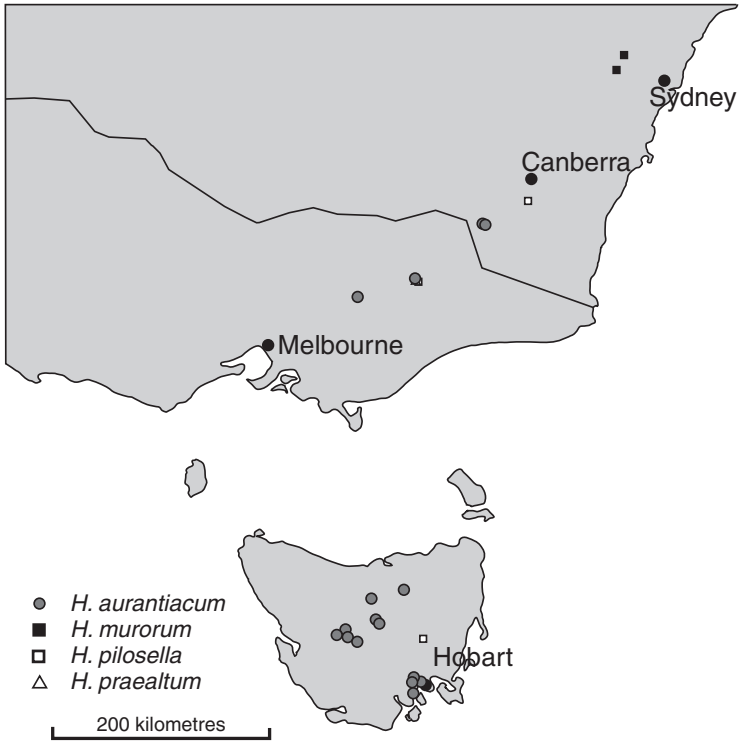

Figure 1. Sites of known naturalizations of *Hieracium* species in Australia.

(Andrew Crane personal communication). *Hieracium aurantiacum* now occurs on roadsides, public open spaces, walking tracks and in private gardens (National Heritage Trust 2003). It generally shows a preference for disturbed areas but may also occur in open woodland (National Heritage Trust 2003). Minor infestations may provide stepping stones for spread, even when surrounding vegetation is resistant to establishment.

New South Wales

In New South Wales, *H. aurantiacum* was sold by nurseries on the South Coast and Southern Highlands (Burton and Dellow 2005). It was first recorded as naturalized in the Toolong Range, Kosciusko National Park in December 2003 (Burton and Dellow 2005, McDougall 2004). This population was found growing in *Eucalyptus pauciflora* Sieber ex Spreng woodland with a grassy understorey (McDougall 2004). Many plants were still present a year after spraying, in December 2004 (Keith McDougall personal communication). More recently, in late 2005, a well-established population of *H. aurantiacum* was found near Ogilvies Creek, 7 km to the south-west, at approximately 1450 m above sea level. It is thought that this population was the source of previously discovered plants. The area is a former Snowy Hydroelectricity Scheme town site, and includes the remains of plantings such as fruit trees. *Hieracium aurantiacum* may have been present here for 40 years prior to its discovery, but is thought to have spread after the January 2003 fires. It established in an area up to 500 m long, and formed a monoculture in some areas (David Lawrence personal communication). Thus far there has only been a single control attempt. Dense vegetation and non-flowering plants means that some individuals were probably missed (Keith McDougall personal communication). Eradication attempts are continuing at these locations, including monitoring and survey beyond the original infestations for further populations (Keith McDougall personal communication).

Victoria

Hieracium aurantiacum was first recorded as naturalized in Victoria in January 1999. It was found 1600 m above sea level in disturbed roadside and ski-field vegetation, and *E. pauciflora* heathy woodland, in the Falls Creek Village during a Melbourne University Field Botany class (Carr *et al.* 2004, Morgan 2000). It is thought to have been growing as a garden plant in Falls Creek Village since at least 1985, from seed deliberately introduced from Europe (Jill Dawson personal communication).

At least ten populations were present in 1999, each of more than 500 individuals, some more than 1 km from the presumed source (Morgan 2000). The majority of these populations were located in, or near, Falls Creek Village (Morgan 2000) but one population was discovered inside the Alpine National Park, at Heathy Spur, two kilometres from the village (Carr *et al.* 2004). This population was located close to a hiking track, and seed may have been transported by a bushwalker (Rudi Pleschutschnig personal communication).

Since 1999, *H. aurantiacum* has spread south to south-east from Falls Creek due to prevailing summer winds. Field surveys conducted in January and February 2004 showed *H. aurantiacum* present in Falls Creek Village and on some ski slopes to the south (Carr *et al.* 2004). Control efforts started around 2000, involving surveying, mapping and spraying populations by resort management and Parks Victoria, and have been widely supported by the local community. Many populations in the Falls Creek area are believed to have been eliminated, although the species still occurs within the Alpine Resort and adjacent parts of the Alpine National Park near Rocky Valley Dam. *Hieracium aurantiacum* has not been found at Heathy Spur since the 1999 record (Carr *et al.* 2004). However, isolated populations have been found in the Basalt Hill area (Carr *et al.* 2004, N. Williams and Lynise Wearne personal observations).

In summer 2002/2003, a population of *H. aurantiacum* was discovered by bushwalkers in a remote area of the Mt Buller ski resort along a narrow black ski run. Although bushwalkers were initially suspected as the source of the infestation, it is now thought that seed was brought to Mt Buller on ski machinery transported from Falls Creek. After prompt seed-head removal and spraying with herbicide, only a few plants were found on the site of the initial infestation in 2004/2005. However, two additional plants, that were also subsequently destroyed, were found along a track leading from the ski run. In summer 2005/2006, surveys revealed the original infestation had spread onto a batter and downslope into native vegetation, predominantly *E. pauciflora* with a reasonably dense *Podolobium alpestre* Crisp & P.H.Weston understorey and scattered boulderfield with *Podocarpus lawrencei* Hook.f. (Louise Perrin personal communication). Control efforts are continuing.

Hieracium aurantiacum has also been recorded in a garden bed containing alpine and arid plants at the Ballarat Botanic Gardens. The size of this infestation was about 15 m^2 and consisted of 20–50 plants. It was originally planted in the Gardens and ongoing eradication efforts have reduced the population. The species has also been found for sale at nurseries in South Gippsland and western Victoria, and growing in private gardens in West Gippsland (Michael Hansford and Randall Robinson personal communication).

Hieracium praealtum Vill. ex Gochnat (King devil hawkweed)

Hieracium praealtum can reach a height of 45 cm (Webb *et al.* 1988) but grows smaller

on poor or shallow soils, or in exposed areas (Blood 2004). The majority of leaves occur in a basal rosette (Webb *et al.* 1988). The species has yellow flowerheads in clusters of 3–35 at the top of the stem (Webb *et al.* 1988). Flowering begins in November in New Zealand (Makepeace 1985a). *Hieracium praealtum* is native to Europe and Asia, and occurs as a weed in New Zealand, Canada and the United States (Blood 2004, Carr *et al.* 2004).

Victoria

In December 2003, *Hieracium praealtum* subsp. *bauhinii* (Besser) Petunn. was found on the edge of the Alpine National Park, adjacent to Falls Creek Resort north of Rocky Valley Dam, at 1600 m above sea level (Blood 2004, Carr *et al.* 2004). The approximately 3 ha infestation of over 200 000 plants was the first record of *H. praealtum* in Australia (Blood 2004, Carr *et al.* 2004). The invasion-source is unknown, but seeds may have been introduced on contaminated equipment imported from New Zealand to construct a nearby ski lift around 2000. Other possible vectors include bushwalkers, campers or overseas visitors (Carr *et al.* 2004). The infested area consists of a partially rehabilitated quarry with vehicle tracks and a picnic area. Control occurred quickly after its identification and over four kilograms of flower and seed-heads were picked before the site was sprayed twice with herbicide (Rudi Pleschutschnig personal communication). The site has been quarantined, interpretation signs installed, is monitored, and regenerating *Hieracium* plants are controlled on a regular basis (Craig Hore personal communication). Further spread of the species was narrowly avoided after soil from the site contaminated with *Hieracium* seed was moved six kilometres east to Langfords Gap, with the intention of using it along aqueducts in the area. The contaminated soil was subsequently quarantined and germinating *Hieracium* plants sprayed with herbicide (Charlie Pascoe personal communication).

During field surveys in January/February 2004, a satellite infestation of *H. praealtum* was found growing in open heathland at Ruined Castle within the Falls Creek Alpine Resort (Carr *et al.* 2004). Further satellite infestations were found in December 2005 close to the track to Wallaces Hut, approximately 2700 m from the original infestation, and on the side of the Bogong High Plains Road near Basalt Hill (Craig Hore personal communication). Given the large source population that produced seeds for at least four years, and the superficial similarity of *H. praealtum* to common exotic species, it seems likely that further populations of *H. praealtum* remain undetected around Falls Creek and adjacent parts of the Bogong High Plains.

Hieracium pilosella L. (mouse-ear hawkweed)

Hieracium pilosella produces a single, pale yellow flowerhead at the top of a 2–15 cm vertical stem. The basal rosette of dull green leaves is white underneath due to dense, stellate hairs (Espie 2001, Webb *et al.* 1988). The species is native to Europe and Asia, and naturalized in New Zealand, Canada, and the United States (US Department of Agriculture 1994). *Hieracium pilosella* has the greatest abundance and widest distribution of the *Hieracium* spp. present in New Zealand (Espie 2001, Svavarsdottir *et al.* 1999). It occurs along the eastern seaboard and in the Great Lakes and Pacific Northwest areas of the United States (NatureServe 2006).

Tasmania

A small population of *H. pilosella* L. subsp. *nigrescens* (Fr.) Nägeli & Peter was discovered in 2001 during a routine botanical survey for proposed road works on the Midlands Highway in southern Tasmania. The infestation extended over 50 m^2 in three patches along a roadside fenceline and a short distance into the adjacent paddock, and had a high density, varying from 40% to 80% cover (Rudman and Goninon 2002). The origin and age of the infestation is unknown. Due to rapid identification and notification, an eradication program was developed and integrated with the road works program. It involved removing the top 15 cm of soil from infested areas and a substantial buffer area, and burying it beneath the roadworks. Subsequent monitoring of the site has not detected any regeneration (Rudman and Goninon 2002).

New South Wales

Hieracium pilosella has been sold by nurseries on the South Coast and Southern Highlands of New South Wales (Burton and Dellow 2005) suggesting that garden and naturalized populations may be present in the region. There is also a specimen collected in 1992 from Nursery Swamp in Namadgi National Park in the Canberra Herbarium. Recent searches of the area have failed to find any existing populations (Trish MacDonald personal communication).

Hieracium murorum L. (wall hawkweed)

Hieracium murorum grows 20–50 cm tall, with the vertical stem supporting 5–15 bright, yellow flowerheads. The original record of the species in Australia was discovered flowering in November (Hosking *et al.* 2003). Leaves are predominantly basal and dark green in colour (Webb *et al.* 1988). Also known as golden lungwort (Espie 2001), *H. murorum* is native to western Asia, the Caucasus and Europe (Tutin *et al.* 1976) and is naturalized in the USA, Canada and New Zealand (NatureServe 2006, Webb *et al.* 1988).

New South Wales

In Australia, *H. murorum* was initially found at Katoomba, New South Wales covering less than one hectare. This population consisted of approximately 1000 plants when it was discovered in 1998 (Hosking *et al.* 2003). Another population was subsequently found at Mt. Irvine and consisted of over 100 plants growing in lawns and a garden around a car park (Hosking *et al.* 2003). This population is now limited, with only two individuals found in 2006 (Chris Graves personal communication). Control of these populations is ongoing. *Hieracium murorum* has not been recorded as naturalized in any other Australian states (Hosking *et al.* 2003).

The ecology of *Hieracium* species

There is a lack of detailed knowledge about the ecology of *Hieracium* spp. in Australia. General information sourced predominantly from international studies and focusing on species from the *Pilosella* group is reviewed below. Consequently, ecological responses may differ under Australian conditions.

Reproductive biology

Hieracium spp. show variation in reproductive strategies, both within and between species (Morgan-Richards *et al.* 2004). Among species in the *Pilosella* group, plants spread vegetatively and via movement of seed (Makepeace 1985a, Webb *et al.* 1988). Vegetative spread occurs via stolons and rhizomes. This strategy leads to dense populations expanding clonally, while seeds allow medium- and long-distance dispersal.

Most members of the *Pilosella* group are facultative apomicts (Bicknell and Borst 1994, Bicknell *et al.* 2003) meaning that they can produce seeds without fertilization (Koltunow and Grossniklaus 2003). Facultative apomicts can take advantage of sexual reproduction, producing genetically diverse offspring, but can also produce seed asexually, allowing for long-distance dispersal in the absence of pollen from conspecifics.

Dispersal, establishment and growth

Long-distance dispersal in *Hieracium* is primarily by wind dissemination of small seeds. Stergios (1976), however, found that the majority of *H. aurantiacum* seeds were deposited within 2 m of the source patch. This suggests that long-distance wind dispersal may be a rare event for this species. *Hieracium* spp. can also be dispersed by animals, water and in mud. The seeds have minute barbs along their ribs that enable them to attach to hair, fur,

clothing and vehicles (National Heritage Trust 2003). Road maintenance and ski equipment have also been implicated in dispersal of seeds and plant fragments (National Heritage Trust 2003). Dispersal modelling is one promising predictive tool that could be more widely applied (Williams *et al.* 2006).

Seeds are normally dispersed within days of maturation (Makepeace 1985a) and most can germinate immediately upon release (Johnson and Thomas 1978, Makepeace 1985b, Stergios 1976, Thomas and Dale 1975). However, germination of late maturing seed is enhanced by cold treatment (Stergios 1976) suggesting some seed is innately dormant (Thomas and Dale 1975) and may remain viable in the soil for up to seven years (Panebianco and Willemsen 1976). Mass germination of *Hieracium* spp. is triggered by rainfall (Johnson and Thomas 1978, Makepeace 1985b). Seedlings have a low probability of survival and are highly sensitive to drought stress (Johnson and Thomas 1978, Makepeace 1985b).

Once established, *Hieracium* spp of the *Pilosella* group can rapidly increase the area they occupy via rhizomes and stolons (Espie 2001, Rinella and Shely 2002). However, spread by this means is influenced by biotic barriers present in the invaded community, such as competition from established plants (Rose and Frampton 1999). Plants generally send out between three and eight stolons early in the growing season, while at the same time producing inflorescences (Makepeace 1985a, Stergios 1976, Wilson and Callihan 1999). Daughter plants form at stolon tips (Makepeace 1985a, Thomas and Dale 1974) but can also form from adventitious root buds in some species (Wilson *et al.* 1999). Vigorous stolon growth can quickly expand colonies forming dense mats of up to 3800 plants per square metre (Thomas and Dale 1974, Wilson and Callihan 1999). The vegetation dynamics of *Hieracium* colonies has been studied in New Zealand, USA and Canada. Plants on the periphery of colonies produce more stolons, flowerheads and seeds than those in the interior which can die off in dry conditions (Makepeace 1985a, Stergios 1976, Thomas and Dale 1974, 1975). This suggests that density-dependent processes are important in regulating hawkweed populations (Wilson and Callihan 1999).

Conditions favourable to Hieracium invasion

The probability that a site will be invaded is a function of suitability for *Hieracium* establishment, current environment, past management, and size of the *Hieracium* propagule rain (Duncan *et al.* 1997). The life history of individual *Hieracium* spp., which have varying colonizing ability related to drought tolerance and competitive ability, is also considered important (Makepeace 1985b). Areas of disturbance in a suitable environment are likely to be sites of initial invasion. These allow production of an increasing number of propagules that invade less favourable adjacent areas (Duncan *et al.* 1997). Although the likelihood of an individual *Hieracium* plant establishing and surviving is low, the large number of seeds produced by established plants makes finding new populations a management priority. For example, *H. praealtum* and *H. pilosella* patches 10 cm^2 in area can produce up to 2700 and 1300 seeds per year respectively (Makepeace 1985a). Consequently, identifying sites in the vicinity of known populations with conditions suitable for *Hieracium* establishment is important.

A number of studies in New Zealand have found that soil moisture is an important predictor of *Hieracium* invasion. Rose *et al.* (1998) found that *H. pilosella* cover tended to peak on sites with intermediate soil moisture. Soil moisture was the only variable that significantly predicted presence of *H. praealtum*, which tended to establish on sites with a higher moisture index (Svavarsdottir *et al.* 1999). This finding was repeated by Duncan *et al.* (1997), who, after taking into account elevation, found that the cover of *Hieracium* species was lower at more xeric sites and on soils with lower moisture holding capacity.

Although not essential for *Hieracium* invasion (Johnstone *et al.* 1999), evidence suggests that *Hieracium* spp. are more likely to establish in areas that have been disturbed (Rose *et al.* 1998, Treskonova 1991). Experiments have found that soil disturbance is essential for establishment of *H. pilosella* (Jesson *et al.* 2000) and that *H. praealtum* germinates most readily on bare soil (Johnson *et al.* 1978, Makepeace 1985b). Sites colonized by *H. pilosella* in eastern Otago, New Zealand tended to be degraded, with a higher percent cover of bare ground and a lower cover of grass tussocks (Johnstone *et al.* 1999). Rabbit activity was a significant predictor of *Hieracium* cover in Canterbury (Duncan *et al.* 1997). Pastoral disturbances, such as burning and grazing, are also thought to have increased vulnerability of New Zealand tussock grasslands to *Hieracium* invasion (Rose and Frampton 1999).

In Europe, hawkweeds are found in pastures, mountain meadows and disturbed areas (Wilson and Callihan 1999). They tend to invade similar environments in New Zealand and North America, with montane and subalpine pasture and rangelands particularly susceptible (Rose and Frampton 1999, Wilson and Callihan 1999). Invaded New Zealand vegetation communities include wasteland, scrub, tall- and short-tussock grasslands, roadsides, lawns, gardens and pastures (Webb *et al.* 1988). In Australia, short-tussock grasslands are thought to be at the greatest risk of invasion (National Heritage Trust 2003) because their structure and composition pose few effective barriers to seedling establishment (Makepeace 1985b, Rose and Frampton 1999). However, *Hieracium* spp. have also been found growing in *E. pauciflora* woodlands and alpine heathlands. Areas of vigorously growing grass and pasture are more resistant to *Hieracium* establishment, and fertilizing and oversowing with pasture species are advocated as effective control techniques in agricultural areas of New Zealand (Espie 2001, Rose and Frampton 1999, Scott 1993).

Conclusion

Four *Hieracium* spp. are naturalized in Australia. Once detected, prompt treatment has reduced most known populations and limited spread of these hawkweeds on mainland Australia. However, it is likely that undetected populations exist. Populations of *H. aurantiacum* in Victoria and New South Wales, *H. praealtum* in Victoria and *H. murorum* in New South Wales were able to set seed and disperse for a number of years prior to their detection and may have established in areas surrounding known populations. In addition, *Hieracium* spp. were sold by nurseries in at least two states providing additional but unknown sources of infestation. Systematic searches in the vicinity of known *Hieracium* infestations, that are informed by the species biology, ecology and invasion history at other sites, will help to prevent their spread in Australia. International liaison and co-ordinated programs including control, monitoring and education will also be important.

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