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Ecology of Old World hawkweeds, *Hieracium* species (Asteraceae), in their homeland and considerations on their potential weediness

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Abstract. *Hieracium* is a large and complex genus comprising hundreds, or a few thousands, of species, depending on the species concept. They can be sexual or apomictic. When *Hieracium* species (Asteraceae, Cichorioideae) (hawkweeds) are adventive, they may become weeds in rangelands and pastures, where they can successfully compete with native tussock grasses, as has happened in New Zealand and they can be a pernicious weed problem. *Hieracium caespitosum, H. pilosella* and *H. aurantiacum* are among the main problem species in the United States of America and New Zealand. Their success over other species is also due to their great genetic plasticity. Allelopathy, geobotany, biology, spread and the potential weed problems are discussed. Because of their hardiness and mode of spread, rapidly invading new areas and dispersing over long distances, *Hieracium* species are difficult to control. The use of herbicides is generally not effective and is not feasible for economic and environmental reasons, especially on non-agricultural land such as within national parks. Herbicides also have a negative impact on desirable pasture species. The possibility of controlling these weeds biologically is under study.

Introduction

The transportation activities of modern society have allowed the movement of plant seeds between distant regions of the world. Such floral interchange has broken the natural barriers that separated geographically-isolated parts of the world for millions of years. Plants have been given new environments and their areas of distribution have changed. The increasing travel and trade among and within countries is leading to an increased rate of establishment of new weeds. About 50% of the North American weeds have been introduced accidentally or intentionally from Europe, South America, Asia and Australia (Reed and Hughes 1970). In the United States of America many of them have become noxious weeds of national or state importance.

Exotic species of *Hieracium* (Asteraceae, Cichorioideae) were introduced accidentally or intentionally into New Zealand, Japan, Patagonia and North America where they have become naturalized and weedy. *Hieracium caespitosum* Dumortier, *H. pilosella* L. and *H. aurantiacum* L. are among the main problem species in the USA and New Zealand (Callihan *et al.* 1989; Scott *et al.* 1990; Roché 1992). In North America they have the potential to become serious weed problems in pastures and native grasslands.

The present contribution is part of a developing effort to study the possibility of controlling these plants biologically. In Europe, studies are in progress at the European Biological Control Laboratory (USDA - ARS), Montpellier, France and at the European Station of the International Institute of Biological Control, Delémont, Switzerland. The geobotany, chorology, phytosociology and biological characteristics of *Hieracium* species and the associated potential weed problems are discussed here. Understanding these characteristics will help to determine the best methods of control and, in the case of biological control, will allow selection of the best natural enemies.

Botanical features and distribution of *Hieracium* species

The genus *Hieracium* L. is in the subtribe Hieraciinae, tribe Lactuceae, of the subfamily Cichorioideae of the Asteraceae, order Campanulales. It has four subgenera: *Hieracium*, *Pilosella* (Hill) S. F. Gray, *Stenotheca* Monn. and *Mandonia* Sch. Pip. The genus includes perennial herbs, usually characterized by a basal rosette of generally elliptical leaves, entire to deeply dentate, rarely lobed and petiolate to sessile, depending on the species. The leaves and stems are often very hairy. The roots are deep and many species have epigeous or ipogeous stolons, especially in the subgenus *Pilosella*. The stems, single to numerous, 2 - 80 cm tall, bear androgynous, ligulated florets, usually yellow, but also reddish orange, green or white, singly or in racemose, paniculate, or corymbose clusters. The achenes are more or less strongly ribbed, never beaked, with a pappus of one or two rows of brownish or whitish hairs. The plant tissues have compound, anastomosed, laticifer tubules and are characterized by a milky sap.

The genus *Hieracium* consists of several subgenera and is exceptionally polymorphic with many species and subspecies, of which a large proportion have resulted from hybridization and these perpetuate by apogamy. Zahn (1921-1923) reported 753 species, but the genus contains many, often difficult to determine, forms. According to some authors it consists of about 1000 species (Zomlefer 1994), or even many thousands, depending on the species concept (Bremer 1994). In fact, in addition to well-defined species whose typical characters are more stable, it comprises many other intermediate taxa and hybrids that are difficult to interpret (Zangheri 1976). The taxonomy of this genus is the most complex of the European flora (Cappelletti 1976), involving interspecific hybridization, polyploidy and apomixis, including agamospermy. This leads to the formation of microspecies and various ambiguous taxa (Johnson 1977).

The plants develop peculiar characters at different locations and following apomixis the identical plants generated as a clone at a given locality could be considered a separate species. In the case of the female gametophyte of *Hieracium* species, apomixis takes place via somatic apospory, in which cells belonging to the vegetative line substitute the impotent cells of the germinal line, producing an aposporic diploid gametophyte. Gonial apospory produces the male gametophyte, as described for *H. boreale* Fries by Cappelletti (1976). Due to apomixis, a multitude of more or less ancient hybrids has been preserved. This is why Zahn (1921 - 1923) and subsequently other specialists of this genus distinguished two taxonomic levels: principal species and intermediate species, with a combination of the morphological characters of two principal species.

Some of the best known species of hawkweeds are as follows. (i) *Hieracium aurantiacum* (orange hawkweed, or red devil, devil's paintbrush, devil's weed), which is a rare species in the European mountains, with clusters of orange flowers in flowerheads and epigeous or ipogeous stolons. Its karyotype is 2n = 18, 27, 36, 45, 54, 63, 72 (Tutin *et al.* 1976). (ii) *Hieracium florentinum* Allioni (king-devil, or yellow hawkweed, yellow paintbrush), with 2n = 18, 36, 45 (Zangheri 1976), which has yellow flowers, with flowerheads in corymbs. This species does not have stolons. (iii) *Hieracium caespitosum* (= *H pratense* Tausch = *H. collinum* Gochnat) (meadow hawkweed, or yellow hawkweed, yellow devil, king-devil) which has yellow flowers in flowerheads in clusters. It has epigeous or ipogeous stolons and 2n = 18, 27, 36, 45 (Zangheri 1976). (iv) *Hieracium pilosella* (= *Pilosella officinarum* Sch. Pip.) (mouse-ear hawkweed), with stolons and yellow flowers in solitary flowerheads, having 2n = 18, 27, 36, 39, 45, 54, 63 (Zangheri 1976). (v) *Hieracium praealtum* Villars *ex* Gochnat subsp. *praealtum* (tall king-devil hawkweed), having 2n = 36, 45 (Tutin *et al.* 1976) which is a vigorous plant with yellow flowers in flowerheads in clusters. Stolons are very short or absent. (vi) *Hieracium floribundum* Wimmer and Grabowski (yellow-devil hawkweed, king-devil), with 2n = 27 (Tutin *et al.* 1976), which has yellow flowers in flowerheads in corymbs. In this species stolons are very short or absent.

The Lactuceae, comprising 98 genera and more than 1550 species (excluding the microspecies of *Hieracium* and *Taraxacum*), are predominantly plants of the Northern Hemisphere, with concentrations of genera in the Mediterranean area, Central Asia and southwestern North America (Bremer 1994). It is difficult to determine if the centre of origin of the Lactuceae is the Mediterranean area or Central Asia (Bremer 1994). The subtribe Hieraciinae is mainly of the Old World. It comprises seven genera, occurring for the most part in Eurasia, but also in Africa and North and South America (Bremer 1994). However, the genus *Hieracium* occurs in temperate regions of the world, except Australasia (Heywood 1978). Most species occur in Europe, with a few in western and northern Asia, Japan, northern Africa (especially the mountains), North America and in the Andes of South America (Fiori 1974). The subgenera *Hieracium* and *Pilosella* occur in Eurasia. The subgenus *Pilosella*, which contains stoloniferous species of European origin, includes most of the species which tend to become weeds in other parts of the world. The species within the subgenus *Hieracium* do not have stolons. The habitats for *Hieracium* species include hill and mountain pastures, meadows, stony places, roadsides and humid or dry sites, from sea level up to 3000 m (Fiori 1974).

Ecology of *Hieracium* species

Climate and phenology

Hieracium species belong to the biological form of hemicryptophytes (Raunkiaer 1934), which are adapted to both temperate and temperate-cold climates. They are arctic-alpine species, cold-hardy plants which originated from the quaternary glaciations and at present have a relict distribution. The huge climatic perturbations of the Quaternary had a strong impact on the flora, which was drastically impoverished. The plants were forced to move southwards, or isolated on nunataks (Cappelletti 1976), where speciation occurred. The new species were particularly well adapted to the cold climate and successfully outcompeted their ancestors, partially or completely, at the end of the glaciations.

The main problems that these plant were able to overcome were the lack of water and the short growing-season. This is the reason why the plants in this genus are perennials, sturdy, able to adapt to various environmental conditions and also resistant to drought (Duquénois *et al.* 1956; Hopkins 1978; Makepeace 1985). Within three months they complete sexual reproduction and store enough energy to survive adverse climatic conditions until the following summer.

The scarcity of water available to the plants arises from a complex of factors, chiefly from the low rainfall, thin soil, strong winds that increase evapotranspiration, evaporation and the freezing of the soil during the winter, which prevents water utilization by the roots. Their deep roots firmly fix the plants to the ground and allow them to resist strong winds. Some species are adapted to degraded soils, impoverished and acidified by intense logging, grazing, etc., such as *Hieracium murorum* L. and *Hieracium racemosus* Waldstein-Kitaibel (Ferrari 1980).

Many species, such as *H. caespitosum*, *H. pilosella* and *H. aurantiacum*, reproduce rapidly, vegetatively. From the basal rosette, they produce stolons with roots at each node and, if broken, or if the mother plant dies, each of these is able to generate a new plant. In Europe, *H. pilosella* was observed to be a pioneer plant on abandoned land, before invasion by graminaceous plants (Guyot 1951), due to its seeds (Makepeace 1985). Once established, they soon cover large areas (Tonzig and Marrè 1976), principally by vegetative reproduction (Makepeace 1985). *Hieracium* species bloom abundantly during the summer and fall. The nictinastic movements of the flowers of *H. pilosella* were observed by Linnaeus, who included this species, which opens at 06h00, in his *Calendarium Florae* (Linnaeus 1757).

Morphological adaptations

The dense down-covering of most *Hieracium* species plays a defensive role in protecting the plants from excessive evapotranspiration, ultraviolet radiation and sudden changes of temperature. These protective trichomes, typically dead, are full of air. This gives them a sericeous brilliance and a white colour and they strongly reflect light. The protective trichomes also maintain relatively immobile air near the plant, which prevents sudden changes of temperature (Cappelletti 1975). In this way they effectively protect the epidermis against solar radiation and reduce evapotranspiration. The latter effect is enhanced by the fact that the dense interlacement of the trichomes, especially abundant on the lower side of *Hieracium* species leaves, restrains a layer of stagnant air which, in contact with the epidermis, fills with humidity and reduces the water vapour released from the stoma (Cappelletti 1975; Tonzig 1968). The procumbent posture of most species in this genus is a defensive adaptation to cold climates and wind. The acaulescent plants, with their rosettes of leaves close to the ground, collect heat from the ground and resist harsh conditions (Tonzig and Marrè 1976). Also, at increasing elevations, the same species has a modified phenotype, usually being dwarfish, to resist adverse meteorological conditions.

Allelopathy

The antagonism of these plants to other species originates from competition for water, nutrients, light and space, from the secretion of phytotoxic substances by the roots and from phytotoxic agents washed into the soil from the leaves. *Hieracium pilosella* contains umbelliferone (7-hydroxycumarin), which is one of the strongest inhibitors of the germination of the seeds of other plants. Extremely low concentrations (1/8000) of this substance, which is released from the roots and washed into the soil from recently-dead leaves (Makepeace *et al.* 1985), prevent, for instance, wheat germination (Haussmann and Scurti 1985). Seven phenolic compounds were found to be released by *H. aurantiacum* on land where allelopathic effects were observed. Three of these compounds were tentatively identified as ferulic acid, vanillic acid and umbelliferone (Dawes and Maravolo 1973). The allelopathy of *H. pilosella* leads to a degradation of the vegetation in the areas invaded by this species. In Europe, Guyot (1951) observed the following pattern of the impact on the surrounding vegetation, proceeding towards the centre of a group of *H. pilosella* plants: (a) at the periphery, a narrow belt where *H. pilosella* grows vigorously and blooms abundantly, in contact with surrounding vegetation, still unmodified; (b) a zone of variable width, where *H. pilosella* grows less vigorously and blooms sparsely, if at all, and where there are also some dwarf and delicate individuals; (c) closer to the centre, a zone with very impoverished vegetation and where *H. pilosella* itself is progressively eliminated; and (d) at the centre, an area completely bare, where every trace of the original vegetation has almost completely disappeared and where sometimes, slowly, re-population begins with annual species (*Ajuga chamaepitys* (L.) Schreber, *Anagallis arvensis* L., *Arenaria serpyllifolia* L., *Euphorbia exigua* L., *Galeopsis ladanum* L., *Geranium columbinum* L., *G. dissectum* L., *Linaria spuria* Miller P., *Mercurialis annua* L., *Papaver rhoeas* L., *Sinapis arvensis* L., *Stachys annua* (L.) L.).

Hieracium umbellatum L. and *Hieracium vulgatum* Fries also are reported to have very strong allelopathic effects (Guyot 1951). Allelopathy in *H. pilosella* was observed also by Makepeace (1976) in a fescue tussock (*Festuca novae-zelandiae* (Hackel) Cockayne) in New Zealand. Leaf material was allelopathic to cocksfoot (*Dactylis glomerata* L.) and white clover (*Trifolium repens* L.) in the laboratory. This allelopathy, which is an additional factor contributing to the success of this species in dominating large areas, was observed also with senescent leaves. A strong allelopathic effect of *H. pilosella* was observed in Europe against *Festuca rubra* L. under natural conditions (Widera 1978). Studies conducted in several grasslands of Wisconsin demonstrated the presence of allelopathy in *H. aurantiacum* (Dawes and Maravolo 1973).

Beneficial attributes

In their homeland, *Hieracium* species are important components of the natural ecosystem. In the Old World they occur in small scattered stands and some species are rare. They never pose a problem as weeds, but often are considered desirable and beneficial, not only for the environment, but also for some of their properties. For instance, *H. pilosella* has medicinal properties. The entire plant at the blooming stage, including the root, is used for infusions (Lodi 1978) and tinctures (Suozzi 1995). The main properties of the fresh plant are diuretic, which are lost after desiccation; only fresh plants, or extracts can be used (Lodi 1978). Following its intake, the amount of urine released is doubled or tripled, with elimination of chlorurates and urea (Viola 1979). The main components are a bitter, active ingredient, tannic (belonging to the group of the pyrocathechin), resinous and mucilaginous substances, umbelliferone (hydroxycumarin) (Duquénois *et al.* 1956; Suozzi 1995), caffeic acid (Duquénois *et al.* 1956), albuminoid substances and manganese (Viola 1979) and, in the flowers, a colouring matter, not well defined, belonging to the flavone group (Duquénois *et al.* 1956; Negri 1964).

The plant has antibiotic properties (Duquénois *et al.* 1956; Suozzi 1995) and is used against dropsy, nephritis, gout, dyspnea, hemoptysis, cardiac oedema, diarrhoea and intermittent fevers (Duquénois *et al.* 1956; Viola 1979). It is active against the bacteria causing brucellosis (Suozzi 1995) and historically, besides ulcers and many serious internal diseases mentioned above, it was used to cure wounds (Durante 1636). The tannins probably play a defensive role in the plant, protecting its tissues from fungal, insect and bacterial attack (Sappa 1959). It has been used to cure abortive epizootics in cattle (Duquénois *et al.* 1956). *Hieracium* species are a source of nectar for honey bees; may be useful for soil conservation, providing a cover to bare ground; can be eaten by livestock, providing a complementary source of food; and are used as ornamentals.

The chemical composition of *Hieracium peleterianum* Merat and *Hieracium piloselloides* Villars is similar to the composition of *H. pilosella*. *Hieracium peleterianum* contains large amounts of umbelliferone and *H. piloselloides*, in addition to umbelliferone, contains caffeic acid and a flavonoid (Duquénois *et al.* 1956). Because of their rapid growth, procumbent posture and sturdy foliage, *Hieracium* species are recommended for recreational grounds. In pastures they are moderately grazed (Corbetta *et al.* 1980).

Habitats

In the Alps, *Hieracium* species occupy well-defined ecological niches and are components of well defined plant associations. For instance the habitat of *H. caespitosum* are the Nardetalia, more or less peaty prairies, with slopes at elevations up to about 1200 m. *Hieracium aurantiacum*, *Hieracium alpinum* L. and *Hieracium glaciale* Reynier, typically alpine plants, occur in the Aveno – Nardetum, at altitudes between 1800 m and 2200 m (Oberdorfer 1959), but they are found also at higher elevations, up to about 2800 m. *Hieracium alpinum* and *H. glaciale* are indicators of acidophil soils (Guinochet and Vilmorin 1984). *Hieracium alpinum* occurs especially on windy crests (Cappelletti 1976). *Hieracium pilosella* is a pioneer plant which occurs in the Nardetum alpigenum, in dry nitrophil prairies at altitudes between 900 m and 1700 m, but it has a wide ecological valence and is present from sea level to over 2000 m. Nevertheless, records for a given species are often erroneous, due to the already-mentioned difficulty in obtaining a precise identification at the species level. Therefore the habitat requirements for a given true species could often be narrower than generally acknowledged. *Hieracium* species belong to the category of persistent species defined by Gross (1984) for secondary successions. This category includes clonating perennial species with a long life-cycle. The seeds are numerous, short-lived, small and disperse long distances. The absence of perennial species in the first phase of the colonization may be due to the short vitality of their seeds.

Potential weediness

Hawkweed characteristics, described in detail in the previous sections, are discussed below in regard to the weedy potential of these plants. Adventitious species of *Hieracium* are not part of the natural plant community, as they were in their homeland. Therefore they have the potential to escape the environmental and biological controls in the new environment and become naturalized. Under these conditions, *Hieracium* species have a competitive advantage over other plants, tending to dominate the plant community. Because of their fast growth, *Hieracium* species rapidly colonize the land where they become established by means of their stolons and through wind and animal distribution of their seeds. In this way and because of the lack of competition, they expand their distribution, compressing autochthonous flora. This is what has already happened in New Zealand, Japan (Suzuki and Narayama 1977) and to some extent in North America (Scott *et al.* 1990). It is also possible that, in some cases, in the area of introduction as alien plants they find previously unoccupied ecological niches. Stoloniferous species from western Europe (Scott *et al.* 1990) are the alien species which have posed a weed problem when accidentally or intentionally introduced to other parts of the world.

The aggressiveness of hawkweeds allows the introduced species to establish and rapidly spread, being troublesome especially in rangelands, pastures and fields. Their rapid spread, thorough monopoly of the soil and genetic plasticity give *Hieracium* species a very high weedy-potential. Their dense mats virtually exclude all other vegetation. *Hieracium* species are capable of adapting to various conditions and thrive almost equally well in all soils, from sandy loam to heavy clay, and at a wide range of altitudes. For instance, *H. aurantiacum* is usually considered to occur at high elevations as it does in Europe (Jones and Orton 1897; Oberdorfer 1959), but after it established at higher elevations, it invaded all types of soils at many elevations (Jones and Orton 1897). The great adaptability and hardiness of *Hieracium* species probably derives from the rigorous selection undergone by this genus through glaciations and has resulted in refined adaptations to extreme environmental conditions, such as lack of water and ultraviolet radiation. Another adaptation is to store nutrients that allow the immediate regrowth after winter. Stored nutrients are then reintegrated towards the end of the vegetative growth period.

Hieracium caespitosum, *H. pilosella* and *H. aurantiacum* rapidly spread by stolons. Vegetative expansion is especially important for the advance of weedy populations of species in the subgenus *Pilosella*, while seeds allow long-distance dispersal. *Hieracium pilosella* is able to exploit the free space in the surrounding vegetation and subsequently displaces other plants. The species has a competitive advantage, which is enhanced by allelopathic effects (see above), especially on infertile, dry, shallow, and overgrazed soil.

Hawkweeds do not persist on cropland, where tillage and herbicides keep them under control. They are a problem in permanent rangelands, pastures, hay-fields and meadows, where they develop dense infestations and replace desirable grasses. They also occur in riparian habitats, tree plantations, urban areas and along roadsides. Hawkweeds drastically reduce the production of rangelands and pastures. In the case of heavy infestations, a pasture yield of 2000 lb per acre (2250 kg per ha) in the absence of the weed, was completely lost (Callihan *et al.* 1989). They are an environmental problem as well, since they displace native plants and modify entire biotopes. High grazing-pressure gives a competitive advantage to *H. pilosella* compared to desirable tussock grasses, whose populations decline (Scott *et al.* 1990).

Hieracium species in New Zealand

In New Zealand, 11 *Hieracium* species are a major weed problem. They were probably introduced as contaminants of crop- or pasture-seeds (Scott 1984). After 1950, adventitious hawkweeds spread rapidly and extensively and displaced forage species and native grasses on tussock grasslands, especially in the South Island (Scott 1984; Makepeace 1985). The dense mats of *H. pilosella* limit sheep grazing (Scott *et al.* 1990) and the inter-tussock vegetation underwent major changes (Treskonova 1991). *Hieracium pilosella* and *H. praealtum*, which are among the most abundant tussock grassland species, are presently the most troublesome.

In New Zealand, range management practices have modified grasslands since the late 1850s (Connor 1964), when sheep were first introduced (O'Connor and Kerr 1978). One of the major changes in the tussock was the decrease of tall species and the increase of short species. Changes in the grassland structure following the felling of trees, fire, and sheep grazing favoured invasion by hawkweeds. *Hieracium pilosella* and *H. praealtum* grow in dense mats which dominate the ground cover, especially in the short tussock grasslands. The main component of these grasslands, intensively used for sheep grazing for over a century, was *Festuca novae-zelandiae*, along with an inter-tussock vegetation represented by other native and introduced grasses, forbs and small shrubs. Both of the above-mentioned hawkweed species rapidly spread vegetatively by means of stolons.

The invasive *H. pilosella* has a flat habitus and displaces the inter-tussock grasses first and subsequently the fescue tussock, reaching up to 80% of the ground cover at some sites (Makepeace 1985). *Hieracium praealtum* is a pioneer plant which grows especially on disturbed soils. It is less tolerant of grazing than *H. pilosella*, but it has become a dominant species in many grassland areas retired from grazing (Makepeace 1985).

Conclusions

Hieracium species are very difficult to control and are resistant to most chemical herbicides (Matthews 1975). Chemical control is too expensive and not environmentally sound, especially because of the risk of contaminating the water-table. Herbicides cannot be used on non-agricultural land such as national parks or other reserves and they have a negative impact on desirable pasture species. Alternative means of control, such as grazing, on rangelands are not feasible because *Hieracium* species, and especially *H. pilosella*, are less palatable than grasses (Roché 1992). The presence of tannins, which are produced in special vacuoles in the tissues of *Hieracium* species, increases their resistance to natural enemies, since these substances have antiseptic properties (Cappelletti 1975; Bell 1981). This, along with morphological and geobotanical characteristics of *Hieracium* species, may have led to the co-evolution of specialized natural enemies associated with the plant and increases the likelihood of success of classical biological control programs against *Hieracium* species in North America. All of the weedy species of *Hieracium* introduced from Europe belong to the subgenus *Pilosella*, but none of the *Hieracium* species native to North America belong to this subgenus, which may enhance the chances of procuring suitably-specific agent species. On the other hand, the extreme taxonomic complexity of the genus, and the ease of hybridization, may complicate a biological control programme.

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