Hawkweeds in the Northwestern United States

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everal species of hawkweed (Hieracium spp.) are recent additions to the weedy flora of the Inland and Pacific Northwest, the region encompassing Washington, northern Idaho and northwestern Montana. Over 60,000 acres are currently estimated to be infested. Private landowner concern about the rapid rate of spread of hawkweeds is shared by public land managers, wildlife managers, timber companies, livestock farmers, and recreationists. Lack of control of these weeds has become a serious land management concern in the last decade. Various chemical and cultural methods have successfully controlled small infestations, but larger, less accessible populations, comprising the bulk of the infestation, are more difficult to control. Biological control is being investigated as a tool with which to combat the increasing hawkweed problem. The purpose of this paper is to summarize what is currently known about the introduced hawkweeds in the United States in order to facilitate future research and management of hawkweeds.

Taxonomy

The hawkweeds (Hieracium spp.) are members of the tribe Lactuceae (= Cichorieae) in the family Asteraceae. The name Hieracium is derived from the Greek 'hierax', meaning hawk; allegedly keen-sighted hawks of yore ate the sap of the brightly colored plants to sharpen their eyesight (Fernald 1950). Hieracium is an extremely diverse genus morphologically. It includes a huge number of taxa in which apomixis, hybridization, and polyploidy are all common (Stebbins 1950). Apomixis, or asexual reproduction, includes both agamospermy (production of seeds without pollen) and vegetative reproduction. These reproductive strategies generate enormous morphological and cytological variation within and among species, making Hieracium one of the most taxonomically difficult genera. Problems with taxonomy are worsened by the lack of clearly defined. stable characters that are important in classifying species within the genus. For example, species are broadly distinguished by the character and amount of pubescence, leaf venation, flower color, stolon morphology, and the size. shape, and color of the inflorescence (Bailey and Bailey 1976, Voss and Böhlke 1978). The result has been the description of a huge number of species, subspecies, varieties, and forms that differ slightly (Sell 1974). Zahn (1921-22) conducted the most comprehensive treatment of the genus in which he described 756 species world-wide. It is estimated that while over 10,000 Hieracium species, subspecies, varieties and forms have been described worldwide, only about 700 species are valid, with the remainder

being genetic forms of a "related" species (Hitchcock et al. 1955)

The genus is divided into 4 subgenera, 3 of which are found in north-temperate flora and are distinguished by the following key (adapted from LePage 1971):

- 1b. North temperate flora
- 2b. Plants not stoloniferous:

There are generally considered to be about 36 species of Hieracium belonging to 3 subgenera in America north of Mexico. About 25 species are native to the United States and Canada and fall into 2 subgenera, Hieracium (3 species) and Stenotheca (22 species) (Table 1). Subgenus Hieracium is circumboreal in distribution, and is represented in North America by H. umbellatum L., H. robinsonii Zahn and H. canadense Michx. Species in this subgenus reproduce sexually and apomictically. Subgenus Stenotheca is restricted to the New World and contains most of our native taxa. Species in this subgenus are strictly sexual. Conflicting characters used to distinguish species have generated considerable debate regarding classification. For example, Guppy (1978) suggested that H. scouleri Hook., H. albertinum Farr., and H. cynoglossoides L. are too closely correlated in characters to be distinguished into separate species, and instead form a complex of species. Similarly, Guppy (1978) suggested that H. umbellatum L.. and its close relative H. canadense Michx., may be 2 forms of the same species. Deardorff (1977) added H. longiberbe Howell and H. nudicale Heller to the H. scouleri complex. The remaining hawkweed species found in the United States and Canada are introduced from Europe and belong to 2 subgenera (Table 2). Four species belong to the subgenus Hieracium: H. murorum L., H. argillaceum Jordan group, H. sabaudum L., and H. groenlandicum Arv.-Touv. Plants in this subgenus have not become weedy in North America. The remaining 7 species belong to the subgenus Pilosella. As in other subgenera, these plants are difficult to distinguish morphologically. From a practical standpoint, however, plants in subgenus Pilosella fall into 3 groups. The first group is represented by H. pilosella, mouse-ear hawkweed, easily distinguished by its single, yellow flower.

Table 1. List of Hieracium species native to America north of Mexico, by subgenus (H=Hieracium, S= Stenotheca).

Species	Subgenus
H. canadense Michx. (Canada h.) = H. columbianum Rydb. = H. umbellatum var. scarbisculum Farw. = H. laevigatum ssp. canadense Zahn.	Н
H. robinsonii (Zahn) Fern (Robinson h.)	Н
H. umbellatum L. (narrow-leaved h.) = H. scabrisculum Schwein. = H. canadense var. scabrum = H. macranthum Nutt. = H. canadense var. angustifolium T. & G. = H. kalmii = H. suksdorfii Gand.	н
H. albiflorum Hook. (white-flowered h.) = H. vancouverianum ArvTouv. = H. helleri Gand. = H. leptopodanthum Gand. = H. candelabrum Gand. = H. albiflorum subvar. rosendahlii Zahn. = H. albiflorum f. lyallii Zahn.	S
H. albertinum Farr (western h.) = H. absonum Macbr. = H. scouleri var. albertinum	S
H. argutum Nutt. (S. California h.)	S
H. bolanderi Gray. (Bolander's h.) = H. siskiyouense Peck.	S
H. carneum Greene	S
H. cynoglossoides L. (houndstongue h.) = H. griseum Rydb. = H. cusickii Gand. = H. flettii St. John & Warren = H. parryi Zahn. = H. rydbergii Zahn. = H. scouleri var. griseum (Rydberg)	S
H. fendleri Schultz (Fendler h.)	s
H. gracile Hook. (slender h.) = H. hookeri Steud. = H. triste var. detonsum	S
H. gronovii L. (hairy h.)	S
H. horridum Fries. (shaggy h.) = H. breweri Gray	S
H. lemmonii Gray	S
H. longiberbe Howell (long-beaked h.) = H. piperi St. John & Warren = H. scouleri var. longiberbe	S
H. longipilum Torr. (long-bearded h.)	S
H. marianum Willd. (Maryland h.)	S
H. paniculatum L. (panicled h.)	S
H. pringlei Gray. (woolly h.)	S
H. rusbyi Greene	S
H. scabrum Michx. (rough h.)	S
H. scouleri Hook. (Scouler's h.) = Pilosella scouleri Schu. & SchuBip. = H. amplum Greene = H. absonum Macbride & Payson	S

= H. cinereum Howell

Species	Subgenus
= H. idahoense Gand.	
= H. nudicale Heller	
= H. paddoense Gand.	
= H. washingtonense Gand.	
= H. cascadorum Zahn.	
= H. chelannense Zahn.	
= H. chapacanum Zahn.	
= H. scouleri var. scouleri	
= H. scouleri var. nudicale (Gray)	
H. traillii (Green's h.)	S
= H. greenei Porter & Britton (? Gray)	
= H. howellii Gray.	
= H. barbigerum Greene	
= H. oregonicum Zahn.	
= H. cinereum Howell.	
H. triste Willd. (alpine h.)	S
H. venosum L. (rattlesnake weed)	S

While predominantly an eastern weed, *H. pilosella* has a limited western distribution in coastal Washington and Oregon (Roché 1992). The second group includes *H. aurantiacum* L., orange hawkweed, the only introduced species with orange flowers. The remaining group consists of species with multiple, yellow flowers and includes *H. pratense* Tausch. (= *H. caespitosum* Dumort), *H. praealtum* Vill., *H. piloselloides* (= *H. florentinum* All.), *H. floribundum* Wimm. & Grab., and *H. flagellare* Willd. (= *H. auricula* L.). Known variously as yellow hawkweed, meadow hawkweed, field hawkweed, king devil hawkweed, and yellow devil hawkweed, this group represents most of the taxonomic complexities.

Until recently, it was thought that only H. pratense (Figure 1) occurred in the Inland Northwest, however, H. floribundum and H. piloselloides have also been identified in the past 6 years. Other populations contain plants that are morphologically similar to *H. pratense* and *H. piloselloides*. Lepage (1967) suggested that H. piloselloides is a hybrid between H. praealtum and H. flagellare. Similarly, he treated H. flagellare as a hybrid between H. pratense and H. pilosella (Lepage 1967, 1971). Guppy (1976) suggested that H. floribundum and H. pratense, distinguishable only by the degree of pubescence, may be different phases of a single species that exhibits a broad morphological range. Lepage (1967) recognized the largest number of hybrids among the introduced hawkweeds, particularly between H. aurantiacum, H. pilosella, H. floribundum and H. pratense. It is likely that the combined influences of morphological variation, polyploidy, frequent apomixis, and widespread hydridization among the introduced species has led to a huge array of intermediate types, and that species distinctions can no longer be made in North America based solely on descriptions from European flora.

Biogeography

H. pratense was likely introduced into the United States in 1828 (Britton and Brown 1970), and is now commonly found from Québec and Ontario (Frankton and Mulligan

Table 2. List of Hieracium species introduced into America north of Mexico, by subgenus (*P=Pilosella*, *H=Hieracium*).

Species	Subgenus
H. aurantiacum L. (orange h.) = H. brunneocroceum Pugsley.	Р
H. floribundum Wimm. & Grab. (yellow devil h., glaucous hawkweed)	Р
H. flagellare Willd. (whiplash hawkweed) = H. auricula L. = H. lactucella Wallr.	Р
H. pilosella L. (mouse-ear h.)	Р
H. piloselloides Vill. (King devil h.) = H. florentinum All. = H. praealtum Vill.	Р
H. praealtum Vill. (King devil h.)	Р
H. pratense Tausch (meadow h., field h., King devil) = H. caespitosum Dumort (Yellow King devil)	Р
H. argillaceum Jordan group (European h.) = H. lachenalii Gmelin (common h.) = H. vulgatum Fries (common h.) = H. molle Pursh. = H. strumosum L.	H
H. murorum L. (wall h., golden lungwort)	Н
H. groenlandicum ArvTouv. (Greenland h.)	Н
H. sabaudum L.(hawkweed)	Н

1970) southward to Georgia and Tennessee (Rickett 1987). The first record of *H. pratense* in the western United States was in Pend Oreille County, Washington, in 1969 (Marion Ownbey Herbarium, Wash. State Univ.). H. aurantiacum was introduced into Vermont in 1875 as an ornamental and within 25 years spread throughout much of northeastern United States and southeastern Canada (Voss and Böhlke 1978). First recorded in Spokane, Washington, in 1945 (Marion Ownbey Herbarium, WSU), H. aurantiacum has been collected from gardens in Nevada County, California (Munz and Keck 1959), on the east slope of the Rocky Mountains in Colorado (Weber 1990), coastal Oregon and Washington (Rickett 1987), and in southwestern British Columbia (Guppy 1976). H. aurantiacum is more widespread than other hawkweed species primarily because it is planted as an ornamental and often escapes cultivation. Both H. piloselloides and H. floribundum were first reported in northern New York 1879 (Voss and Böhlke 1978) and 1900 respectively (Kennedy 1902).

Introduced hawkweeds infest similar habitats in Washington, Idaho, Montana, and British Columbia. Found predominantly in mountain meadows and clearings in forest zones, hawkweeds also infest permanent pastures and hayfields, cleared timber units, and abandoned farmland where the soil is well drained, coarse-textured, and moderately low in organic matter. They are found at elevations ranging from 1,500 feet to over 5,000 feet, with the largest infestations occurring around 3,300 feet. None of the introduced species are found in the natural grasslands or shrubsteppe of the northern Intermountain West, and are not expected to become problem weeds in any dry habitat usually associated with western rangelands.

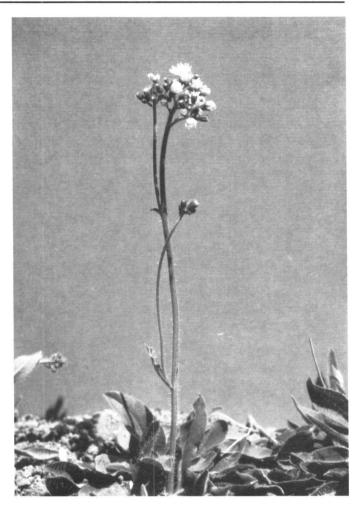


Fig. 1. Meadow hawkweed (Hieracium pratense)

In Idaho, *H. pratense* and *H. aurantiacum* are now widely distributed throughout the 6 northern counties, and is reportedly spreading south. In Washington, *H. pratense* and *H. floribundum* are found primarily west of the Cascade Mountains as well as in the 4 northeastern counties. Montana reports *H. aurantiacum*, *H. pratense*, and *H. piloselloides* variously distributed in 5 northwestern counties in addition to both Glacier and Yellowstone National Parks (Robin Cox, Vegetation Manager, Glacier National Park, pers.comm.)

Morphology and Biology

Hawkweeds are perennial, stoloniferous plants that contain a milky sap. Among the introduced species, only *H. piloselloides* is not stoloniferous. Each young plant consists of a rosette of 5 to 12 hairy leaves arising from a short, thick rhizome, with a shallow, fibrous root system. Rosette leaves are oblong to elliptical, entire to dentate. Plants produce 1 to several flowering stalks with 5 to 20 ligulate heads arranged in compact corymbs. Cauline leaves, if present, are much smaller and are arranged alternately along the lower half of the stalk. The flowers are yellow or orange (*H. aurantiacum*). The involucre is cylindrical, with unequal

bracts arranged in 2 or 3 imbricated rows. Achenes are spindle-shaped, slender, and have a pappus of a single circle of slender, tawny bristles.

Aspects of the biology and ecology of introduced hawkweeds have been studied in the United States, Canada and New Zealand. Seeds that germinate in the spring have a higher survival rate than fall germinated seeds (Panebianco and Willemsen 1976). After a rapid period of rosette growth in the spring and early summer, and following sufficient exposure to long days (Yeung and Peterson 1972), plants flower in late June and form viable seed shortly after anthesis. Under favorable conditions, a single generation can be completed in about 4 months. The plant will overwinter as a rhizome and regrow the following spring. In greenhouse experiments conducted in 1996 by the senior author, plants flowered an average of 61 days following germination.

Long-distance transport of seeds is likely through the activities of birds and animals (including man). In field experiments with *H. aurantiacum*, Stergios (1976) observed that about 95% of seeds fell within 3.5 feet of the patch, and thus were not carried far by the wind. While seeds are physiologically ready to germinate in the summer following a short period of afterripening, dry soil conditions in the summer and cool temperatures in the fall cause most seeds to delay germination until the following spring (Panebianco and Willemsen 1976).

Stolons develop only after flowering is initiated (Yeung and Peterson 1972). Each of the 1-6 leafy stolons arises from axillary buds at the base of rosette leaves. Depending on plant health, time of year, and environmental conditions, stolons will either terminate with rosettes of leaves or develop into a secondary flowering stalk (Thomas and Dale 1976). If a new rosette is formed, it will establish roots, and as the stolon degenerates the rosette becomes an independent plant.

The stoloniferous habit of hawkweeds results in the formation of dense mats of weeds that can persist for 30 years and reach densities of 3,500 plants m⁻² (Thomas and Dale 1975). In *H. piloselloides*, axillary buds develop into secondary flowering shoots rather than stolons. Another means of vegetative reproduction by introduced hawkweeds is by adventitious root buds. Plants derived from root buds have been reported for *H. pratense* (L. M. Wilson and J. P. McCaffrey, unpubl. data) and *H. florentinum* (Peterson and Thomas 1971).

The proportion of flowering plants in the population, the number of flower heads, seed production, the number and length of stolons, and leaf size are all highly density-dependent (Thomas and Dale 1975, Stergios 1976) Thomas and Dale (1975) showed that only 10% of the rosettes in the center of a patch flowered in a given year, and that more plants on the periphery of the patch flowered than at the center. Moreover, they reported that only 1% of the rosettes in an established population are derived from seedlings, and concluded that vegetative reproduction is more important than seeds to the maintenance of older patches. Similar phenomena have been reported for *H. pilosella*

(Bishop and Davy 1994) and *H. aurantiacum* (Stergios 1976).

Hawkweeds have long been used in the study of apomixis and cytology. Having a base chromosome number of 9, polyploids range from triploid (2n = 27) to decaploid (2n = 90). The introduced species are typically triploid (2n=27), tetraploid (2n = 36) or pentaploid (2n = 45) (Skalinska 1967). Skalinska and Kubien (1972) reported that while all of the polyploid *H. pratense* they examined from Poland were apomictic, the diploid biotypes (2n = 18) were strictly sexual. Deardorff (1977) stated that *H. pratense* is sexual, but he did not report the geographic origin of the specimens he collected. Diploids have not been reported for the other introduced hawkweeds.

The tribe Lactuceae is well known for its diverse flavonoid chemistry. In the genus *Hieracium*, umbelliferone and a number of other phenolic compounds have been identified and are known to have phytotoxic properties (Dawes and Maravolo 1973). Some researchers have even suggested that a chemotaxonomic treatment of the genus is valid based upon the high degree of correlation between chemically derived characters (Bate-Smith et al. 1968). In New Zealand, Makepeace (1976) studied the chemical ecology of mouse-ear hawkweed and attributed much of its competitive ability to allelopathy.

Control

A number of studies in both North America and New Zealand have addressed problems with hawkweed control. The use of herbicides, while effective, is limited to relatively accessible sites. Herbicides such as 2,4-D, clopyralid, and picloram have resulted in the greatest degree of control when applied at the normally recommended rate for perennial pasture weeds (Noel et al. 1979, Lass and Callihan 1992). Studies conducted at the University of Idaho showed that over 50% control was achieved for 6 years following treatment with a one pint rate of clopyralid (Lass and Callihan 1992). Other herbicides either failed to control hawkweed or suppression was achieved for fewer than 3 years (Lass and Callihan 1992).

Marked reductions in hawkweed density and vigor have been obtained by fertilizer treatments in the United States (Reader and Watt 1981), Canada (Hay and Ouellette 1959), and New Zealand (Scott et al. 1990 a, 1990b). However, Reader and Watt (1981) found that repeated fertilizer application had no effect on dense patches of hawkweed that contained few grasses or other forbs. It appears that the best results of hawkweed control are achieved where fertilizer and herbicides are applied together.

Soil analyses from hawkweed infestations in British Columbia indicated that soils there are low to deficient in sulfur. Similar analyses from Benewah County, Idaho, while preliminary, showed that upland meadow soils are universally deficient in sulfur, whether inside or outside a hawkweed patch. However, the Idaho studies showed that soils under hawkweed are low in organic matter (L. Wilson and

J. P. McCaffrey, unpubl. data). More detailed analyses are needed to characterize these soil-hawkweed relationships.

Most of the hawkweed infestations in the Inland Northwest occur in areas with limited access where the use of herbicides and fertilizers is impractical. These areas may be better suited to classical biological control. Interest in such a program has spread quickly in the Inland Northwest and has resulted in the formation, in 1992, of the Hawkweed Action Committee, Inc. in St. Maries, Benewah County, Idaho. Exploration for insects attacking hawkweeds in their native ranges is being conducted by USDA-ARS scientists in France, and the International Institute of Biological Control (IIBC) in Delémont, Switzerland.

One of the major constraints often limiting the introduction of one or more natural enemies is host specificity. It must be shown that insects selected for biocontrol feed only on the target weed. Host specificity problems may arise with hawkweed since the native flora is replete with Hieracium species, some of which are threatened and endangered. Furthermore, closely related genera such as Crepis. Taraxacum, Tragopogon, Cichorium, and Lactuca are well represented in the native flora and may further complicate host specificity testing. However, since most of the introduced hawkweeds are stoloniferous and belong to the subgenus Pilosella, potential biological control agents need only be specific to the subgenus level. Insects that attack stolons would be particularly beneficial as these structures are specific to most of the species in subgenus Pilosella. Flower head insects may be less important in a program for biological control of hawkweeds because sexual reproduction has been shown to contribute little to the population dynamics of these weeds, and the risk of attacking native hawkweeds may be greater.

Plant taxonomy and biology studies will be required to properly address host specificity testing to ensure the accurate evaluation of insect-host associations. Pre-release surveys were conducted by University of Idaho scientists during 1994-1995 to identify insects associated with the native and introduced hawkweeds in northern Idaho (Wilson, Johnson and McCaffrey, in prep.). These studies revealed a suite of insects that feed on a number of native hawkweed species. Two species of tephritid flies and 1 species of moth were found in the flower heads, and a gall wasp was found in the axils of leaf petioles, in the leaf mid-ribs, and inside the flower stalk. Insects were also found in similar structures of H. pratense, but only where it occurred with the native species. Future surveys and continued testing will determine the range of feeding by these insects. These studies coincide with research presently underway by the USDA-ARS in Montpellier, France, and the IIBC in Delémont, Switzerland. A successful biological control program for hawkweeds in the United States will require the coordinated inputs of scientists and land managers in the United States, Canada, Europe, and New Zealand.

Currently, research by the authors at the University of Idaho includes field and greenhouse studies to determine how hawkweeds compensate for damage, especially in combination with interspecific competition and variable fertility. Additional research is planned to conduct hybridization studies and to examine polyploidy in plants from selected populations around the region.

Summary

Moist, humid regions in the northwestern United States are likely to be highly susceptible to invasion by the aggressive, rapid-spreading hawkweeds. The spread of introduced hawkweeds in the Inland Northwest during the past decade has alerted land managers to the need to develop long-term management strategies to limit further hawkweed spread and to control the larger areas of infestation. The tools available to accomplish this include biological, chemical, and cultural control. Cultural practices include fertilizing, good grazing practices, early detection and control of small hawkweed infestations. Good land stewardship practices will be imperative to ultimately manage the introduced hawkweeds at an acceptable level.

Biological control of hawkweeds may be more easily achieved with natural enemies that attack stolons and/or are specific to the subgenus *Pilosella*. If a biological control program is established, it will be a valuable component of an integrated program of hawkweed management because it can impact remote and inaccessible infestations.

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