

# MULLEIN (VERBASCUM THAPSUS): THE SPREAD AND ADAPTATION OF A TEMPERATE WEED IN THE MONTANE TROPICS

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## ABSTRACT

Common mullein (*Verbascum thapsus*) is a rosette, biennial weed native to temperate Eurasia and naturalized worldwide in suitable mid-latitude environments, where it frequently is considered a pest. The species tolerates a wide range of environmental conditions and is particularly adapted as an early successional pioneer in disturbed dry and rocky sites. *Verbascum thapsus* was introduced to the island of Hawai'i sometime around 1900 and has since spread into dry montane environments on the slopes of Mauna Kea, Mauna Loa, and Hualālai volcanoes. On the Indian Ocean island of La Réunion (environmentally similar to Hawai'i), mullein has also recently become established in comparable montane zones. A quantitative survey of roadside mullein populations along the Saddle Road ascending the slopes of Mauna Kea and Mauna Loa resulted in determination of the morphological variation along steep topo-climatic gradients. Over the elevational range of occurrence (5,330 to 10,800 ft or 1,625-3,300 m), roadside mullein densities reached a maximum of 9-17 plants/100 ft<sup>2</sup> (100-180/100 m<sup>2</sup>) in the zone between 5,900 and 6,560 ft (1,800-2,000 m). The altitude-density relationship for mullein on the island of La Réunion is nearly identical to that on Hawai'i and demonstrates the vulnerability of other tropical mountain areas to invasion. Over the elevational range of mullein on Mauna Kea the species exhibits striking variation in gross morphology and life history. Both mean rosette diameter and plant height increase with elevation. Above 8,200 ft (2,500 m) "gigantism" is common, with some plants reaching nearly 13 ft (4 m) in height, double the maximum height recorded for this species in its native European habitat. Additionally, with increasing elevation there is a strong tendency toward polycarpy and extreme stem fasciation, resulting in increased woodiness. These morphological trends appear consistent with an adaptive model proposed to explain the development of insular arborescence in rosette weeds. Control and eradication of mullein is made difficult by extensive seed viability (up to 100 years). In order to develop eradication strategies, the spatial configuration and population structure of selected *V. thapsus* colonies were documented prior to removal in order to facilitate long-term study of recolonization and site persistence.

## INTRODUCTION

Common mullein (*Verbascum thapsus*: Scrophulariaceae), a monocarpic and biennial Eurasian weed, is widely naturalized in North America and other temperate areas of the world including Australia and New Zealand. Various medicinal properties and other folk culture uses (e.g., piscicide) are attributed to the plant and may, in part, explain its widespread introduction (Wilhelm 1974). In its native European habitat and other temperate areas, mullein is an early succession colonizer of disturbed dry and rocky sites and is able to survive under a broad range of environmental conditions (Williams *et al.* 1975; Semenza and Evans 1978; Reinartz 1984a).

The species is generally characterized as an obligate biennial, with flowering dependent on the number of growing seasons required to reach a critical size. However, naturalized populations in North America range from annuals (Georgia) to triennials (Canada) as a function of both environmental and competitive factors (Gross 1981; Reinartz 1984b). The flowering spike (up to 6.5 ft or 2 m in height) may produce 150,000 seeds of comparatively small size (0.03 in. or 0.65-0.75 mm) with no specific adaptations for dispersal (Baskin and Baskin 1981). Indeed, studies have shown that under normal conditions more than 80% of all seedfall occurs within 23 ft (7 m) of the parent plant (Gross and Werner 1978). It appears that the early successional strategy of mullein rests more on extreme seed viability (50-100 years or more) than on long-distance dispersal (Kivilaan and Bandurski 1933; Manning 1965). Mullein cannot compete under situations of dense herbaceous groundcover, but seeds can remain dormant in the soil until vegetation disturbance provides suitable conditions for germination.

Mullein has become an aggressive adventive in most temperate areas of introduction, but little has been written on the impact of this species in the montane tropics. It may be argued that climatic barriers protect tropical mountains from invasion by temperate weed species to some extent. Inadvertent introductions in the tropics would be more likely to occur in the lowlands (rather than isolated mountain peaks), and plants would necessarily face the difficulty of dispersing upward into environmentally favorable montane zones. Wester and Juvik (1983) have shown that in Hawai'i the alien roadside weed flora along a highway ascending Mauna Loa Volcano changes gradually with elevation from a species assemblage dominated by pantropical lowland weeds to one composed primarily of extratropical temperate species at higher elevations. At least in the case of Hawai'i, introduced temperate weed species appear able to successfully colonize the climatically favorable montane zone. Some pest species such as gorse (*Ulex europaeus*) have been directly introduced into montane pastures.

On the island of Hawai'i, mullein provides a classic example of an introduced temperate weed that has successfully spread throughout mid- and high-elevation areas of the Island, achieving serious pest status (Smith 1985). First established in the Kona district of Hawai'i sometime between 1900 and 1910, it is unclear whether the species was an intentional or

inadvertent introduction (L.W. Bryan, pers. comm. 1983). The first documented herbarium accession (B.P. Bishop Museum, Honolulu) of mullein in Hawai'i was for specimens collected near the summit of Hualalai Volcano (elev. 8,270 ft or 2,520 m) by L.W. Bryan in 1932. Other Bishop Museum accession sheet comments indicate that the species was "dominant on the South Slope of Hualalai between 7,700-7,900 ft" by 1946 and had spread into the central plateau or saddle area between Mauna Kea and Mauna Loa by 1948. Over the past several decades mullein has expanded its range in both roadside habitats and remote upland areas on Mauna Kea, extending to above 10,800 ft (3,300 m) along the summit access road (Fig. 1).

This study presents results of a quantitative analysis of roadside *V. thapsus* populations along steep altitudinal gradients on the slopes of Mauna Loa and Mauna Kea. The study was undertaken to define both the elevational range and the ecologically optimal zone of the species. In addition, the incidence of morphological abnormalities was recorded for correlation with altitude/climate gradients on the mountain slopes. The Hawai'i data were compared with roadside *V. thapsus* populations sampled along an elevational gradient on the Indian Ocean island of La Réunion (Fig. 2), which is environmentally similar to Hawai'i (Cadet 1974, 1980). The observations are used to illustrate the vulnerability of other tropical montane areas of the world to *V. thapsus* invasion.

This paper also reports on problems associated with *V. thapsus* control and eradication efforts undertaken from 1984 through 1986 on Mauna Loa and Mauna Kea.



Figure 1. *Verbascum thapsus* colonization of roadside areas on Mauna Kea (elevation 2,500 m) near sampling site 6, 1983.

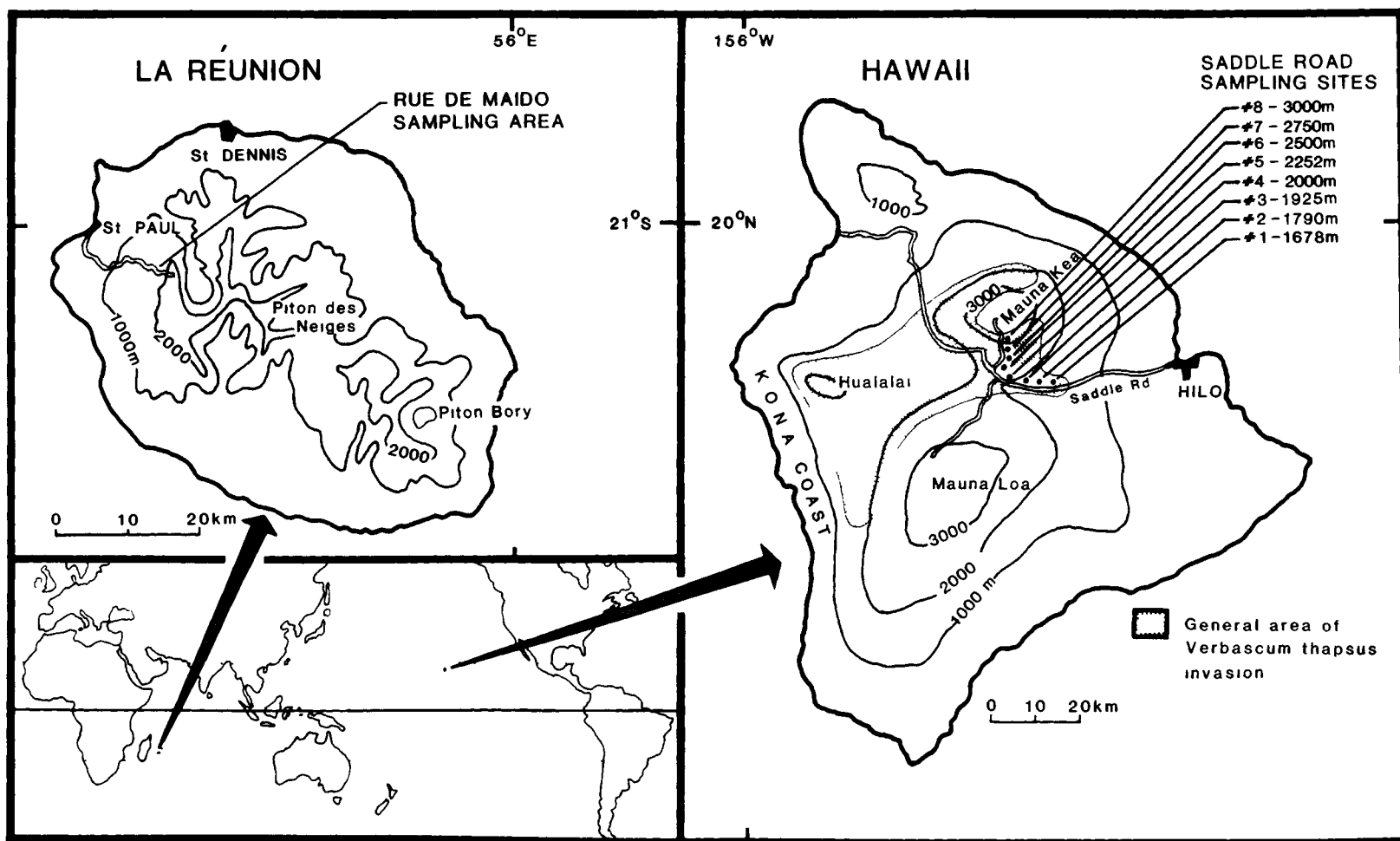


Figure 2. Location of study areas in La Réunion and Hawai'i.

## MATERIALS AND METHODS

A review of published and unpublished references and local herbarium accessions of mullein was undertaken to document the early introduction and spread of this species on the island of Hawai'i. The general limits of distribution of the species in the uplands of Hawai'i were extracted from mountain vegetation surveys (114 transects with 7,438 sampling stations) established in conjunction with the U.S. Fish and Wildlife Service Hawai'i Forest Bird Survey (Jacobi and Scott 1985).

Intensive quantitative sampling of roadside mullein populations was undertaken during 1985 at eight sites along the Saddle Road and Mauna Kea summit road between the elevations of 5,500 and 9,850 ft (1,678 m-3,000 m) (Fig. 2). Along the Saddle Road, sample sites were established at odd-numbered mile markers between the lower elevational limit of the species (5,500 ft or 1,678 m at the 21-mile marker) and 6,560 ft (2,000 m) (27-mile marker). Above 6,560 ft (2,000 m) on the Mauna Kea summit road, sampling sites 5-8 were located at altitudinal intervals of 820 ft (250 m). At each sampling site, belt transects 6.6 ft (2 m) wide and of variable lengths were laid out on the roadside verge, parallel to and 1.65 ft (0.5 m) from the pavement. Identical sampling areas were established on both sides of the highway at each site. Total sampling area varied from site to site depending on mullein density and was controlled to insure that each sample included a minimum of 100 live plants and at least 30 mature plants (flowering or fruiting). Site sampling areas ranged from 34,660 ft<sup>2</sup> (3,220 m<sup>2</sup>) in areas of sparse mullein occurrence to 2,150 ft<sup>2</sup> (200 m<sup>2</sup>) in high-density situations. Within each sampling area, all plants with a rosette diameter of 1.97 in. (5 cm) or larger were measured for rosette diameter, height of flowering spike (if present), reproductive state (budding, flowering, seeding, senescence), presence of any anatomical abnormalities including degree of fasciation, and the presence of polycarpy (basal, medial, or terminal secondary rosettes or flowering spikes).

Sampling in the Rue de Maito area of La Réunion Island (where the species is relatively uncommon as compared with Hawai'i) was restricted to recording mullein abundance in 1.24 mi x 3.24 ft (2 km x 1 m) roadside transects between road kilometer markers over the elevational range 4,920 to 6,890 ft (1,500-2,100 m). No unusual anatomical abnormalities were observed in the La Réunion mullein populations, so morphological data comparable to that collected in Hawai'i were not obtained. Relevant climatological data for the transect areas in Hawai'i and La Réunion were extracted from recent compilations (Hawaii Department of Land and Natural Resources 1970; Juvik *et al.* 1978; Cadet 1980; Hawaii Department of Planning and Economic Development 1985).

## RESULTS AND DISCUSSION

### General Distribution

The major areas of heavy mullein invasion on the island of Hawai'i generally include the leeward uplands (3,940 to 9,840 ft or 1,200-3,000 m) of Mauna Loa, Mauna Kea, and Hualālai (Fig. 2). The species also occurs

sporadically in areas outside this zone, including windward Mauna Loa and even a few sea level locations on the arid west coast of the Island. The area of major mullein invasion and spread corresponds generally to that part of the Island with a temperate, summer-dry climate analogous to that found in the species' native range (Mediterranean Europe). As an example of this striking climatic similarity, Humu'ula, a meteorological station within the study area (elevation 6,700 ft or 2,043 m, near sampling site 4), has a mean annual temperature of 52 F (11 C) and annual rainfall (winter concentrated) of 40 in. (1,013 mm). These values are very similar to Mediterranean locations like Milan, Italy (57 F or 13.7 C and 38 in. or 960 mm). The hot, dry summers of the upland interior of Hawai'i result from a strengthening of the subsidence inversion over the Islands, which generally restricts significant summer rainfall to areas below 5,900 ft (1,800 m). However, this summer-dry condition is somewhat mitigated by frequent mist and fog (undetected in the rainfall records) associated with orographic clouds that hug the middle slopes of the mountain (Juvik *et al.* 1978). Mullein appears to thrive in this climatic regime and has successfully invaded an area of over 770 mi<sup>2</sup> (2,000 km<sup>2</sup>) in less than 70 years. On the island of La Réunion, *V. thapsus* has not yet achieved widespread distribution and pest status comparable to that found in Hawai'i. No information is available on the date of introduction in La Réunion; however, its limited distribution would suggest a comparatively recent arrival. Currently restricted to roadside areas of the Rue de Maïdo between 4,920 and 6,890 ft (1,500-2,100 m) elevation, the species has yet to colonize the more extensive volcanic ash and cinder areas surrounding the active volcano at Piton Bory (Fig. 2).

### Altitudinal Range and Abundance

In windward areas of the Saddle Road above Hilo, the species reaches its low-altitude limit at 5,330 ft (1,625 m) (Table 1). Below this elevation, mullein appears to be usually excluded from the roadside verge by other aggressive weeds better adapted to warm and wet conditions (Wester and Juvik 1983). The competitive exclusion hypothesis appears confirmed by the fact that mullein has recently been able to sporadically colonize lower windward locations (down to 2,620 ft or 800 m) along the Saddle Road verge where road-widening projects cleared all existing verge vegetation in 1986. Mullein densities in the roadside verge reach 15-18 plants/100 ft<sup>2</sup> (160-190/100 m<sup>2</sup>) in the zone between 6,230 and 6,560 ft (1,900- 2,000 m) (Fig. 3). The substantially lower densities (of about 8.3 plants/100 ft<sup>2</sup> or 90 plants/100 m<sup>2</sup>) recorded between 7,380 and 8,200 ft (2,250-2,500 m) (sites 5 and 6) may be a result of the open cattle range in this area, where managed pasture grasses may act to reduce mullein densities along the verge. The plant does not appear to be eaten by cattle even under poor forage conditions, as *V. thapsus* colonies were well distributed throughout pastures even in overgrazed areas. Roadside mullein densities diminished rapidly above 9,020 ft (2,750 m) elevation, where the species reaches its present limit at 10,830 ft (3,300 m) on Mauna Kea.

Along the Rue de Maïdo sampling area on La Réunion, plant densities were much lower than on Hawai'i (Table 2), reaching a maximum of only 0.86 plants/100 ft<sup>2</sup> (9.3/100 m<sup>2</sup>) at the road summit (6,890 ft

**Table 1. Characteristics of *Verbascum thapsus* populations in roadside habitats on Mauna Loa and Mauna Kea, island of Hawai'i.**

Sample Sites <sup>1</sup>	Elevation (m)	Sample Area (m <sup>2</sup> )	Live Plants <sup>2</sup>	Density/ 100 m <sup>2</sup>	Relative Density <sup>3</sup> (%)	Rosette Diameter: <sup>4</sup> mean and (range) (cm)	Height: <sup>5</sup> mean and (range) (cm)	Extreme Fasciation % of mature plants <sup>6</sup>	Multiple Shoots % of mature plants <sup>7</sup>
1	1,678	3,220	179	5.6	2.9	17.4 (5-46)	79.6 (48-183)	0	11.8
2	1,790	3,220	382	11.9	16.6	17.3 (5-48)	70.3 (37-143)	0	27.5
3	1,925	688	1,107	160.9	83.8	12.6 (5-36)	71.5 (34-194)	0	6.0
4	2,000	200	384	192.0	100.0	12.9 (5-62)	84.5 (61-198)	4.8	14.2
5	2,250	500	474	94.8	49.4	18.7 (5-65)	96.8 (30-220)	7.7	46.1
6	2,500	250	217	88.6	46.1	25.9 (5-110)	140.7 (51-323)	35.1	40.8
7	2,750	250	276	110.4	57.5	20.8 (5-70)	108.7 (25-245)	31.5	57.4
8	3,000	1,000	135	13.5	7.0	27.3 (5-148)	111.1 (34-178)	9.1	59.1

1 Location of sampling sites shown in Figure 2.

2 Only *V. thapsus* plants with a basal rosette diameter >5 cm were recorded. Standing dead plants were also recorded but not included in this tabulation.

3 Relative density = density expressed as a percentage of highest density recorded (Site 4).

4 For the two altitudinal sampling sites (3 and 8) showing the greatest difference in mean rosette diameter, differences are statistically significant ( $t = 8.4$ ;  $p < 0.01$ ). For altitudinally adjacent sampling sites 2-3, 4-5, 5-6, 6-7, and 7-8, differences in mean rosette diameter are also statistically significant ( $p < 0.01$ ).

5 Height data were recorded only for mature plants with an inflorescence spike (including standing dead plants). For the two altitudinal sampling sites (2 and 6) showing the greatest difference in mean plant height, differences were statistically significant ( $t = 8.8$ ;  $p < 0.01$ ). For the altitudinally adjacent sampling sites 5-6, and 6-7, differences in mean plant height were also statistically significant ( $p < 0.01$ ).

6 Extreme fasciation was arbitrarily defined as stem flattening sufficient to produce a maximum cross-sectional diameter more than three times the minimum cross-sectional diameter (non-fasciated stems are generally cylindrical; see Figure 9).

7 Included are plants with either (or both) multiple basal rosettes or multiple flowering spikes.

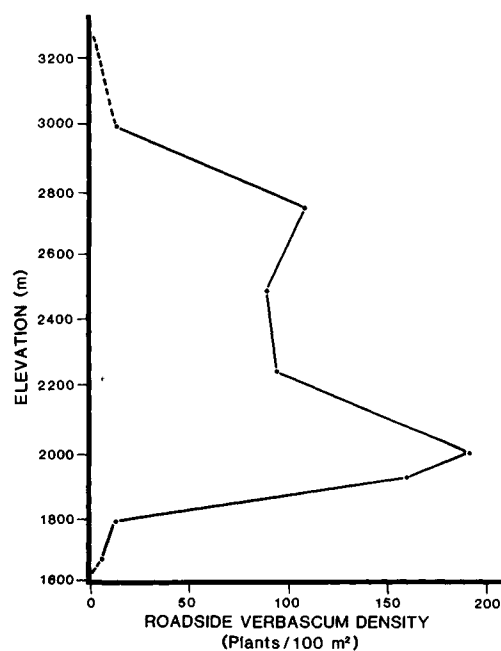


Figure 3. Variation in roadside *Verbascum thapsus* density at different elevations on Mauna Loa and Mauna Kea, 1985.

Table 2. Common mullein density in roadside habitats along the Rue de Mado, La Réunion.

Sample Site*	Elevation** (m)	Live plants	Density/ 100 m <sup>2</sup>	Relative Density (%)***
1	1,500	3	0.15	1.6
2	1,664	6	0.30	3.2
3	1,840	32	1.60	17.3
4	1,973	177	8.85	95.6
5	2,085	185	9.25	100.0

\* Sampling areas were 2,000 m<sup>2</sup>, consisting of roadside verge area 1 m wide x 2 km long.

\*\* Mid-point elevation within each 2-km long sample area.

\*\*\* Site density expressed as % of site 5 density.

or 2,100 m). For general comparative purposes, the Hawai'i and La Réunion data were converted to "relative density," where densities at each elevation were expressed as a percentage of the value at the site of the highest density (i.e. site 4 at 6,560 ft (2,000 m) in Hawai'i and the summit site at 6,890 ft (2,100 m) in La Réunion). The striking similarities in altitude-relative density relationships between the two sites (Fig. 4) mirror the environmental similarity of these geographically disparate islands and the apparent preference for mid-elevation, tropical montane sites climatically analogous to southern Europe. The parallel invasion patterns in Hawai'i and La Réunion suggest the general susceptibility of other high-elevation tropical montane environments.

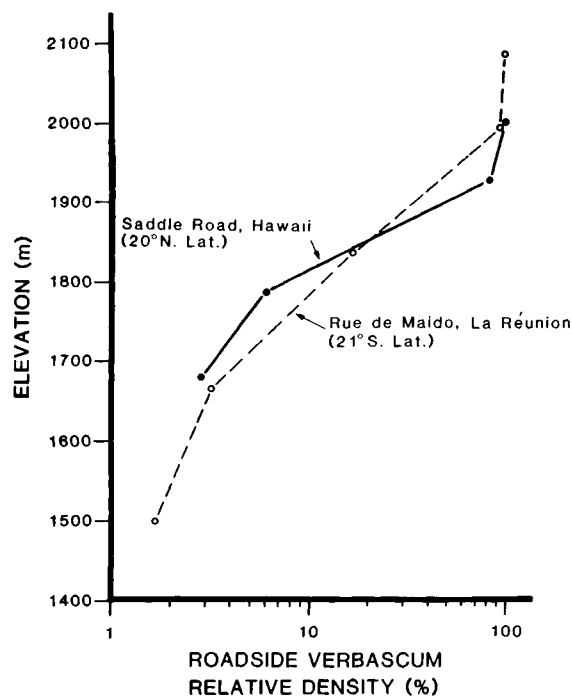


Figure 4. Variation in relative density (see text) of *Verbascum thapsus* along altitudinal transects in Hawai'i and La Réunion.

### Plant Size in Relation to Altitude

Mean rosette diameter of mullein increased with elevation to a maximum of 10.75 in. (27.3 cm) at the highest sampling site (8, at 9,840 ft or 3,000 m) in Hawai'i (Fig. 5). This value is more than double the mean rosette diameter at lower elevation sites 3 and 4, and differences are statistically significant (Table 1). While a large number of young plants at some lower elevations might account for the observed trend in sample means, examination of the maximum rosette diameter recorded at each site confirms the same relationship (Table 1). Below 6,560 ft (2,000 m), the largest rosette diameters recorded at different sites were 14.2 to 18.9 in. (36-48 cm), while at 8,200 ft (2,500 m) and above, maximum rosette diameters ranged from 27.6 to 58.3 in. (70-148 cm).

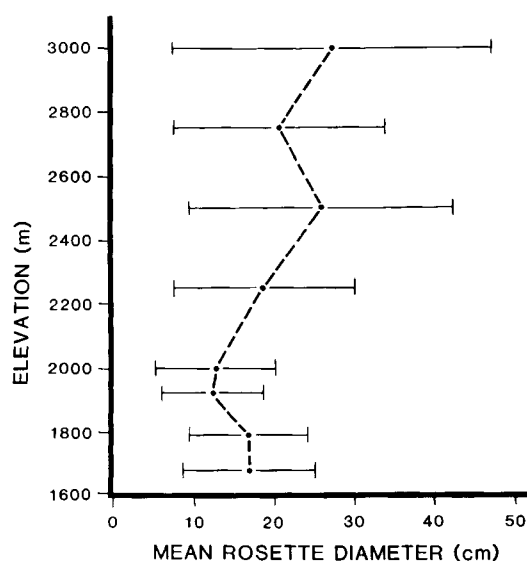


Figure 5. Altitudinal variation (mean  $\pm$  1 std. dev.) in mean rosette diameter of *Verbascum thapsus* on Mauna Loa and Mauna Kea, 1985. (Only plants with rosette diameters  $\geq$  5 cm were measured.)

For mature plants bearing an inflorescence spike, mean plant height data show an altitudinal pattern similar to rosette diameter (Fig. 6). A maximum mean height of 55.4 in. (140.7 cm) was recorded at 8,200 ft (2,500 m), approximately double that recorded for mature plants at elevations below 6,560 ft (2,000 m) (Table 1). An elevational trend toward gigantism is clearly evident in both the height and diameter data. It should be noted that the maximum height of mullein within its native Eurasian range is generally given as 7.6 ft (2.3 m) (Manning 1965; Gross and Werner 1978). On the upper slopes of Mauna Kea specimens exceeding 10 ft (3 m) and occasionally 13 ft (4 m) in height are not unusual. The increase in plant stature with elevation may be related to optimal conditions for increased net photosynthesis in the Hawaiian subalpine zone, since solar radiation increases with elevation (Hawaii Department of Planning and Economic Development 1985), while air temperature (and hence plant respiration losses) decrease.

### Morphological Abnormalities

Stem fasciation involves abnormal flattening of the main shoot axis resulting from the gradual expansion of the growing point in one plane. Sinnott (1960) reported fasciation in a wide range of plants resulting from a variety of factors, including mutilation and wounds, application of growth substances, and such environmental factors as short day length. Il'yenko (1982) observed fasciation in *V. thapsus* "adapting to new conditions" under cultivation. On Mauna Kea extreme fasciation of the flowering spike is common at high elevation and frequently produces grotesquely deformed and twisted flowering heads (Fig. 7). No fasciation was noted on mature plants growing below 6,560 ft (2,000 m), while at 8,200 to 9,020 ft (2,500-2,750 m) elevation, extreme fasciation was exhibited by 31-35% of all mature plants (Fig. 8). One of the consequences of extreme

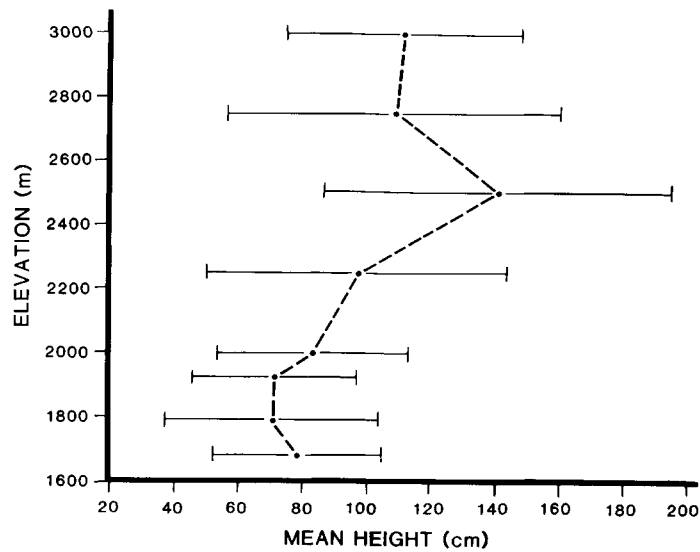


Figure 6. Altitudinal variation in mean height ( $\pm 1$  std. deviation) of *Verbascum thapsus* flowering stocks on Mauna Loa and Mauna Kea, 1985.



Figure 7. *Verbascum thapsus* plants illustrating extreme fasciation and multiple axillary shoots at high elevation on Mauna Kea.

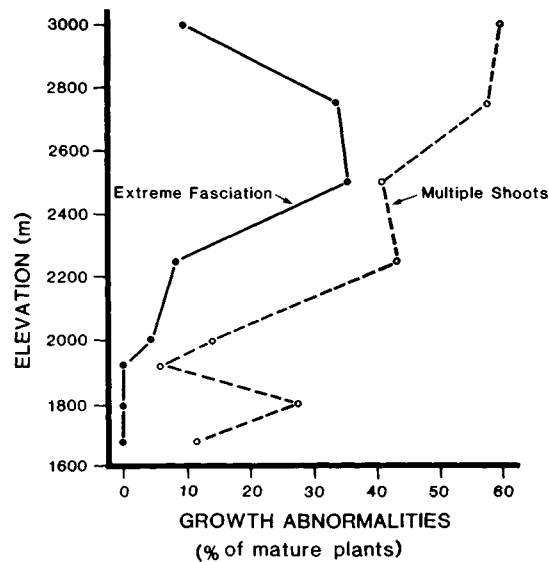


Figure 8. Altitudinal variation in percentage of mature *Verbascum thapsus* plants exhibiting growth abnormalities including extreme fasciation and multiple axillary shoots, 1985.

fasciation is a dramatic increase in stem bulk and woodiness (Fig. 9). Carlquist (1974 and pers. comm. 1986) has reported the effect of severe frost on the growth of several monocarpic Canary Island *Echium* species under cultivation at Claremont, California. Although *Echium* species, native to high elevations, evidenced little frost damage, one mid-elevation species, *Echium pininana* (native to frost-free areas), exhibited leaf damage and subsequent fasciated stem growth by all individuals. *Verbascum thapsus* in its native European range does not normally experience diurnal frosts during the active summer growing season. On Mauna Kea, diurnal frosts may occur throughout the year at high elevation but are rare at elevations below 9,020 ft (2,750 m). The elevational pattern in observed mullein fasciation (Fig. 8) is generally consistent with a frost damage hypothesis.

Although usually described as a monocarpic plant, *V. thapsus* may exhibit a variety of polycarpic growth forms, including multiple basal rosettes and multiple flowering shoots situated basally, medially, or terminally from the primary flowering spike or from separate basal rosette clusters (Fig. 7). The tendency toward a multiple shoot growth habit also shows a strong elevational trend, generally similar to that of fasciation. However, the percentage of mature plants with multiple shoots continues to increase above 9,020 ft (2,750 m), reaching a maximum of 59% near the upper limit of the species range at 9,840 ft (3,000 m) (Fig. 8).

Over the comparatively short period of time since mullein first began colonizing the upper slopes of Mauna Kea in the 1940s, significant



Figure 9. Plane and cross sectional views of *Verbascum thapsus* flowering spikes illustrating normal (lower) and fasciated (upper) forms. Both plants were collected at 2,500 m elevation on Mauna Kea.

morphological responses to the altitudinal/climatic gradient have begun to appear. (An alternative explanation is that founder populations with these adaptations survived.) Characteristics include gigantism, fasciation (with resultant increases in stem woodiness), and polycarpic growth forms, as well as a shift from biennial to perennial habit. All these adaptations conform to the conditions given by Carlquist (1974) as potentially leading to development of insular arborescence in rosette herbs. Carlquist (1974) listed examples of insular arborescence from the family Scrophulariaceae, including *Hebe* in New Zealand and *Lytanthus* in the Canary Islands. At present there are no data to determine whether the elevation-morphology trends of mullein on Mauna Kea are mere environmental variants (as might be expected given the short history of the species on the mountain), or genetically differentiating ecotypes. Studies of naturalized populations of *V. thapsus* in North America indicate that morphological and life history variations along latitudinal gradients are largely genetically based (Reinartz 1984b). Future research on *V. thapsus* in Hawai'i will concentrate on "common garden" experiments to distinguish genetic and environmental components of the observed morphological variations with altitude.

### Control and Eradication

With the exception of efforts documented here, few governmental or private efforts to control or eradicate *V. thapsus* in the mountainous areas of Hawai'i have occurred to date. On both Mauna Kea and Mauna Loa,

the plant occurs only along the edges of access roads at the upper elevational limit, suggesting that the automobile (tire tread mud) may be a significant mode of dispersal at high elevation, since the seeds of mullein are not specifically adapted for long-distance dispersal.

Recent efforts to restrict the spread of *V. thapsus* at high elevation have centered on removal of all roadside plants near the upper altitudinal limits of distribution. From 1984 to 1986, student volunteers from the University of Hawaii at Hilo Geography Club undertook eradication work along 3.1 mi (5 km) of the Mauna Kea summit road above Hale Pōhaku (9,840 to 10,830 ft or 3,000-3,300 m), and 6.2 mi (10 km) of the Mauna Loa access road (6,230 to 6,890 ft or 1,900-2,100 m). More than 5,000 plants were uprooted and destroyed during these eradication efforts (Anonymous 1984). Before removal, the spatial configuration and population structure of selected mullein colonies were fully documented to facilitate long-term studies of site persistence and reinvasion rates, in light of the extremely long seed viability in this species (Juvik and Juvik, unpub. data). Follow-up of seedling growth rates over the next few years should indicate the interval between initial control and first flowering of the subsequent generation, and thus the best retreatment interval for further control efforts. The possibility of biological control for heavily infested areas of Hawai'i also bears serious investigation. The weevil *Gymnetron tetrum* is a major seed predator of *V. thapsus* throughout its natural range and may prove a viable control agent in Hawai'i.

Recent comments (Smith 1985) that population size and range of *V. thapsus* have been significantly reduced by a gall-forming insect are not supported by our data. There are presently no significant insect predators, and the species continues to expand its range and population size in favorable upland environments.

## CONCLUSIONS

Over the past 70 years, mullein has rapidly invaded montane areas on the island of Hawai'i. As an early successional colonizer of disturbed sites, the successful spread of *V. thapsus* has been greatly facilitated by native forest and ground cover disturbance associated with the grazing and browsing of both feral and domestic ungulates (Juvik and Juvik 1984). Mullein is continuing to expand its range on Mauna Kea, where the ash and cinder substrates are more favorable than the fresh lava flows of upper Mauna Loa. The potential invasion of summit cinder cones of Mauna Kea would be an aesthetic blight (notwithstanding recent tourist literature that has touted the "particularly photogenic" qualities of the "furry leafed" mullein, e.g., Uprichard 1986) and would have serious ecological consequences. It is particularly ironic that mullein appears to be filling a niche similar to that vacated by Hawai'i's endemic "rosette species," the silversword (*Argyroxiphium sandwicense*), which unlike the unpalatable *Verbascum* has been nearly eradicated from Mauna Kea by browsing of feral ungulates.

The similar mullein invasion on the Indian Ocean island of La Réunion emphasizes the general vulnerability of other tropical montane areas around the world. In Hawai'i every effort should be made to prevent establishment of this species on the island of Maui, since Haleakalā Crater possesses the altitudinal range (7,220 to 9,890 ft or 2,200-3,000 m) and cinder substrate preferred by *V. thapsus*. The recent discovery and removal (Hawaiian Botanical Society 1986) of an immature mullein plant from the roadside verge at 9,510 ft (2,900 m) in Haleakala National Park confirms the need for continued vigilance to prevent successful establishment of this species in the subalpine zone on Maui.

The altitudinal trends in morphological variation described in this paper may illustrate incipient adaptive stages in a general evolutionary model for the development of woody, arborescent, tropical alpine rosette plants. Mauna Kea mullein clearly evidences gigantism, increased woodiness, and shifts to perennial habit. The genetic significance of these morphological variations must await further study.

### ACKNOWLEDGMENTS

We would like to thank J. Jacobi for extracting *Verbascum thapsus* distributional data from unpublished botanical results of the U.S. Fish and Wildlife Service Hawai'i Forest Bird Survey. We further express our appreciation for the field assistance and *V. thapsus* eradication work undertaken by students of the University of Hawaii at Hilo Geography Club. We also thank Sherwin Carlquist for his critical review of the manuscript.



## Literature Cited

- Anonymous. 1984. Exotic plant eradication. *Hawaii Tribune-Herald* Oct. 21:26.
- Baskin, J.M., and C.C. Baskin. 1981. Seasonal changes in germination responses of buried seeds of *Verbascum thapsus* and *V. blattaria* and ecological implications. *Can. J. Bot.* 59:1769-1775.
- Cadet, T. 1974. Étude sur la vegetation des hautes altitudes de l'île de La Réunion (Ocean Indien). *Vegetatio* 29(2):121-130.
- Cadet, T. 1980. *La vegetation de l'île de La Réunion*. St. Denis, Réunion: Imprimerie Cazal.
- Carlquist, S. 1974. *Island biology*. New York: Columbia Univ. Pr.
- 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., and P.A. Werner. 1978. The biology of Canadian weeds. 28. *Verbascum thapsus* L. and *Verbascum blattaria* L. *Can. J. Plant Sci.* 58:401-413.
- Hawaii Department of Land and Natural Resources. 1970. *An inventory of basic water resource data: island of Hawaii*. Rep. 34. Honolulu.
- Hawaii Department of Planning and Economic Development. 1985. *Hawaii sunshine map*. Honolulu.
- Hawaiian Botanical Society. 1986. Mullein discovered in Haleakala National Park. *Newsletter, Haw. Bot. Soc.* 25(3):89.
- Il'yenko, O.O. 1982. Botanical properties of some species of the Scrophulariaceae family during their cultivated growth. *Ukr. Bot. Zh.* 39(5):24-28 (in Ukrainian with Russian and English summaries).
- Jacobi, J.D., and J.M. Scott. 1985. An assessment of the current status of native upland habitats and associated endangered species on the island of Hawai'i. In *Hawai'i's terrestrial ecosystems: preservation and management*, ed. C.P. Stone and J.M. Scott, 3-22. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit. Honolulu: Univ. Hawaii Pr.
- Juvik, J.O., and S.P. Juvik. 1984. Mauna Kea and the myth of multiple use: endangered species and mountain management in Hawaii. *Mountain Res. and Devel.* 4(3):191-202.
- Juvik, J.O., D.C. Singleton, and G.G. Clarke. 1978. Climate and water balance on the island of Hawaii. In *Mauna Loa Observatory: a 20th anniversary report*, ed. J. Miller, 129-139. Washington, D.C.: U.S. Dep. Commerce.
- Kivilaan, A., and R.S. Bandurski. 1933. The ninety-year period of Dr. Beal's seed viability experiment. *Amer. J. Bot.* 60:140-145.

- Manning, S.A. 1965. *Systematic guide to flowering plants of the world*. New York: Taplinger Pub. Co.
- Reinartz, J.A. 1984a. Life history variation of common mullein (*Verbascum thapsus*). I. Latitudinal differences in population dynamics and timing of reproduction. *J. Ecology* 72:897-912.
- Reinartz, J.A. 1984b. Life history variation of common mullein (*Verbascum thapsus*). II. Plant size, biomass partitioning and morphology. *J. Ecology* 72:913-936.
- Semenza, R.J., and R.A. Evans. 1978. Influence of light and temperature on the germination and seedbed ecology of common mullein (*Verbascum thapsus*). *Weed Sci.* 26(6):577-581.
- Sinnott, E.W. 1960. *Plant morphogenesis*. New York: McGraw-Hill.
- Smith, C.W. 1985. Impact of alien plants on Hawai'i's native biota. In *Hawai'i's terrestrial ecosystems: preservation and management*, ed. C.P. Stone and J.M. Scott, 180-250. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit. Honolulu: Univ. Hawaii Pr.
- Uprichard, B. 1986. High atop Mauna Kea. *Hawaii* 5(7):45-48.
- Wester, L., and J.O. Juvik. 1983. Roadside plant communities on Mauna Loa, Hawaii. *J. Biogeography* 10:307-316.
- Wilhelm, G., Jr. 1974. The mullein: plant piscicide of the mountain folk culture. *Geogr. Rev.* 64(2):235-252.
- Williams, G.J. III, R. Lazor, and P. Yourgrau. 1975. Temperature adaptations in the hill reaction of altitudinally and latitudinally diverse populations of *Verbascum thapsus* L. *Photosynthetica* 9(1):35-39.