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**COMMON MULLEIN (*VERBASCUM THAPSUS*): A LITERATURE REVIEW**  
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*Verbascum thapsus*, common mullein, is a biennial weed of roadsides, pastures and open and semi-open natural habitats. This report reviews the autecology of *V. thapsus* in its native range (Eurasia) as well as in Hawai'i and elsewhere where it has naturalized. *V. thapsus* exhibits many characteristics of an ideal weed; broad germination conditions, self-compatibility, high seed output and a long-lived seed bank. Populations can vary substantially in life history characters, which may have allowed the species to spread over such a wide geographical range, including most temperate parts of the world. *V. thapsus* was introduced to the island of Hawai'i about 100 years ago, and it still appears to be spreading. It has invaded sites from sea level to the summit of Mauna Kea, but the densest populations occur in upper montane and subalpine habitats. Outside of Hawai'i, it is a poor competitor in many habitats, relying on continuous disturbance to maintain its populations. In contrast, in Hawai'i common mullein appears to have spread in little-disturbed native habitats, particularly where vegetation is sparse such as on relatively recent lava flows. Little is known about the impact this may have on the native biota. Further studies are needed to determine if the spread of *V. thapsus* depends on disturbance in Hawai'i. Extreme stem and inflorescence fasciation in *V. thapsus* appears to be unique to Hawai'i; its cause and how it affects life history characteristics are not known. While certain herbicides are effective in killing common mullein, long-term control is very difficult due to its abundant, long-lived seeds. No biocontrol agents have been introduced to Hawai'i, although a number of insects and pathogens attack it and its seeds elsewhere.

## BIOLOGY AND ECOLOGY OF *VERBASCUM THAPSUS*

### Taxonomy

*Verbascum thapsus* L. belongs to the family Scrophulariaceae. The genus *Verbascum* is palaeartic in origin and consists of more than 250 species, mostly from southeastern Europe and southwestern Asia (Pennell 1935). *Verbascum* is considered representative of the subgenus *Verbascoideae*, previously *Pseudosolanidae*, with nomenclature based on certain similarities to the family Solanaceae (Juan *et al.* 1997). The genus consists of biennial or perennial herbs forming a taproot, many of which are widely naturalized. Eight of the 250 species are known to be introduced to North America, the most prevalent of which are *V. thapsus* and *V. blattaria* (Gross & Werner 1978). Tutin *et al.* (1972) listed 3 subspecies for *Verbascum thapsus*: *V. thapsus* subsp. *thapsus*, has shortly petiolate basal leaves, long-decurrent lower cauline leaves, ovate corolla lobes and lower stamens with glabrous or sparsely hairy filaments; *V. thapsus* subsp. *crassifolium* (Lam.) has petiolate basal leaves with scarcely decurrent lower cauline leaves, oblong corolla lobes and lower stamens with densely villous filaments; *V. thapsus* subsp. *giganteum* (Willk.) has subsessile basal leaves with long-decurrent lower cauline leaves, ovate corolla lobes and lower stamens with densely villous filaments.

*Verbascum* is probably a corrupted form of the Latin word *barbascum* meaning bearded plant, referring to the plant's beardlike filaments (Mitch 1989). *Thapsus* probably comes from the Sicilian Isle of Thapsos where *V. thapsus* was gathered in abundance during ancient times or from the Tunisian island Thapsus. The species name *thapsus* could also have been derived from the Greek word '*thapsinos*' meaning yellow, since *V. thapsus* has yellow flowers. *Verbascum thapsus* has numerous common names including: common mullein, candlewick, hedge-taper, lungwort, feltwort, blanketleaf, hare's-beard, velvetplant, Jacob's-, Jupiter's- or Peter's staff and old man's flannel (Mitch 1989).

Basic chromosome numbers for the genus *Verbascum* are  $X=8, 9, 11, 15, 17$  (Darlington & Wylie 1955, Löve & Löve 1961, Gross & Werner 1978,). *V. thapsus* from Europe had chromosome numbers of  $2n = 34$  and  $2n = 36$  (Darlington and Wylie 1955) while plants from Ottawa and British Columbia are reported as  $2n = 36$  (Mulligan 1961, Packer 1964).

### Plant morphology

Common mullein is a stout, erect, biennial plant from 0.3-2 m tall (Polunin 1969, Tutin *et al.* 1972), densely covered with whitish to yellowish woolly tomentose (Webb 1967, Schischkin & Bobrov 1997). Webb (1967) reports the plants 0.6-0.9 m tall. The basal leaves of the rosette are elliptical to obovate-oblong, obtuse, 8-20 cm long, 2.5-4 cm wide with entire to finely crenate margins. The upper cauline leaves become progressively decurrent towards the inflorescence on the stem (Tutin *et al.* 1972). According to Schischkin & Bobrov (1997) the leaves are 15-30 cm long and 5-10 cm broad with the radical leaves having 3-6 mm long petioles. The inflorescence is usually an unbranched spike, with densely clustered yellow or rarely white flowers. Bracts are 12-18 mm, ovate to lanceolate, acuminate; pedicels are partly adnate to stem. Calyx has 5 lanceolate lobes, 8-12 mm long. The corolla is nearly regular with very short tube and spreading lobes, 12-35 mm in diameter (Polunin 1969). Plants in the USSR have corollas about 12-20 mm across with very distinct pellucid glands (Schischkin & Bobrov 1997). The five stamens are all fertile and decurrent, with the upper three having whitish or yellowish hairs. Anthers are obliquely attached and partly fused to the filaments and

the stigmas are capitate. The fruit is a capsule 7-10 mm long, elliptical-ovoid (Webb 1967, Tutin *et al.* 1972). The seeds range between 0.5-0.8 mm in length and on average weigh 0.067 mg (Darlington & Steinbauer 1961, Gross & Werner 1978).

### **Geographic distribution**

*Verbascum thapsus*, native to Europe and Asia is now widely distributed in the mid latitudinal parts of the world (Gross & Werner 1978). According to Tutin *et al.* (1972) it occurs in most of Europe, except the extreme north and much of the Balkan Peninsula. It is not reported from Iceland or Crete and is rare in Northern Scotland (Gross & Werner 1978). In the east, its range extends into Russia (Tutin *et al.* 1972), the Caucasus Mountains, Western Himalayas (Murbeck 1933) and China (Jingwei 1982). *V. thapsus* subsp. *thapsus* occurs throughout the range of the species, *V. thapsus* subsp. *crassifolium* occurs in the mountains of south and central Europe and from Portugal to the eastern Alps, and *V. thapsus* subsp. *giganteum* occurs in the mountains of south and southeast Spain.

In North America, *V. thapsus* occurs in southern Ontario, Quebec, British Columbia and in other eastern provinces of Canada, with scattered populations throughout the central plains region. In the continental United States, it has been introduced several times, both intentionally as a medicinal herb and accidentally. Wilhelm (1974) reported that it was introduced as a piscicide in the mid 1700's by a few families in the Blue Ridge Mountains of Virginia. Since then the species has naturalized and spread widely in the United States. It has also naturalized on the Island of La Reunion in the Indian Ocean (Juvik & Juvik 1993) and in Australia and New Zealand (Parham & Healy 1976).

In the Pacific *V. thapsus* had been reported only on the Island of Hawai'i in the Hawaiian archipelago (Juvik & Juvik 1993). Plants have been found and destroyed immediately on Haleakala, Maui, (Nagata, pers. comm.). Plants have occasionally been offered for sale on Maui but promptly withdrawn after complaints from conservationists (Medeiros, pers. comm.).

### **Life history**

#### Germination

*Verbascum thapsus* seeds germinate under a wide range of environmental condition. Semenza & Evans (1978) investigated the influence of temperature and light on germination using seeds from western Nevada and northern California. They found that seeds did not have any temperature-related after ripening period. They germinated seeds under 55 temperature regimes in both dark and in light. Each temperature regime consisted of a 16-hour cold temperature alternating with an 8-hour warm temperature. The temperatures ranged from 0°-40°C. In the dark, seeds germinated in 47% of the 55 temperature regimes they tested. Maximum germination (94%) occurred at 15/40°C through 35/40°C temperature regimes after 4 days. Optimum germination (defined as not significantly different from the maximum) occurred at 23% of the temperature regimes tested. The addition of light did not increase the rate of germination compared to the dark in the range of temperatures from 15/40 to 35/40 °C. With cold periods below 10°C, seeds did not germinate in the dark. However, under similar temperature regimes but with the addition of 8-hour light periods *V. thapsus* seeds germinated even at strong fluctuating temperatures of 0/35°C and 0/40°C. These results indicate that *V. thapsus* seeds can germinate on the soil surface even under extreme diurnal fluctuations. Few plants of temperate environments will germinate both at such extreme

diurnally fluctuating temperatures and at a constant high temperature of 35°-40°C (Semenza & Evans 1978).

*Verbascum thapsus* seeds collected from different sites can have different germination properties. Seeds collected from 1 of 3 sites tested by Semenza & Evans (1978) showed greater emergence when they were sprinkled over a layer of litter (84%) compared to when sprinkled on bare soil surface (58%). Germination of seeds from the other two sites, however, did not significantly differ between bare soil and litter surfaces. Seeds from 2 of the 3 sites showed reduced emergence when sown under a 1 cm layer of litter (27% and 24%). Bost & Reader (1995) found that litter did not inhibit germination but it inhibited seedling establishment by preventing shoot extension. Gross (1980) also found that seeds of *V. thapsus* will germinate under a canopy cover of forbs and grasses, but most germinants do not survive.

Baskin & Baskin (1981) studied the seasonal changes in germination responses of buried seeds of *V. thapsus*. They buried *V. thapsus* seeds packed in nylon bags to a depth of 15 cm within clay pots in a greenhouse. Seeds were exhumed at monthly intervals, and germination tests were done in the dark and in light at 4 alternating temperatures corresponding to diurnal fluctuations typical of March (15/6°C), April (20/10°C), May and June (30/15°C), July and August (35/20°C), September (30/15°C), October (20/10°C) and November (15/6°C). All exhumed seeds that were incubated in darkness showed seasonal patterns of germination. There was maximum germination (81-100%) at 30/15°C and 35/20°C in the dark from early autumn to late spring and no germination in summer. However, at these temperatures in light, maximum germination (86-100%) occurred through all seasons except from mid to late autumn. These results suggest that when light is available, *V. thapsus* seeds are capable of germinating at most times throughout the year. Curiously, when the seeds were left buried in the bags, fewer than 15% of the seeds germinated even at warm temperatures; Baskin and Baskin (1981) concluded that there is some other factor associated with burial besides darkness, that prevents germination of buried *V. thapsus* seeds.

Vanlerberghe & Van Assche (1986) investigated the factors that were responsible for the seasonal changes in germination responses observed by Baskin & Baskin (1981). They incubated *V. thapsus* seeds on filter paper in petri dishes at a temperature chain of 4°C → 10°C → 20°C → 10°C → 4°C. Each temperature treatment lasted for one month at the end of which samples were taken for germination tests. Seeds were germinated in light and dark at 3 alternating (12/12hr) temperatures: 15/6, 20/10 and 35/20°C. Similar to previous studies (Semenza & Evans 1978, Baskin & Baskin 1981), their experiment showed that light-treated *V. thapsus* seeds, in general, have a higher percent germination than seeds kept in dark. However, they showed that light stimulus for germination could be partially replaced by alternating temperatures. After an incubation period of 4°C, seeds germinated at wide range of conditions including low temperatures. However seeds incubated at higher temperature (spring and summer conditions, 20°C) got into 'deeper dormancy' and needed a stronger stimuli (light and 35/20°C) to germinate. The seeds became less dormant again when the incubation temperature was lowered. They concluded that the seasonal changes in germination responses observed by Baskin & Baskin (1981) were mostly due to prolonged changes in temperatures. Seeds exhibit different levels of dormancy which are linked to the different temperature cycles of the season. Changing levels of dormancy with temperature allows long-lived *V. thapsus* seeds to germinate in appropriate seasons (Vanlerberghe & Van Assche 1986).

#### Growth and development

In addition to germinating over a wide range of conditions, *V. thapsus* can also grow and establish in a wide variety of environments. In continental areas, it grows best with cool summers where the mean annual temperature of the warmest month is less than 22°C, with at least 4 months over 10°C (Gross & Werner 1978). The mean annual precipitation required is 500 - 1500 mm, with a growing season of at least 140 days. *V. thapsus* grows best on dry, sandy, rocky or highly calcareous soils within a pH range from 6.5 to 7.8 (Gross & Werner 1978).

*Verbascum thapsus* is strictly monocarpic (flowering once, then dying), and it is usually a biennial. In general, during the first summer after germination it produces a rosette of leaves and a tap root. It continues to grow vegetatively into late autumn and overwinters as a rosette (Gross & Werner 1978). Common mullein has been reported to require a cold period (vernalization) (Glier & Caruso 1973), after which it begins to bolt, growing an upright stalk that bears the flowers in the second spring or summer. Flowering proceeds from the bottom of the indeterminate raceme upwards, with mature capsules forming at the bottom while flower buds are still being produced at the top. In temperate regions, flowering begins around June, and plants may flower and fruit throughout summer until frost sets in, upon which most seeds are released, and the plant dies.

#### Reproductive biology

The size of rosette after the first growing season determines the fate of the plant in the following year. In a study conducted by Gross (1981), rosettes less than 9 cm in diameter did not flower in the second season. However, the probability of flowering steadily increased with rosette size. All rosettes with a diameter greater than 14 cm at the end of the first growing season flowered the following year (Gross 1981).

The flowers are ephemeral, opening before dawn and closing by mid-afternoon of the same day (Gross & Werner 1978). The two anterior stamens provide most of the pollen while the posterior stamens provide a foothold for bees. Pollen is transferred from the anterior stamens to the lower abdomen of the bee (McLean & Ivimey-Cook 1956). Although visited by a wide variety of insects, only bees are known to be effective pollinators (Pennell 1935). The flowers are facultatively autogamous (self-pollinating in the absence of pollinators). Autogamy takes place at the end of the day as the stamens bend towards the style and the corolla closes, pushing the receptive stigma against the anthers (Gross & Werner 1978). Taller plants tend to attract more pollinators than short plants (Donnelley *et al.* 1998). Donnelley *et al.* (1998) compared the growth of artificially selfed and artificially crossed plants in both the greenhouse and in the field, concluding that the plants were fully self-compatible with no early acting inbreeding depression. However they did not rule out the possibility of inbreeding depression in the later life stages. Their experiments indicate that *V. thapsus* has a mixed mating system with various levels of outcrossing possible, depending on pollinator availability. Vegetative reproduction does not occur in *V. thapsus* (Gross & Werner 1978, Gross 1980).

*V. thapsus* forms natural hybrids with *V. lychnitus* and *V. nigrum*, although not commonly (Clapham *et al.* 1952). Hybrids between *V. thapsus* and *V. lychnitus* are morphologically intermediate between the parents, and they are uniformly sterile (Darwin 1889). Koelreuter, in 1762, is reported to be the first to create artificial hybrids in the genus *Verbascum* (Gross & Werner 1978). Hybrids within the genus can be produced readily, although they are almost universally sterile (Arts-Damier 1960). Other species with which *V. thapsus* is reported to hybridize with are *V. vibratum*, *V. phlomoides*, *V. pulverulentum* and *V. blattaria* (Stace 1975). Of these, *V. blattaria* and *V. vibratum* are present in Hawai'i.

### Dispersal and seedbank

Each *V. thapsus* plant produces about 100,000 to 180,000 seeds (Gross 1980). The small seeds are pitted or roughened and lack a mucilage coating (Darlington & Steinbauer 1961, Gross & Werner 1978). The seeds do not have any specialized morphological adaptations for dispersal. Movement of the stalk by wind or by animals is required to release the seeds from the capsules (McLean & Ivimey-Cook 1956). Although seed dispersal was observed as far as 11 m, 93% of seeds fall within 5 m of the parent plant and 75% of them within 1 m (Gross & Werner, 1978).

*Verbascum thapsus* seeds remain viable in the soil for long periods of time thereby creating a persistent seedbank. Seeds from 41 weeds including *V. thapsus* that are commonly found in the Great Plains region of the United States were buried in Nebraska in 1976. *V. thapsus* showed the highest seed survival among the 41 weeds with 95% germination of seeds exhumed after 17 years of burial (Orvin *et al.* 1996). In the Duvel buried seeds experiment Toole & Brown (1946) found seeds to be viable after 39 years. In Denmark, viable seeds were collected from soil samples archeologically dated from 1300 AD (Odum 1965).

### **Evolution of the biennial habit**

Biennial plants like *V. thapsus* complete their life cycle in two years (Harper 1977, Hirose 1983, Kelly 1985) growing vegetatively in the first year and reproducing in the second year. The flora of North America provisional checklist of species lists 200 biennials (1.4%) of a total of 14,500 species (Hart 1977), indicating that the biennial life history strategy is rare. Silvertown (1983) showed that although biennials appear to be rare on a continental basis, they are more common in certain plant families. Over 11% of umbellifers (Apiaceae) and 5% of composites (Asteraceae) in the European flora are biennials.

Life histories are shaped by tradeoffs between allocation to growth and reproduction (Ricklefs 1997). Charnov & Schaffer (1973) proposed a mathematical model to explain the evolution of annual and perennial life histories. Their model predicts that populations that experience relatively high adult survival should be perennials, while populations with a low probability of first year survival should adopt an annual life history. They proposed that high adult survival is associated with more stable environments, like late successional forest habitats, so such habitats favor perennials; whereas in more open habitats, when disturbance is frequent, there is a high probability of seedling establishment, but a low probability of survival over more than one growing season, so an annual life history should be favored (Charnov & Schaffer 1973).

Hart (1977) proposed a model for the evolution of a biennial life history. He built on the model of Charnov & Schaffer (1973) and showed that for a biennial life history to evolve, first season and second season survival rates would both need to be moderate. This situation is most likely in early- to mid-successional stages (Hart 1977). A survey by Salisbury (1942) supports the predictions of the models. Closed communities (late successional) were composed of nearly 90% perennials, open communities (early successional) were composed of over 90% annuals, and biennials had the highest frequency in intermittent or semi-open habitats. According to Hart's (1977) model, the relative advantage of a biennial habit is a delicate balance that can tip to favor an annual or perennial habit with a small change in the ratio of adult to juvenile survival. Hence life history variation within biennial species should be expected. Biennials may behave as annuals under some conditions or delay their reproduction by several years under other

conditions, depending on which strategy results in the highest reproductive success (Hart 1977).

### ***Verbascum thapsus* ecology**

#### Population dynamics and community association

*Verbascum thapsus* is a weed of roadsides, old fields and pastures (Gross & Werner 1978, Gross 1980). Rapid germination and a biennial habit make it a colonizer of early successional stages. Gross & Werner (1982) experimentally introduced seeds into 1 year, 5 year and 15 year-old fields and monitored the fate of the seedlings over time. The amount of bare ground rapidly declined with the age of the field, from 66% in the 1 year-old field to less than 1% in the 15 year-old field. *V. thapsus* establishment decreased as the availability of ground cover decreased, with no seedling establishing in the 15 year-old field. However when bare ground was experimentally created in the 15 year-old field, *V. thapsus* seedlings were able to establish, indicating that the ability of *V. thapsus* to establish depends on the availability of open space rather than on the successional age of the area *per se*.

Populations may become locally extinct within 2-3 years unless the area is continuously disturbed. Gross (1980) studied the impact of various competitors on the colonization of *V. thapsus* in an old field in Michigan. She categorized competitors into three groups: biennials and winter annuals, perennial dicotyledons and perennial grasses. Species belonging to each of these categories were removed singly and in two-way or three-way combination from separate plots, and the ability of *V. thapsus* to colonize was assessed. Seedlings of *V. thapsus* germinated under all treatments, indicating that the presence of vegetation *per se* did not prevent germination; however, the number of seeds germinating increased with the amount of vegetation removed. Juvenile survival rate also increased with increasing vegetation removal. Among the different removal treatments, *V. thapsus* seedling density was the greatest when biennials were removed, intermediate in the absence of dicotyledons; and lowest when grasses were removed. Overall, the probability of a *V. thapsus* plant flowering and producing seeds increased with the amount of vegetation removed. Reinartz (1984c) found that the time since disturbance can affect the germination dynamics of *V. thapsus* populations. The amount of germination and density of seedlings and rosettes decreased in the second and third years after disturbance compared to in the first year. The fraction of seedlings surviving to the end of their first growing season was also greater in the first year after disturbance than in the second and third years after disturbance. These difference in the germination dynamics in the first, second and third years following disturbance were a function of the time since disturbance rather than year to year climatic fluctuations (Reinartz 1984c).

#### Life history variation in *V. thapsus*

*Verbascum thapsus* has three distinct life stages: rosette, bolting and flowering. The length of each of these stages varies considerably due to genetic and/or environmental effects. Reinartz (1984a, b, c) conducted detailed studies on its life history in the continental U.S. and Canada, exploring the genetic and environmental basis for several life history characteristics. After making observation on *V. thapsus* across North America, Reinartz concluded that triennials were most prevalent in the northern populations of Canada, while annuals were found only in the southern Texas populations; North Carolina populations behaved as biennials.

Seeds from 24 natural populations ranging from the plant's northern limit in Canada to the southern limits in Texas and Georgia were also grown in a common

garden. The common garden plants maintained latitudinal differences in life history, indicating a genetic basis. Reinartz suggested that the delay in flowering among the northern populations is an adaptation to the short but predictable growing season. Annual genotypes are favored in the southern populations where survival in the second year is more uncertain because of drought and increased competition. The relative numbers of biennials versus annuals or triennials were also correlated with the amount of bare ground available. More triennials were found in areas with sparse vegetation while annuals were prevalent in areas with thick ground cover. Reinartz (1984a) suggested that the genetic differentiation in the life history characteristics of *V. thapsus* may have evolved as a result of differences in climate, habit productivity and the degree of competition for light with surrounding vegetation.

Plant size affects the proportion of biomass devoted to reproduction. Reinartz (1984c) found that larger plants had greater reproductive effort and smaller root to shoot ratio and flowered earlier in the growing season than smaller plants. The greater amounts of carbohydrates stored in the caudex (swollen stem base) of larger plants may bring about their earlier flowering (Glier & Caruso 1973). Root growth occurs together with the rosette growth; however, growth in both ceases when bolting begins (Reinartz 1984c). Along the latitudinal range surveyed by Reinartz (1984b), higher (northern) latitude plants had larger caudices than lower latitude plants. Roots of the southern latitude populations made up a greater fraction of the total plant biomass than the roots of the northern populations. The relatively well-developed root system in the southern populations was explained as an adaptation for continued flowering during late-season drought (Reinartz 1984b).

The southern population had a greater number of capsules per plant, longer flowering stalk and a lower density of capsules (per 2 cm). The lower density of capsules in the southern population was due to the development of only two out of the four flower buds at each node. Only the top and the bottom buds developed and although the axillary flower buds were present, they never developed. Northern populations typically produced 4 capsules per node. This variable pattern of flower development has been suggested as a mechanism to maximize reproductive effort. In southern populations, growth is often cut short by drought, and developing fewer capsules at a time may be advantageous under water-limited conditions (Reinartz 1984b).

Plant size and biomass partitioning in *V. thapsus* vary with the year of establishment after disturbance. Although plants established in the second and third years after disturbance are smaller than plants establishing in the first year, they allocate more biomass to stem and leaves, which are longer and narrower than first year plants. This may be an adaptation to reduce shading from competitors during the later successional stages (Reinartz 1984c).

#### Physiological adaptations in *V. thapsus*

The wide distribution and broad ecological amplitude in *V. thapsus* has been attributed to its ability to photosynthesize over a broad range of temperatures (Williams & Kemp 1976). Plants from different latitudes and altitudes in North America exhibited similar rates of photosynthesis over a temperature range from 15-40°C. Williams & Kemp (1976) suggested that the absence of photosynthetically temperature sensitive ecotypes of *V. thapsus* among the North American populations has aided its ability to colonize thermally diverse sites.

Wuenscher (1970) compared leaves with their pubescence shaved off to unshaved leaves and found that unshaved *V. thapsus* leaves had higher leaf temperatures and reduced transpiration associated with an increased boundary layer resistance to water loss. On evaluating Wenscher's (1970) work, Parkhurst (1976) showed that the leaf hairs allowed increased stomatal resistance, thereby reducing water loss with only a slight increase in boundary layer resistance. Woodman & Wilson (1991) suggested that greater leaf pubescence on younger leaves in *V. thapsus* forms an evapotranspirative barrier. The hairier younger leaves, which have a relatively greater number of stomata per unit area, were more protected from stomatal water loss. Based on a CO<sub>2</sub> compensation point of 58 ppm and on leaf anatomy Williams *et al.* (1975, 1977) concluded that *V. thapsus* has a C<sub>3</sub> photosynthetic pathway. But based on leaf anatomy and the high temperatures at which *V. thapsus* is capable of photosynthesizing, Parkhurst (1976) hypothesized that *V. thapsus* probably follows the C<sub>4</sub> pathway. Glier & Caruso (1973, 1977) showed that lowering temperatures below 20°C induced the degradation of starch in the roots of *V. thapsus*. They suggested that the breakdown of starch provided cryoprotective chemicals during late autumn that helped the overwintering rosette survive.

In a greenhouse study of *V. thapsus* from different altitudes, Williams & Horwitz (1972) showed that plants from higher elevation (2341m) had a physiological mechanism for protecting their photosynthetic system from harmful UV radiation, while those from lower elevations (456 and 1672 m) were more susceptible to damage from UV light. They also found a higher concentration of flavonoid compounds in plants from 2341 m than those from lower altitudes, which suggested that flavonoid pigments may be involved in protection from UV radiation. These adaptations appear to be genetic in nature, as all plants were grown from seeds in a common greenhouse (Williams & Horwitz 1972). In a greenhouse study, Tosserams *et al.* (1997) showed that enhanced UV-B radiation (simulating 45% stratospheric ozone reduction) did not adversely affect germination and seedling development in *V. thapsus*.

Strong apical dominance in *V. thapsus* leads to its typical growth habit with one upright stem (Lorite & Aarssen 1997, Naber & Aarssen 1998). Branching inflorescences not known when the apical meristem remains intact. Lortie & Aarssen (1997) found that nutrient addition alone did not induce branching in *V. thapsus*. But a combination of damage to the apical meristem and nutrient addition resulted in branching. The authors suggested that branching in natural populations could be due to herbivore damage to the apical meristem. In a later study, Naber & Aarssen (1998) tested the effect of mechanical damage (clipping) and herbivory on branching, biomass and reproduction in *V. thapsus*. Although destroying the apical meristem induced branching, it did not lead to an increase in biomass or an increase in reproductive output. Interestingly, the seeds of clipped plants were heavier than those of unclipped plants, and this may have been due to overcompensation by *V. thapsus* (Naber & Aarssen 1998). Unclipped plants were mostly unbranched but a few formed branches. Branches were more likely in the tallest plants. Also fruits on the main stalk of taller branched plants were more heavily infested by a curculionid weevil (*Gymnetron tetrum*) suggesting that taller plants are more attractive to weevils, and weevil damage had induced branching in these plants (Naber & Aarssen 1998).

#### Predation

The weevil *Gymnetron tetrum* (Coleoptera: Curculionidae), native to Europe, is a seed predator specific to *V. thapsus* (Buchanun 1937, Sleeper 1954, Gross & Werner 1978, Julien & Griffiths 1998). The female oviposits in the ovaries and the larvae of *G.*

*tetrum* mature in the capsules and destroy up to 50% of the seeds (Sleeper 1954). Eight other species of Coleoptera found in Poland have been reported to be injurious to *V. thapsus* (Gross & Werner 1978).

*Haplothrips verbasci* (Thysanoptera: Phlaeothripidae) occurs only on *Verbascum* species among which *V. thapsus* is the chief host plant (Bailey 1939, Heming 1968). According to Bailey (1939) this thrip was introduced to North America from Europe but did not spread as rapidly as its host. *H. verbasci* was also found to occur on other hosts in North America like corn, cherry, ceonothus and black-eyed daisy, however these are transitional hosts, as it appears to feed exclusively on *V. thapsus* (Bailey 1939). Eggs are laid among the forked hairs of the basal leaves and among the flowers. The adults and larvae feed on tender portions of the plant away from sunlight. Adults hibernate in the dry seed pods and basal leaves in winter. Injury to *V. thapsus* by *H. verbasci* appears as "yellow blotches" on the leaves, slight browning around the base of individual flowers and on smaller leaves in the rosette. Bailey (1939) however does not mention any effects of *H. verbasci* on *V. thapsus* survival or plant densities. Heming (1968) found both sexes of *H. verbasci* occurring in large numbers on the flower spikes of *Verbascum* species in late summer in North Carolina, however their impact on *V. thapsus* was not examined.

*Campylomma verbasci* (Heteroptera: Miridae) causes extensive damage to apple and pear trees during winter, and in summer the adults feed on herbaceous hosts, preferably *V. thapsus* (Thistlewood *et al.* 1990). In the second year of their study Thistlewood *et al.* (1990) found all life stages of *C. verbasci* on *V. thapsus* with a positive correlation with higher numbers of *C. verbasci* associated with larger inflorescences. The authors suggested that the strong association (> 100 per plant) of *C. verbasci* with *V. thapsus* was due to higher nitrogen and phosphorous availability compared with neighboring plants and also due to the availability of insect prey like *Haplothrips verbasci* that feeds on *V. thapsus*. This bug may be both an herbivore and a predator, and the impact of *C. verbasci* on *V. thapsus* and its associated insects is not known.

Adults of *Euschistus servus* and *E. variolarius* species (Hemiptera: Pentatomidae) have been reported to feed and copulate on leaves of *V. thapsus* (Munyaneza & McPherson 1994).

The wheat bug *Nysius huttoni* (Hemiptera: Lygaeidae) is also reported to aggregate and overwinter under the dead leaves of *V. thapsus* (Farrell & Stufkens 1993).

The leaf hairs in young leaves of *V. thapsus* serve as a defense against many generalist herbivores. Woodman & Wilson (1991) showed that younger leaves with their pubescence shaved off were attacked by grasshoppers and suffered epidermal damage while the leaves with intact pubescence showed few signs of damage. Due to the density of leaf hairs, cattle and sheep generally also do not graze on *V. thapsus* (Whitson *et al.* 1991),

#### Disease

The 'Index of Plant Diseases in the United States' (United States Department of Agriculture 1960) lists the following pathogens associated with *V. thapsus*:  
*Cercospora verbasci* Ell and Ev., (leaf spot) (Fungi Imperfecti: Moniliales)  
*Phyllosticta verbasci* (leaf spot) (Fungi Imperfecti: Sphaeropsidales)  
*Ramularia variabilis* (Fckl.). (leaf spot) (Fungi Imperfecti: Moniliales)  
*Mycosphaerella verbasci* (Schw.) Fairm., (leaf spot) (Ascomycetes: Sphaeriales)  
*Phyotrichium omnivorum* (Shear) Dug., (rot disease) (Fungi Imperfecti: Moniliales)

*Phoma thapsi* (Ell. And Ev.), (rot disease) (Basidiomycetes: Agaricales)  
*Erisphye cichoracearum* D. C. (powdery mildew) (Ascomycetes: Erysiphales)  
*Heterodera maroni* (Cornu) Goody, nematode (Heteroderidae)  
*Meloidogyne sp.*, nematode (Meloidodera)

In addition to the above, *Perenospora sordida* (downy mildew) (Phycomycetes: Basidiophora), *Septoria verbasicola* (leaf spot) (Fungi Imperfecti: Sphaeropsidales) and *Oidium pyrinum* (powdery mildew) (Ascomycetes: Erysiphales) and *Annulus zonatus* (tomato ring spot virus) have been reported on *V. thapsus* (Wescott 1990). Most of these pathogens also cause disease in other economically important plants. For example, *Erysiphe cichoracearum* D. C. (powdery mildew) affects a variety of vegetables and ornamental plants like species of *Cucumis*, *Helianthus* and *Dahlia*. *Phymatotrichum omnivorum* (Shear) Dug. (root rot) is pathogenic to cotton. Bruckart & Lorbeer (1976) reported *Marmor cucumeris*, cucumber mosaic virus to have naturally infected *V. thapsus* plants growing near lettuce and celery fields in New York. This was the first report of infection of *V. thapsus* by *M. cucumeris*; however, this virus infects a large number of economically important plants like cucumber, squash, melon and spinach.

#### Status and Control

*V. thapsus* is considered a weed of roadsides and pastures in regions where it has been introduced and naturalized. Although impacts of *V. thapsus* on the native biota have not been reported, it is listed as a noxious weed by the Arizona Interagency Noxious Weed Coordinating Committee. It is not considered a serious threat to native species since dense populations generally only occur in disturbed areas. Probably for this reason, it has been removed from the noxious plant list in California (Reichard, pers comm).

Repeated mowing of *V. thapsus* prevents bolting and flowering. However this practice increases the rosette size, and when mowing is stopped the rosette bolts, often with axillary branches that also bear flowers and fruits (Gross & Werner 1978). Clipping the flowering stalk is not an effective control either, since the clipped plants can produce side branches that flower and fruit. When *V. thapsus* plants were clipped they produced significantly greater number of branches, with a greater pooled branch length (Naber & Aarssen 1998). Uprooting the plants before they flower or cutting the rosette and tap root below ground probably are the most effective forms of mechanical control. However if a significant portion of the tap root remains in the soil re-sprouting may occur (S. Ansari, personal observation).

Chemical control of *V. thapsus* has been reported to be difficult because the leaf hairs hold the herbicide away from the plant, rendering it ineffective (Gross & Werner 1978, Naber & Aarssen 1998). However, some herbicides have been suggested for the control of *V. thapsus* (Table 1).

*Gymnetron tetrum* a potential biocontrol agent, was accidentally introduced into the United States before 1942, but it has not been deliberately released anywhere for biological control (Buchanan 1937, Julien & Griffiths 1998). According to Julien & Griffiths (1998) it is well established in Washington and causes extensive damage to the seeds of *V. thapsus*; however, it has negligible impact on *V. thapsus* in California. It is also reported in Oregon, Idaho, South Dakota and Wyoming but its impact on *V. thapsus* in these states is not known. From the literature it appears that this weevil has variable impact on *V. thapsus*, and there are no records of this species destroying a population of *V. thapsus*. A study by Myers & Risley (2000) indicated that reduced seed production due to a biological control agent does not always translate to reducing

population density of the target weed. They studied the interaction between diffuse knapweed, *Centaurea diffusa* and insects introduced for its biocontrol: two gall flies; *Urophora affinis* and *U. quadrifasciata* and a root boring beetle *Sphenoptera jugoslavica*. These biocontrol agents primarily reduce seed production in diffuse knapweed. Myers & Risley (2000) modeled the population dynamics of diffuse knapweed plants and showed that reduced seed production in knapweed due to the biocontrol insects alone did not reduce the density of flowering plants. In fact, improved seedling survival compensated for reduced seed production and led to the increase in the density of flowering knapweed plants. The authors suggest that seed predators are not always the best biocontrol agents for weeds that produce high number of seeds and successful biocontrol agents are probably those that kill plants.

#### Medicinal uses

*V. thapsus* is widely used as a medicinal herb (Millspaugh 1974, Gross & Werner 1978). The boiled leaves are used as tea that is a remedy for coughs and diarrhea. The leaves may provide some stimulatory effects when smoked (Wilhelm 1974). Plant extracts from *V. thapsus* have antiviral activity against herpes virus type 1 (McCutcheon *et al.* 1995).

## **VERBASCUM THAPSUS IN HAWAII**

### **Introduction and distribution**

Three species of *Verbascum* are known to occur in Hawaii: *V. thapsus*, *V. blattaria* and *V. virgatum*. Of these *V. thapsus* is the most common and widespread (Wagner *et al.* 1990). Of the three subspecies only *V. thapsus* subsp. *thapsus* is known to occur in Hawaii. It is not clear whether *V. thapsus* was an intentional or inadvertent introduction to Hawai'i. Juvik & Juvik (1993) report that it first occurred in Kona (Hawai'i) between 1900 and 1910. By 1946, it was common on the south slopes of Hualalai (2,300 m, 19°41'30"E & 155°52'20"N), and by 1948 it had spread into the central plateau, the saddle area between Mauna Loa and Mauna Kea. Over the past several decades, *V. thapsus* has spread along the roadside of the Mauna Kea summit road and in remote upland habitats up to 3,800 m.

In the Hawaiian archipelago *V. thapsus* occurs only on the Island of Hawai'i though several plants have been found on Maui and destroyed immediately. It is one of only a few alien species in Hawai'i that has colonized habitats from sea level to near the summit of Mauna Kea (about 4596 m). In Kona, populations occur along Highway #19 (Queen Ka'ahumanu Highway, 152°55'30"E & 119°51'30"N). In 1997 populations were discovered in the Ocean view estate (155°47'30"E & 19°7'30"N) in South Kona (Juvik, pers comm). As of July 2000, populations along the Saddle road (State Highway 200 or Kaumana Road) occurred as low as about 1200 m (mile 20 marker), where the plants primarily occur in a 'belt' of about 2.5 m. on either side of Saddle road. On Mauna Kea, *V. thapsus* has colonized pastures and open mamane (*Sophora chrysophylla*) woodland and *Deschampsia nubigena* grassland. *V. thapsus* also grows in association with native *Chenopodium oahuense* and *Agrostis sandwicense*. Scattered populations of *V. thapsus* occur in the dry montane zone of Hawai'i Volcanoes National Park between 1500 and 2500 m. The populations are mostly confined to Ke'eamoku lava flows near Kipuka Kulalilo (155°22'30"E & 19°30'45"N), surrounded by koa forests and *Deschampsia nubigena* grassland.

### **Population dynamics**

Very little is known about the germination and population ecology of *V. thapsus* in Hawai'i. In a quantitative survey, Juvik & Juvik (1993) found that mean rosette diameter and plant height of *V. thapsus* increased with elevation. Giant plants reaching a height of nearly 4.3 m., double the maximum height recorded for the species in its native range, were observed above an elevation of 2,500 m. Also, increasing branching, extreme stem fasciation (see section on fasciation) and woodiness, were associated with increasing elevation. The rosettes at higher elevations also appear to require more time to flower and set seed (S. Ansari, personal observation). Higher elevations are drier and subjected to diurnal frost while lower elevations are warmer and wetter. The strong topoclimatic gradient on Mauna Kea may influence the life history of *V. thapsus* populations in a similar way to the latitudinal gradient in the continental United States (Reinartz 1984a). Unlike populations in the native range and in the continental U.S. that quickly decline in the absence of disturbance, the populations in Hawaii seem to persist over time at high densities. It is possible that the open nature of the high elevation and volcanic substrate, combined with disturbances by feral ungulates on Mauna Kea, support these unusually dense, persistent populations. The impact of *V. thapsus* on the native vegetation is not known.

### **Fasciation**

An interesting and prominent feature of *V. thapsus* in Hawai'i is the occurrence of stem and inflorescence fasciation. Fasciation is an abnormal morphological change generally occurring in the stem and/or the inflorescence wherein the affected region becomes flat, banded or ribbon shaped and is mostly associated with unregulated and distorted tissue growth (White 1945). In *V. thapsus* in Hawai'i, fasciation distorts only the vegetative tissue. Rosettes and the stalk bearing flowers become flattened and/or twisted but the individual flowers and fruits appear to be normal in proportions. Fasciation in *V. thapsus* varies in intensity, with the width of fasciated inflorescence ranging anywhere from 5 and 50 cm. Schischkin & Bobrov (1997) reported that some *V. thapsus* in Russia showed stem fasciation, which is the first report of fasciation in *V. thapsus* and in the family Scrophulariaceae. The first published report of fasciation in Hawai'i was by Juvik & Juvik (1993). About 20 to 25% of *V. thapsus* plants in Hawai'i show fasciation, but the frequency varies among populations from 0 to about 45% (Ansari and Daehler, unpublished data). There are a few anecdotal reports of low frequencies of mild fasciation in some mainland U.S. populations, but extreme fasciation has not been observed in *V. thapsus* in its native range in Europe (Daehler, pers. comm.) nor in other introduced populations (Reinartz 1984a, b, c; Juvik & Juvik 1992). Even on the tropical island of La Reunion in the Indian Ocean, which is climatically similar to Hawai'i, *V. thapsus* does not exhibit fasciation (Juvik & Juvik 1993). Frequent and extreme stem and inflorescence fasciation in *V. thapsus* appears to be unique to the populations in Hawaii.

### **Control efforts in Hawai'i**

Very few governmental or private efforts have been made to control or eradicate *V. thapsus* in Hawai'i. About 5000 plants were uprooted and destroyed by student volunteers from 1984-1986 (Juvik & Juvik 1993) along the 5 km of the Mauna Kea summit road above Hale Pohaku (3000 -3300 m) and 6.2 km along the Mauna Loa access road (1900 - 2100 m). Manual removal of the plants before flowering and seed set appears to be a sure way of removing *V. thapsus* from an area. But, this method is quite labor intensive. Huge expanses of *V. thapsus* and the presence of cattle on Mauna Kea would make herbicide treatment of *V. thapsus* on Mauna Kea difficult. In Hawai'i

Volcanoes National Park, *V. thapsus* densities are about one-tenth of those found on Mauna Kea at similar elevation (Loh *et al.* 2000). It is in a relatively early stage of invasion in the park and has not reached its potential range. According to Loh *et al.* (2000), the large expanse that *V. thapsus* covers, its remoteness and the difficult terrain (a'a lava flows) make manual control very difficult. They recommend aerial surveys to identify and control peripheral populations and development of alternative methods to control in densely populated areas. A concentration of 10% Roundup herbicide applied to *V. thapsus* in the Hawaii Volcanoes National Park, killed the plants (Loh, pers. comm.). Herbicide treatment that inhibits seed germination and establishment has been suggested as a potentially effective means to control *V. thapsus* in the park. Obviously, such a treatment would potentially affect native species establishment as well. Long-term studies needed to understand both the potential impact of *V. thapsus* on native vegetation and the effectiveness of different control strategies.

TABLE 1. Herbicide treatments for control of *Verbascum thapsus*.

Herbicide	Rate	Time	Remarks	Reference
Mixture of 2, 4-D & 4, 5-T	16oz/acre	June or early September	Provides control. Not harmful to livestock.	Gross & Werner (1978).
Tebuthiuron	4-6 lb./acre initially with repeated application at half the rate.		Suppresses growth.	Gross & Werner(1978).
Diquat or Paraquat	1 lb. plus nonionic wetting agent	Seedling stage in autumn or early spring. 2 <sup>nd</sup> year plants must be in full rosette stage.	-	Mathews (1975)
Field master (Premix) (2 lb./gal acetochlor & 1.5 lb./gal atrazine & 0.75 lb./gal.	3.5-5 lb./ active ingredient/acre 7-10 pt./acre	Before, during or after planting but prior to crop emergence.	Rate varies by soil type.	Weed Control Manual 2000
Touchdown(5L or 6L) (sulphosate)	0.5-4lb. active ingredient/acre 0.8-6.4 pt. 5L/acre 0.66-5.33 pt. 6L/acre	Pre-plant, pre-emergence and post emergence	Addition of non-ionic surfactant required. Rate varies by weed species.	Weed Control Manual 2000
Glyphosate	0.38-1.5 lb. active ingredient/acre 0.56-2.25 pt. 5-4WS/acre. 0.75-3 pt. 4WS/acre.	Pre-plant, pre-emergence, spot treatment.	Rate varies by weed species. Larger weeds need higher rates. One of the constituents: Round up RT not listed for use in Hawaii.	Weed Control Manual 2000
Ally (DF) (metsulfuron-methyl)	0.1-0.3 oz. DF/acre	Post-emergence. In early spring when weeds are small & actively growing.	For use in all states except California.	Weed Control Manual 2000
Escort (DF) (metsulfuron methyl)	0.3-2 oz. DF/acre	Applied anytime except when ground is frozen.	Provides non-selective control; used for wide variety of broad-leaf weeds. Use restricted to certain states.	Weed Control Manual 2000
Telar (DF) (shlorsulfuron)	0.25-3 oz. DF/acre. On unimproved industrial turf:	Applied when weeds are actively growing	Not for use in certain areas of Colorado.	Weed Control Manual 2000

## LITERATURE CITED

- Arts-Damler, T. 1960. Cytogenetical studies on six *Verbascum* species and their hybrids. *Genetica* 31: 241-328.
- Bailey, S. F. 1939. The Mullein thrips. *Pan-Pacific Entomologist*. 15: 111-116.
- Baskin, J. M. & C. C. Baskin. 1981. Seasonal changes in germination responses of buried seeds of *Verbascum thapsus* and *V. blattaria* and ecological implications. *Canadian Journal of Botany* 59: 1769-1775.
- Bosy, J. L. & R. J. Reader. 1995. Mechanisms underlying the suppression of forb seedling emergence by grass (*Poa pratensis*) litter. *Functional-Ecology* 9(4): 635-639.
- Bruckart, W. L. & J. W. Lorbeer. 1976. Cucumber mosaic virus in weed hosts near commercial fields of lettuce and celery. *Phytopathology* 66: 253-259.
- Buchanan, E. L. 1937. Notes on Curculionidae (Coleoptera). *Journal of Washington Academy of Science* 27: 312-316.
- Charnov, E. L. & W. M. Schaffer. 1973. Life history consequences of natural selection: Cole's result revisited. *American Naturalist* 107: 791-793.
- Clapham, A. R., T. G. Tutin & E. F. Warburg. 1952. *Flora of the British Isles*. University Press. Cambridge.
- Daehler, C. C. 1999. Department of Botany. University of Hawaii at Manoa. *Personal communication*.
- Darlington, H. T. & G. P. Steinbauer. 1961. The eighty year period of Dr. Beal's seed viability experiment. *American Journal of Botany*. 48: 321-325.
- Darlington, C.D. & A. P. Wylie. 1955. *Chromosome atlas of flowering plants*. 2<sup>nd</sup> ed. Allen and Unwin Ltd. London.
- Darwin, C. R. 1889. *The different forms of flowers on plants of the same species*. D. Appleton and Co. New York.
- 
- Donnelly S. E., J. L. Christopher & L. W. Aarssen. 1998. Pollination in *Verbascum thapsus* (Scrophulariaceae): The advantage of being tall. *American Journal of Botany* 85(11): 16168-1625.
- Farrell-J-A, & M. W. Stufkens. 1993. Phenology, diapause, and overwintering of the wheat bug, *Nysius huttoni* (Hemiptera: Lygaeidae), in Canterbury, New Zealand. *New Zealand Journal of Crop and Horticultural-Science* 21(2): 123-131.
- Glier, J. H. & J. L. Caruso. 1973. Low temperature induction of starch degradation in roots of a biennial weed. *Cryobiology* 10: 328-330.
- Glier, J. H. & J. L. Caruso. 1977. Influence of gibberellin on activities of starch degradative enzymes and phosphatase in *Verbascum thapsus*. *Plant Physiology* 39: 21-24.

- Gross, K. L. & P. A. Werner. 1978. The biology of Canadian weeds 28. *Verbascum thapsus* L. and *V. blattarai* L. *Canadian Journal of Botany* 58: 401-413.
- Gross, K. L. 1980. Colonization by *Verbascum thapsus* (mullein) of an old field in Michigan: Experiments in the effects of vegetation. *Journal of Ecology* 68: 919-927.
- Gross, K. L. 1981. Predictions of fate from rosette size in four 'Biennial' plant species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota* and *Tragopogon dubius*. *Oecologia* 48: 209-213.
- Gross, K. L. & P. A. Werner. 1982. Colonizing abilities of "biennial" plant species in relation to ground cover: implications for their distribution in a successional sere. *Ecology* 63: (4): 921-9-31.
- Harper, J. L. 1977. *Population Biology of Plants*. Academic Press Inc. San Diego, California
- Hart, R. 1977. Why are Biennials so few? *The American Naturalist*. 111: 792-799.
- Heming, B. S. 1968. Postembryonic development of the female reproductive system in *Frankliniella fusca* (Thrippidae) and *Haplothrips verbasci* (Phlaeothripidae) (Thysanoptera). *Mullein thrips in Miscellaneous publications of the Entomological Society of America* vol 7 no 2.
- Hirose, T. 1983. A graphical analysis of life history evolution in biennial plants. *The Botanical Magazine* 96: 37-47.
- Jingwei, Z. 1982. *The alpine plants of China*. Science press, Beijing, China.
- Julien, M. H. & M. W. Griffiths. 1998 *Biological Control of Weeds: a world catalog of agents and their target weeds*. CABI. Wallingford, UK.
- Juvik, J. O. & S. P. Juvik. 1993. Mullein (*Verbascum thapsus*) the spread and adaptation of a temperate weed in the montane tropics. In *Alien plant invasions in native ecosystems of Hawaii, Management and Research*, ed. C.P. Stone, C.W. Smith and T. Tunnison, 254-270. University of Hawaii Cooperative National Park Studies Unit. Honolulu: University of Hawaii Press.
- Juvik, J. O. 1999 Univeristy of Hawaii at Hilo. Hilo. *Personal communication*.
- Juan, R., I. Fernandez & J. Pastor. 1997. Systematic consideration of microcharacters of fruits and seeds in the genus *Verbascum* (Scrophulariaceae). *Annals of Botany* 80: 591-598.
- Kelly, D. 1985. On strict and facultative biennials. *Oecologia* 67: 292-294.
- Loh, R. 1999. Vegetation Management Program, Hawaii Volcanoes National Park, Hawaii. *Personal communication*.

- Loh, R., A. Ainsworth, B. Miner, J. Makaie & J. T. Tunison. 2000. Mullein survey and removal efforts on Mauna Loa in Hawaii Volcanoes National Park. University of Hawaii Cooperative National Park Studies Unit. Honolulu Technical Report 126, Honolulu, HI.
- Lortie, C. J. & L. W. Aarssen. 1997. Apical dominance as an adaptation in *Verbascum thapsus*: effects of water and nutrients on branching. *International Journal of Plant Sciences* 158(4): 461-464
- Lortie, C. J. & L. W. Aarssen. 1999. The advantage of being tall: Higher flowers receive more pollen in *Verbascum thapsus* L. (Scrophulariaceae). *Ecoscience* 6 (1): 68-71.
- Löve, A. & D. Löve. Chromosome numbers of central and northwest European species. *Opera Botanica* 5:1-581.
- Mathews, L. J. 1975. *Weed Control Manual*. Government printer, Wellington, New Zealand.
- McCutcheon, A. R., T. E. Roberts, E. Gibbons, S. M. Ellis, L. A. Babiuk & R. E. W. Hancock. 1995. Antiviral screening of British Columbian medicinal plants *Journal-of-Ethnopharmacology* 49 (2) 101-110.
- McLean, R. C. & W. R. Ivimey-Cook. 1956. *Text book of theoretical botany*. Vol II. Longmand, Greene and Co., London.
- Medeiros, A. 1998. USGS Pacific Islands Ecological Research Center. Haleakala. *Personal communication*.
- Mitch, L. W. 1989. Common mullein - the roadside torch parade. *Weed Technology* 3: 704-705.
- Millsbaugh, C. F. 1974. *American medicinal plants*. Dover Publishing. Inc. New York.
- Mulligan, G. A. 1961. Chromosome numbers of Canadian Weeds. *Canadian Journal of Botany* 37: 1057-1066.
- Munyaneza, J. & J. E. McPherson. 1994 Comparative study of life histories, laboratory rearing, and immature stages of *Euschistus servus* and *Euschistus variolarius* (Hemiptera: Pentatomidae). *Great-Lakes-Entomologist* 26(4): 263-274.
- Murbeck, Sv. 1933. *Monographie der Gattung Verbascum*. [In Swedish and Latin]. Lunds Univers. Arsskr., N. F., Avd. 2, 29: 1-630.
- Myers, J. H. & C. Risley. 2000. Why reduced seed production is not necessarily translated into successful biological weed control, in *Proceedings of the X International Symposium on Biological Control of Weeds*. N. Spencer, editor. Montana State University, Bozeman, Montana.
- Naber, A. C. & L. W. Aarssen. 1998. Effects of shoot apex removal and fruit herbivory on branching, biomass and reproduction in *Verbascum thapsus* (Scrophulariaceae). *American Midland Naturalist* 140: 42-54.

- Nagata, R. 2000 Haleakala National Park. *Personal communication*.
- Odum, S. 1965. Germination of ancient seeds. *Dansk Botanisk Arkiv* 24: 70.
- Orvin, C. B., R. G. Wilson, W. Weisberg & K. G. Hubbard. 1996. Seed longevity of 41 weed species buried 17 years in eastern and western Nebraska. *Weed Science* 44: 74-86.
- Packer, J. G. 1964. Chromosome numbers and taxonomic notes on Western Canadian and Arctic plants. *Canadian Journal of Botany* 42: 473-494.
- Parham, B.E.V. & A. J. Healy. 1976. *Common weeds in New Zealand - An illustrated guide to their identification*. Government printer, Wellington, New Zealand.
- Parkhurst, D. F. 1976. Effects of *Verbascum thapsus* L. Leaf hairs on heat and mass transfer: A reassessment. *New Phytologist*. 76: 453-457.
- Pennell, F. W. 1935. The Scrophulariaceae of eastern north temperate America. *Academy of Natural Science Monograph*. No 1. George W. Carpenter Fund. Philadelphia.
- Polunin, O. *Flowers of Europe*. 1969. Oxford University Press, London.
- Reichard, S. 1999. University of Washington, Seattle, Washington. *Personal communication*.
- Reinartz, J. A. 1984a.. Life history variation of common mullein (*Verbascum thapsus*) I. Latitudinal differences in population dynamics and timing of reproduction. *Journal of Ecology* 72: 897-912.
- Reinartz, J. A. 1984b. Life history variation of common mullein (*Verbascum thapsus*). II. Plant size, biomass partitioning and morphology. *Journal of Ecology* 72: 913-925.
- Reinartz, J. A. 1984c. Life history variation of common mullein (*Verbascum thapsus*). III. Differences among sequential cohorts. *Journal of ecology* 72: 927-936
- Ricklefs R. E. 1997. Life Histories in *The Economy of Nature*. 231-253. W. H. Freeman and Company. New York. USA
- Salisbury, E. J. 1942. *The reproductive capacity of plants*. Bell, London.
- Schischkin, B. K. & E. G. Bobrov. 1997. Solanaceae and Scrophulariaceae. Vol 22, in *Flora of USSR*. Amerind publishing co. pvt. ltd., New Delhi, India.
- Semenza, R. J. & R. A. Evans. 1978. Influence of light and temperature on the germination and seedbed ecology of common mullein (*Verbascum thapsus*). *Weed Science* 26(6): 577-581.
- Silvertown, J. W. 1983. Why are Biennials sometimes not so few? *American Naturalist* 121: 448-453.
- Sleeper, E. L. 1954. A European weevil in North America. *Entomological News* 65: 129-130.

- Stace, C. A. 1975. *Hybridization and the flora of British Isles*. Academic Press. London.
- Thistlewood, H.M.A., J. H. Borden & R. D. McMullen. 1990. Seasonal abundance of the mullein bug, *Campylomma verbasci* (Meyer) (Heteroptera: Miridae), on apple and mullein in the Okanagan valley. *The Canadian Entomologist* 122:1045-1058.
- Toole, E. H. & E. Brown. 1946. Final results of the Duvel buried seed experiment. *Journal of Agricultural Research* 72: 201-210.
- Tosserams, M., E. Bolink & J. Rozema. 1997. The effect of enhanced ultraviolet-B radiation on germination and seedling development of plant species occurring in a dune grassland ecosystem. *Plant Ecology* 128: 138-147.
- Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters & D. A. Webb . 1972. Diapensiaceae to Myoporaceae, Vol 3 in *Flora Europea* . Cambridge University Press. Cambridge.
- Unites States Department of Agriculture. 1960. *Index of plant diseases*. USA Agricultural Handbook. 165. U.S. Govt Print Office, Washington D. C.
- Vanlerberghe, K.A. & J. Van Assche. 1986. Dormancy phases in seeds of *Verbascum thapsus* L. *Oecologia* 68(3): 479-480.
- Wagner, W. L., D. R. Herbst & S. H. Sohmer. 1990. *Manual of flowering plants of Hawaii*. University of Hawaii Press. Honolulu.
- Webb, D. A. 1967. *An Irish flora*. Dundalgan Press, Ltd. Dundalk.
- Weed Control Manual 2000*. Meister Publishing Co., Salem, MA.
- Wescott, C. L. 1990. *Plant disease handbook*. P. van. Nostrand Co.Inc. Princeton, N. J.
- Whitson, T. D., L. C. Burrill, S. A. Dewey, D. W. Cudney, B. E. Nelson R. Lee & R. Parker. 1991. *Weeds of the west*. Pioneer of Jackson Hole. Wyoming.
- Wilhelm, G. Jr. 1974. The Mullein: plant piscicide of the mountain folk culture. *Geographic Review* 64: 235-252.
- Williams, G. J. III. & P. R. Kemp. 1976. Temperature relations of photosynthetic response in populations of *Verbascum thapsus* L. *Oecologia* 25: 47-54.
- Williams, G. J. III & B. A. Horwitz. 1972. Ecological implications of bioelectric response action spectra of high and low elevation populations of *Verbascum thapsus* L. *Photosynthetica* 6(4): 394-400.
- Williams, G.J., P. R. Kemp & K. Oulton. 1977. Anatomical, physiological and biochemical evidence for the C<sub>3</sub> pathway in *Verbascum thapsus*. *New Phytologist* 79: 489-492.

Williams, G. J., R. Lazor & P. Youngrau. 1975. Temperature adaptations in the Hill reaction of altitudinally and latitudinally diverse populations of *Verbascum thapsus*. *Photosynthetica* 9:35-39.

Woodman, R. L. & F. G. Wilson. 1991. Differential mechanical defense: herbivory evapotranspiration, and leaf-hairs. *Oikos* 60: 11-19.

White, O. E. 1945. The Biology of Fasciation and its relation to abnormal growth. *Journal of Hereditary* 36: 11-22.

Wuenschel, J. E. 1970. The effect of leaf hairs of *Verbascum thapsus* on leaf energy exchange. *New Phytologist*. 69: 65-73.