

Upper-montane plant invasions in the Hawaiian Islands: Patterns and opportunities

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Received 30 March 2005; accepted 29 August 2005

Abstract

In the Hawaiian Islands, massive volcanoes have created extreme elevation gradients, resulting in environments ranging from nearly tropical to alpine, spread across a distance of only a few dozen kilometers. Although the Hawaiian Islands are widely recognized for opportunities to study lowland tropical forest invasions, less attention has been paid to invasions of Hawaii's upper-montane forest, sub-alpine and alpine environments. This study synthesizes current knowledge of plant naturalization in upper-montane environments of the Hawaiian Islands in order to (1) determine whether patterns of tropical versus temperate species invasion change with elevation, and (2) evaluate whether upper-montane invaders are having significant impacts on native plant communities. A total of 151 naturalized plant species have been recorded at 2000 m or higher. Most species (93%) are herbaceous, and over half (52%) are native to Europe/Eurasia. Twenty-one species (14%) are reported to be disruptive in native plant communities, mainly by forming dense stands that appear to inhibit recruitment of natives, but also by altering vegetation structure or causing changes in ecosystem processes. Fourteen species (9%) were first recorded within the past 30 years, indicating that new invasions of upper-montane habitats are ongoing. At 1200 m elevation, only 38% of naturalized species are temperate in origin, but the proportion of temperate species increases linearly with elevation up to 3000 m (alpine habitat), where all naturalized species are temperate in origin and over 80% are native to Europe/Eurasia. Declining temperature along the elevation gradient probably drives this pattern. The extreme elevation gradients in the Hawaiian Islands provide specific opportunities for comparative studies on the ecology and evolution of temperate invaders while also creating a unique field environment for understanding interactions between temperate and tropical species.

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Keywords: Alpine; Elevation gradient; European weeds; Montane tropical forest; Sub-alpine; Tropical mountains

Introduction

Most tropical and sub-tropical montane habitats around the world have been greatly modified by a long history of human disturbance (Ellenberg, 1979; Kappelle and Juarez, 1995). On-going activities in upper tropical montane habitats include logging, cattle ranch-

ing, plantation cropping and agriculture. All these activities are likely to introduce alien plant propagules, and when combined with disturbance, invasions can be expected. Burke (2003) recognized upper-mountain regions as bioclimatic and biogeographic 'islands' and identified invasion by alien species as a serious threat to tropical mountains.

Future climate change has been predicted to increase invasions in tropical montane environments, even more

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so than in temperate montane environments (Bortenschlager, 1991). Nevertheless, few studies have examined plant invasions in high montane ecosystems of the tropics or subtropics. Ellenberg (1979) mentioned the occurrence of a “remarkably stable” community of introduced *Trifolium repens* and *Lolium perenne* in the Andean highlands of South America, while also noting, in general terms, the spread of thorny, poisonous, or less palatable plants. Some of these plants must have been aliens. A more detailed vegetation survey of disturbed grasslands in the Andes has recently identified some naturalized species there (Quiroga-Mendiola, 2004). In the central Andes of Columbia (2000 m), introduced *Pinus patula* and *Cupressus lusitanica* were observed reproducing in the immediate vicinity of plantations (Cavelier and Tobler, 1998), but broader-scale surveys were not undertaken. Taking a more systematic approach, Stadler et al. (2000) used information from a published flora to examine general relationships between the numbers of naturalized and native wildflowers in the high mountains of Kenya (> 1500 m); they concluded that native species richness does not increase the resistance to invasions. Although several overviews of plant invasions in the Hawaiian Islands are available (Smith, 1985; Loope and Mueller-Dombois, 1989; Wester, 1992), little emphasis has been placed on patterns of invasion in montane habitats (but see Loope et al., 1992).

Climatic and vegetation characteristics of Hawaiian montane environments

The Hawaiian Islands have vertical elevation gradients spanning more than 4000 m, with climatic regimes that range from nearly tropical in the lowlands, to alpine environments with snow and freezing temperatures only a few dozen kilometers away. Montane forests, shrublands and wetlands occur on all the main islands (Hawaii, Maui, Oahu, Molokai, and Kauai) at elevations ranging from 1000 to 2260 m (Gagné and Cuddihy, 1990; Loope and Giambelluca, 1998). Sub-alpine and alpine habitats are restricted to the islands of Hawaii and Maui, which have volcanoes exceeding 1800 m in elevation (Fig. 1). The rainfall regime at any particular elevation varies greatly, depending on aspect. Rainfall is lowest on leeward aspects (300–1200 mm year⁻¹) where prolonged drought is typical in summer months (April–September). Windward aspects receive significantly more rain (2500–7000 mm year⁻¹) and seasonal soil water deficits are rare below the trade wind inversion layer (Gagné and Cuddihy, 1990).

General vegetation and climatic patterns across an elevation gradient from 1000 to 4200 m are illustrated for windward slopes on the Island of Hawaii (Fig. 2). The wet montane forest occurs from 1000 to almost

2000 m. The climate diagram for Camp Kulani is representative of conditions in the wet montane forest (Fig. 2). Most months are characterized by excessive rainfall and saturated soils, as indicated by the black shading on the climate diagram. The two most common trees in the montane wet forest are *Metrosideros polymorpha* (Myrtaceae) and *Acacia koa* (Fabaceae), both endemic to the Hawaiian Islands. Sub-alpine shrubland and forest occur primarily above the trade wind inversion layer (1800–3000 m); they are seasonally dry with rainfall primarily between October and March. The most common woody species are *Sophora chrysophylla* (Fabaceae, endemic), and *Styphelia tameiameia* (Epicradaeaceae, indigenous). The endemic grass, *Deschampsia nubigena* is also common in this zone. In the upper sub-alpine zone, the shrubland becomes sparse. Finally, the alpine zone is reached just above 3000 m on windward Mauna Kea (Fig. 2) or as low as 2600 m in some places (Medeiros et al., 1998). The alpine zone is characterized by high wind, frequent overnight frosts (with winter snow) and drought. Although the climate diagram for the alpine zone (Fig. 2) suggests extreme water deficits only in summer (where rainfall curve undercuts the temperature curve), the porous cinder substrate drains water very quickly, and high levels of solar radiation and persistent winds make the tropical alpine habitat effectively arid year round (Leuschner, 2000). The alpine vegetation is usually sparse, consisting of endemic grasses, such as *Agrostis sandwicensis*, and the endemic silversword, *Argyroxiphium sandwicense* (Asteraceae), a monocarpic perennial with a massive flowering stalk that can reach 3 m in height. Mueller-Dombois and Fosberg (1998) and Gagné and Cuddihy (1990) provide more detailed descriptions and finer-scale classification of Hawaiian vegetation zones.

Anthropogenic disturbance in Hawaiian upper-montane habitats

On both Maui and Hawaii, ungulates have had major impacts on the upper-montane vegetation. By the mid-1800s herds of feral cattle (*Bos taurus*) and goats (*Capra hircus*) were abundant on the slopes of Mauna Loa, Mauna Kea. In 1937, an estimated 40,000 feral sheep (*Ovis aries*), were roaming as high as 3960 m the alpine zone of Mauna Kea (Tomich, 1986). The sheep were eradicated in 1981, and feral goat and cattle populations are now greatly reduced; however, mouflon (*Ovis musimon*) were released on Mauna Kea in 1964, and they are now a source of disturbance up to 2800 m (Cuddihy and Stone, 1990). In the montane forest zone (1000–2000 m), feral pigs have been a major source of disturbance for at least a century, despite efforts to reduce their numbers (Tunison et al., 1994). Introduced

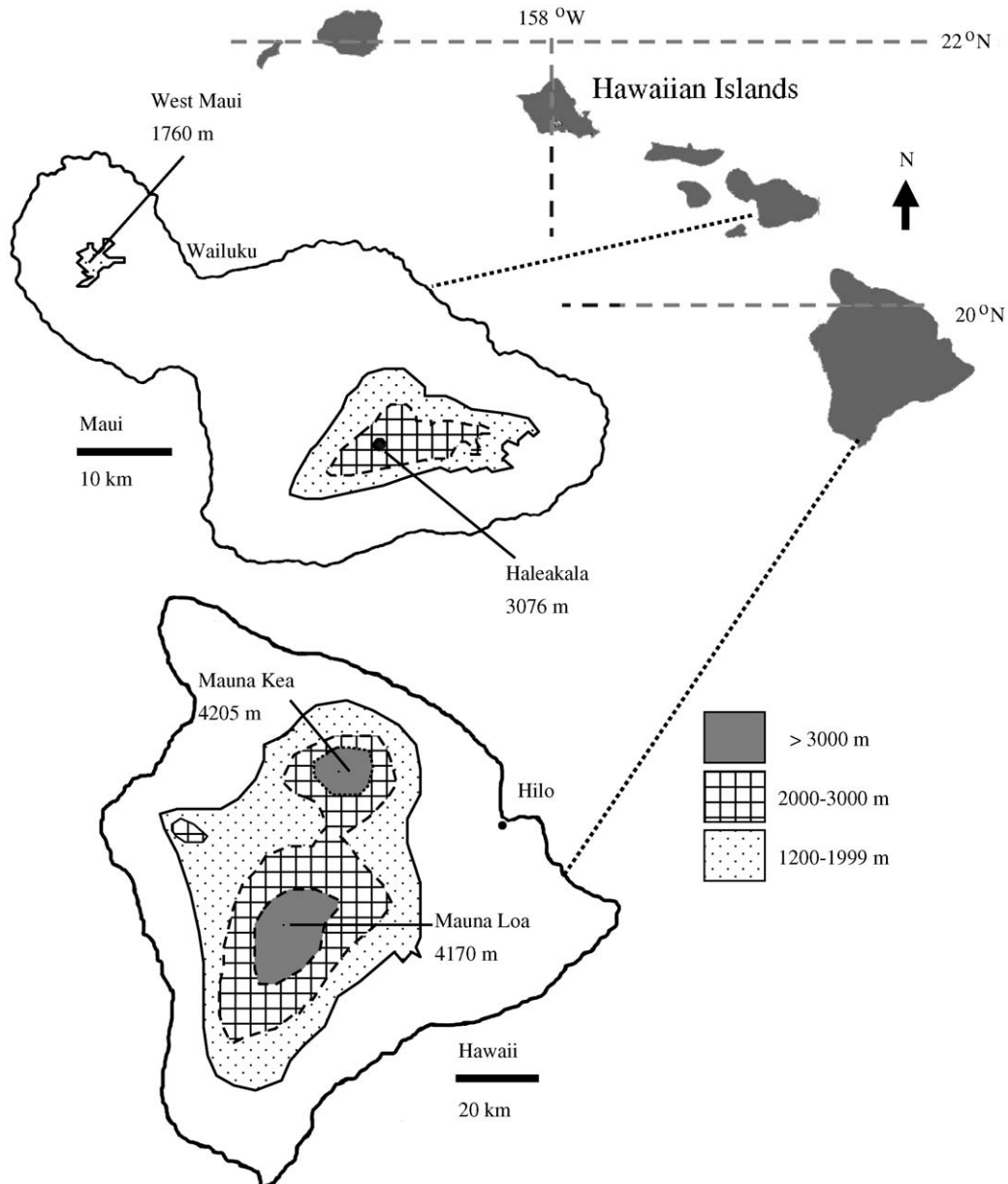


Fig. 1. Map of the Hawaiian Islands, showing locations on Maui and Hawaii that exceed 1200 m elevation. Note that the scales differ for Maui and Hawaii.

mice (*Mus domesticus*, up to 3950 m) and black rats (*Rattus rattus*, ubiquitous in forested areas up to the subalpine zone) act as seed and seedling predators as well as seed dispersers for some alien plants (Tomich, 1986).

Although most humans live in cities and towns below 1500 m elevation, there are some significant human disturbances at higher elevations. In the upper saddle region between Mauna Kea and Mauna Loa, the US Army operates the Pohakaloa Training Area, which covers an area of nearly 50,000 ha, spanning an elevation range of 1300–2600 m. In the training area, there are frequent disturbances from foot soldiers,

military vehicles, and explosives, and there are occasional fires sparked by live munitions (Shaw, 1997).

Human activities and introduced animals have clearly been major sources of disruption in Hawaiian upper-montane habitats over at least the past two centuries, facilitating the dispersal, establishment and persistence of upper-montane plant invaders (Scowcroft and Hobdy, 1987), but no overview of upper-montane invasions is available. One roadside survey of native and naturalized plants up to 2500 m was conducted on Mauna Loa (Wester and Juvik, 1983). The study identified 51 introduced plant species, 22 of which occurred at 2000 m elevation or higher. Wester and

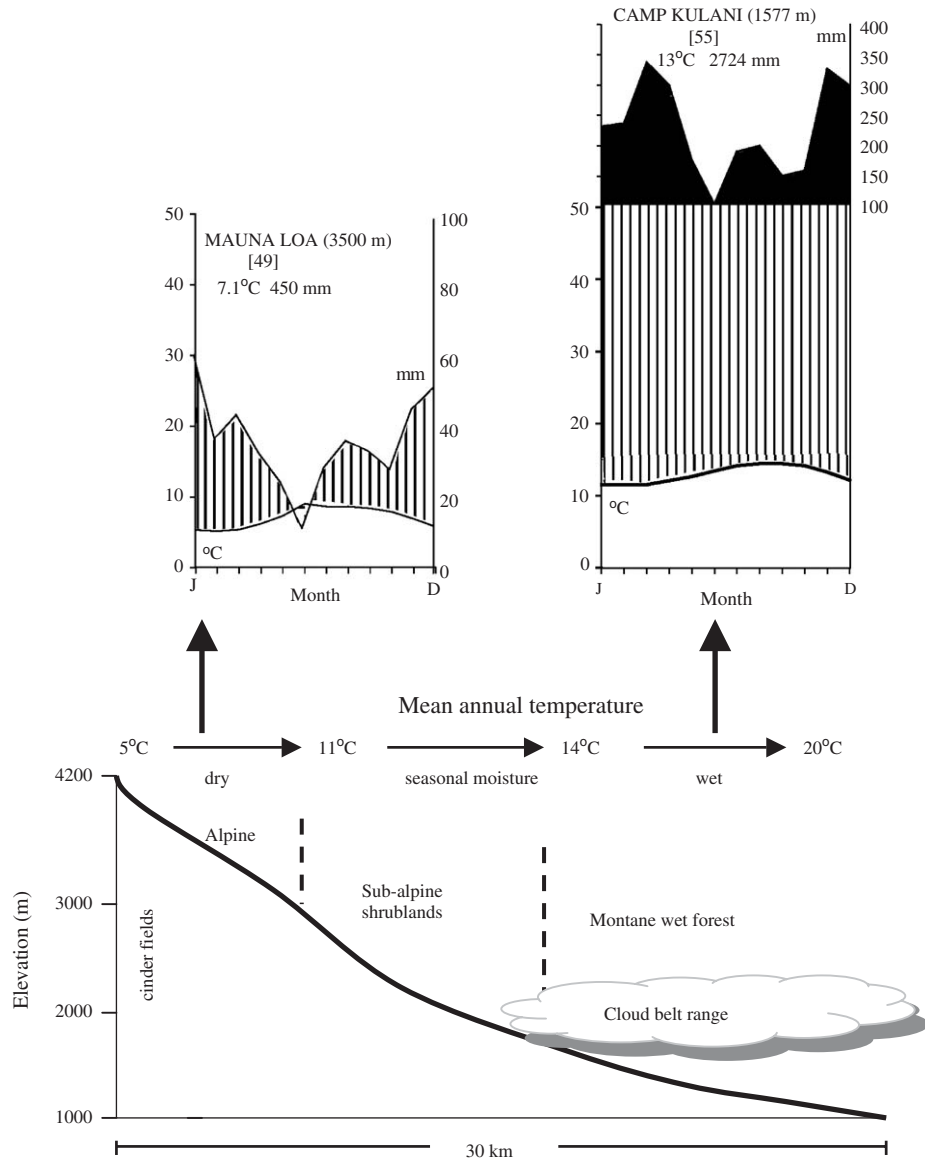


Fig. 2. Climatic variation and generalized vegetation zones across the upper windward slopes of Hawaii (modified from an east-facing slope depicted in [Mueller-Dombois and Krajina, 1968](#)), and climate diagrams ([Walter and Lieth, 1967](#)) for the upper-montane wet forest (Kulani Camp, Mauna Loa) and alpine habitat (Mauna Loa summit).

[Juvik's \(1983\)](#) study is outstanding because it involved systematic, quantitative sampling, but it covered only one road, which traversed a limited elevation range on Mauna Loa.

Here, I compile published and unpublished records of plant naturalizations and invasion in montane habitats (> 1200 m) across the Hawaiian Islands, with particular emphasis on invasions above 2000 m. The objectives of this study are (1) to synthesize current knowledge of upper-montane plant invaders and their impact in the Hawaiian Islands, (2) to assess the relative establishment of tropical versus temperate invaders in tropical montane and alpine habitats of the Hawaiian Islands, and (3) to highlight opportunities to use tropical

mountains for testing basic hypotheses in invasion biology.

Methods

Information on naturalized angiosperms and gymnosperms occurring at elevations of 1200 m or higher in the Hawaiian Islands was compiled from a variety of published sources and local technical reports ([Wester and Juvik, 1983](#); [Higashino et al., 1988a](#); [Stone et al., 1991](#); [Anderson et al., 1992](#); [Loope et al., 1992](#); [Tunison et al., 1994](#); [Shaw, 1997](#); [Higashino et al., 1988b](#);

Medeiros et al., 1998; Wagner et al., 1999; Belfield and Pratt, 2002). Among the above references, Wagner et al. (1999) represents the cumulative knowledge of more than 100 years of specimen collections from around the Hawaiian Islands that have been deposited at the Bishop Museum herbarium, Honolulu (BISH). The remaining references describe occurrences of invaders within specific areas, such as National Parks and other Federal lands in Hawaii. No further documentation of high elevation invasions in Hawaii was found. The reports include all discrete peaks in the Hawaiian Islands >1200 m elevation (Fig. 1), and although some rare invaders were undoubtedly missed, the composite record extracted from these sources is expected to yield an unbiased and substantially complete sample of all montane invaders in the Hawaiian Islands. A minimum elevation of 1200 m was chosen because it clearly lies within the montane forest vegetation zone throughout the Hawaiian Islands; however, emphasis was placed on identifying patterns among naturalized species occurring in the upper-montane forest, subalpine, and alpine zones above 2000 m.

For each species, the highest elevation record was noted, and when available, the lower elevation limit was also recorded. When the elevation was not provided by the original source, the elevation was estimated based on the specific location. Plants that had only been observed or collected from one localized population were classified as 'rare'. The year of the first naturalized record was noted, along with the native range of each species. Based on native range, species were classified as having tropical or temperate affinities (or unassigned for species with native ranges that clearly spanned from tropical to temperate), and patterns of climatic affinity at different elevation limits were examined. Finally, species appearing to have important detrimental effects on native plant communities through their dense growth were classified as 'disruptive'. The disruptive species were further categorized based on specialized impacts (1) altering vegetation structure, (2) altering ecosystem processes by promoting fire, or (3) smothering growth.

Results

A total of 349 naturalized species were recorded as occurring at 1200 m or higher in the Hawaiian Islands, while 151 species were recorded from upper-montane environments of 2000 m or higher (Appendix). The number of naturalized species declined exponentially with increasing altitude (Fig. 3). In contrast, the proportion of species of European or Eurasian origin appeared to increase linearly with elevation, from 38% among all species occurring above 1200 m to 53% above 2000 m and 90% above 3000 m (Fig. 3, $r^2 = 0.96$,

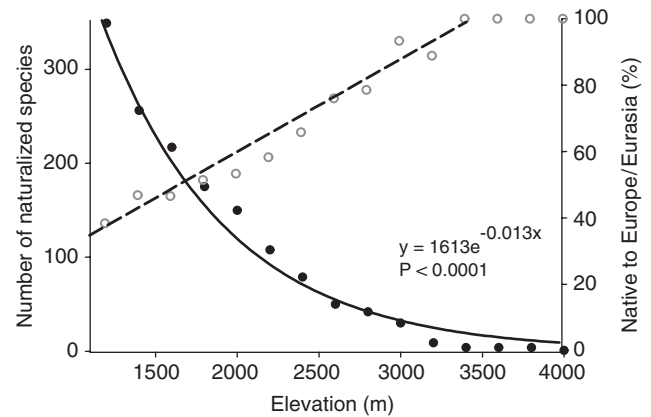


Fig. 3. Total number of naturalized species (closed circles) and percentage of species of European origin (open circles) versus altitude.

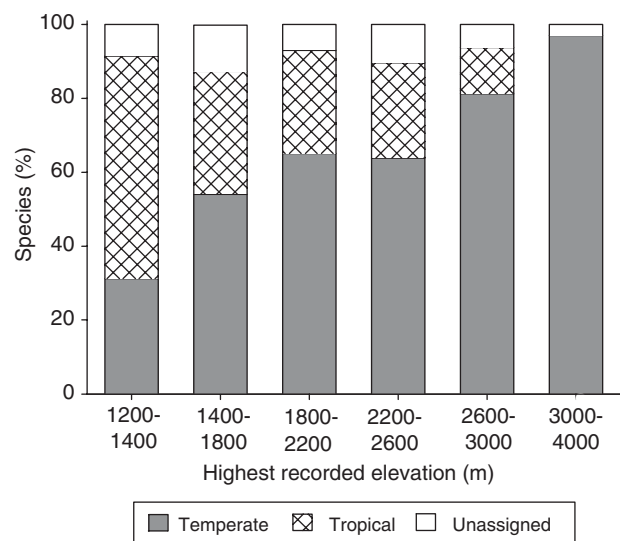


Fig. 4. Changes in the percentage of naturalized species having tropical and temperate affinities as related to the species' maximum elevation record.

$P < 0.001$). Most (60%) of the species having their upper limit in the lowest elevation range (1200–1400 m) were tropical (Fig. 4), nevertheless, a large fraction (31%) of species having an upper limit in the 1200–1400 m range were species with temperate affinities. Among the species occurring above 2000 m, 93% were herbaceous and 27% are grasses. Twenty-one species (14%) were identified as disruptive invaders of native communities; most of these species form dense stands that appear to inhibit recruitment of natives, but some are new life forms that alter community structure (e.g. tall pine trees invading native shrublands), while others are grasses that alter the natural fire cycle by promoting frequent, intense fires (Appendix). Among the species having tropical affinities, *Pennisetum setaceum* (fountain grass) has invaded at the highest elevation (2745 m), but a

temperate species, *Verbascum thapsus* (common mullein) occurs across the broadest elevation range, from near sea level up to 3965 m. *Poa pratensis* has the highest elevation record at 4040 m, approaching Hawaii's highest peak (4205 m). Fourteen species (9%) were first recorded within the past 30 years, indicating that new invasions of upper-montane habitats are ongoing.

Discussion

Susceptibility of Hawaii's upper-montane environments to invasion

Although some studies have suggested that upper-montane tropical environments are relatively resistant to invasion by introduced plants (e.g. Cavelier and Tobler, 1998), there are hundreds of naturalized species in Hawaii's montane environments above 1200 m, and dozens of species have been reported as disruptive invaders of native montane plant communities. Disturbances by introduced feral ungulates appear to have facilitated establishment by many invaders, but invasions are also occurring in protected habitats. An additional factor that may influence susceptibility to invasion is the presence of glaciers, at least on Mauna Kea, as recently as 13,000 years BP, with snowfall occurring as low as 900 m elevation during this period (Porter, 1979; Gavenda, 1992). This means Hawaii's upper-montane habitats have been relatively recently colonized by the limited pool of native species that migrated from lower elevations. In comparison, other mainland tropical mountains may not have been recently glaciated, and their well-developed floras were derived from a larger pool of colonizing species.

Despite the broad success of non-native species in Hawaii's montane habitats, the number of naturalized species declined exponentially with increasing elevation. This pattern was probably due to two factors (1) the decreasing total area available to invade at increasing elevations (species–area effect), and (2) increasing severity of climate (drought, cold and radiation) with increasing elevation. The pattern of declining species richness with elevation is also exponential for native species (C. Daehler, unpublished data), suggesting that the exponential decline in naturalized species is not due to temporary limitation of dispersal into higher elevation habitats.

A shift from tropical species to temperate species

The increasing proportion of naturalized temperate species at increasing elevations is very similar to the pattern reported by Wester and Juvik (1983) for introduced roadside weeds on Mauna Loa. One

difference is that among roadside weeds above 1200 m, Wester and Juvik (1983) found only around 20% of the species to be tropical in origin, whereas when distribution records were pooled across all habitats (this study), 44% of naturalized species above 1200 m were of tropical origin. This suggests that roadside weeds are biased towards temperate species. In fact, Hawaii's roadside weeds are predominately European species at elevations as low as 1000 m (Wester and Juvik, 1983); whereas, among naturalized records pooled across all habitats, European species become the majority only above 2000 m. In the Eastern Himalayas, Das (1985) reported an ecotone between tropical and temperate species near 1800 m elevation. In contrast, the transition from tropical to temperate communities in Hawaii is more gradual across the elevation range of 1000–3000 m. The elevation records from Hawaii were pooled from different aspects (windward and leeward) and different islands. This could have led to smoothing of the tropical–temperate transition; however, a gradual tropical–temperate transition in Hawaii was apparent from Wester and Juvik's (1983) single road survey. I speculate that roadways (and associated disturbed roadsides) have allowed many European weeds to extend their ranges to lower elevations, where they would otherwise be out-competed by tropical species. If this were the case, a clear tropical–temperate ecotone would not be expected.

Although there is a definite replacement of tropical species by temperate species with increasing elevation, the mechanisms underlying this change have been little studied. It is well known that most tropical plants have poor tolerance to frost, and freezing nighttime temperatures in the alpine zone must prevent most tropical plants from surviving there. Historical weather data from the 1200 to 2000 m elevation range are sparse; however, at Camp Kulani (1577 m, Fig. 2) the probability of experiencing below freezing temperatures in a given year was only 18%, based on records from the past 55 years. When freezing temperatures did occur, they were brief (a few hours at night) and did not fall below -2°C (National Climatic Data Center, 2005). The shift from tropical to temperate invaders begins below 1500 m, suggesting a role of other factors in addition to freezing temperatures.

At cooler temperatures, temperate species may have higher photosynthetic rates than tropical species (Allen and Ort, 2001). Temperate weeds may also be able to germinate at lower temperatures than tropical weeds (Sauerborn and Koch, 1988). Under the warmer conditions typical of low elevations, tropical species may have higher biomass production rates than temperate species (Lowe and Bowdler, 1984), allowing them to dominate. In general, tropical plants have smaller genome and chromosome sizes than temperate plants (Levin and Funderburg, 1979), and this may allow for shorter cell cycle duration and higher potential

growth rates in tropical plants, but small genome size is also correlated with poor frost tolerance (Macgillivray and Grime, 1995), suggesting a trade-off. Although a number of hypothetical mechanisms have been proposed to explain the transition from tropical to temperate species with increasing elevation, further experimental studies are clearly needed to sort out the various lines of correlative evidence that have been reported thus far. It is interesting to note that despite only minimal seasonal fluctuation in temperature in Hawaii, temperate species often maintain winter dormancy patterns typical of their temperate native ranges. In contrast, most tropical species do not display winter dormancy. This difference in behavior could be important in understanding interactions between tropical and temperate species, while also influencing ecosystem productivity if tropical–temperate plant ecotones are shifted by climate change.

Why so many herbaceous plants?

Over 90% of the naturalized plants above 2000 m elevation are herbaceous, while among native plants common in sub-alpine vegetation, only 28% are herbaceous (Gagné and Cuddihy, 1990). The high frequency of herbaceous plants in the naturalized flora probably is related to two factors: (1) frequent physical disturbances by ungulates and humans promote the success of fast-growing herbaceous species that can get established and recover quickly, and (2) many of the naturalized herbaceous species are associated with ranching, suggesting a non-random pool of introductions. Species like *Carduus pycnocephalus*, *Chenopodium album*, and *Melinis repens* were probably imported as contaminants of grass seed used to plant pastures. Others are associated with livestock and may have arrived as seeds attached to imported animals (e.g. *Emex spinosa*, *Bidens* spp.) or as contaminants of hay fed to animal during their voyage to Hawaii. Still others were deliberately planted as fodder and then became naturalized (*Anthoxanthum odoratum*, *Dactylis glomerata*, *Pennisetum clandestinum*, *Trifolium* spp). Thus, the high proportion of herbaceous invaders is a reflection of land use patterns in disturbed habitats. At the same time, there appears to have been little or no incentive for deliberately introducing large woody plants above 2000 m, (L. Loope, pers. comm.).

Disruptive invaders

Despite the dominance of herbaceous plants in the naturalized flora, the woody plants that have naturalized above 2000 m are notable because 73% of them were identified as disruptive invaders of native communities, whereas only 9% of the herbaceous species were



Fig. 5. *Pinus radiata* invasion (left) of native shrubland near 2000 m elevation, on the slope of Haleakala, Maui. Photo: Forest and Kim Starr (USGS).

disruptive. Several woody invaders alter native vegetation structure by adding a new life form. Of particular concern are the *Pinus* species, especially *Pinus radiata* (Fig. 5), which was first introduced for forestry purposes. Staff at Haleakala National Park have been controlling *Pinus radiata* in an attempt to limit its upslope spread from plantation trees at lower elevations (Medeiros et al., 1998), but large areas of Haleakala are threatened by *Pinus* invasions. *Pinus radiata* is relatively wind resistant (Somerville, 1980) and can grow to >25 m in height in areas where native vegetation reaches a maximum height of only 5 m. As a result, *Pinus radiata* transforms the structure of remaining native sub-alpine communities as it invades. Medeiros et al. (1998) consider *Pinus radiata* to be a particular threat to moist upper-montane ecosystems, but it can also tolerate very dry conditions, as has been reported in Australia (Dawson et al., 1979). Another forestry introduction, *Eucalyptus globulus*, which can grow to 70 m in height, also towers over native vegetation and occurs in habitats similar to those invaded by *Pinus radiata*.

Some smaller woody plants are also significant problems, as they form dense stands or exhibit smothering growth, restricting native plant growth and recruitment. *Ulex europaeus* is a spiny shrub that has been targeted with several biocontrol agents (Markin et al., 1992), but *U. europaeus* still forms impenetrable thickets in higher elevation, open habitats including pastures and native shrublands on Mauna Kea and Haleakala. *Rubus argutus* and *Passiflora tarminiana* (a smothering vine, formerly *P. mollissima*) can cover large areas; their greatest impacts are seen in mesic to wet forest below 2000 m (Loope et al., 1992; Wagner et al., 1999), but they can occur above 2000 m. *Cotoneaster pannosus* has only recently been recorded as naturalized

in Hawaii. This large, bird-dispersed shrub is spreading on Haleakala, where it is reported to form dense stands in native *Sophora* shrublands (Starr et al., 2003). Other temperate shrubs (e.g. *Heteromeles arbutifolia*) have recently been reported as naturalized just below 2000 m (Wagner et al., 1999), and they may also prove to be disruptive invaders of native sub-alpine communities in the future.

The disruptive invaders categorized as altering ecosystem processes were mainly grasses. Because of their flammability, they can alter the frequency and intensity of fires, which affects persistence of native communities while also altering nutrient cycling (D'Antonio and Vitousek, 1992). Most grass species are expected to decline if disturbance due to feral ungulates is removed, but some disruptive species like *Anthoxanthum odoratum*, *Pennisetum clandestinum*, and *Ehrharta stipoides* (just below 2000 m) appear to maintain dense swards for decades (Cuddihy and Stone, 1990; Tunison et al., 1994), while other grasses (e.g. *Melinis minutiflora*) can greatly increase in abundance following feral ungulate exclusion (Scowcroft and Hobdy, 1987). Some grasses, sedges and rushes are invading unique high-elevation bog communities. *Holcus lanatus* and *Kyllinga brevifolia* can be locally dominant in these wet habitats. *Cyperus haspan* and *Juncus planifolius* are disruptive in upper-montane bogs somewhat below 2000 m elevation (Medeiros et al., 1998). Endemic *D. nubigena* grasslands in the sub-alpine zones of Haleakala and Mauna Loa are also threatened by invaders. So far, at least *Holcus lanatus* and *Anthoxanthum odoratum* have become persistent, significant components of these grasslands even in the absence of feral ungulates (Jacobi, 1981; Karpa and Vitousek, 1994). Overall, 14% of naturalized species were considered disruptive, and this is comparable to results from mountain transects in the Canary Islands, where 8–11% of naturalized species were considered transformer species (Arévalo et al., 2005).

Among the 14 species first recorded as naturalized within the past 30 years, three species (21%) were considered disruptive, and all of these were escapes from deliberate plantings. Because new disruptive invaders are establishing from deliberate introductions, a screening system could be effective in identifying high-risk species to be excluded from future forestry plantings or landscaping around mountain homes (Daehler et al., 2004). Some of the disruptive invaders such as *Pennisetum setaceum*, *Verbascum thapsus*, and *Cortaderia jubata*, are not yet established on all mountain peaks, and preventing their establishment in new areas through early detection and eradication is a high priority (e.g. Loope et al., 1992). Although the management and control options for mountain invaders are generally the same as for lowland invaders, tropical mountain invasions offer unique opportunities for addressing broad questions in invasion biology.

Opportunities

In the Hawaiian Islands, extreme elevation gradients occurring across short distances are combined with an unusually well-documented flora (rarely available in tropical environments) to present unique research opportunities. Temperate invaders are challenged with an extreme range of environments, from tropical to alpine. This situation provides an opportunity to assess the relative roles of phenotypic plasticity versus genetic differentiation in determining the success of a large suite of temperate invaders (Parker et al., 2003). As temperate species extend their ranges into lower montane habitats, they are challenged by biotic factors (increasing competition from tropical species). The particular mechanisms or trade-offs involved in tropical plant–temperate plant competitive interactions have been little-studied, but their investigation across elevation gradients in Hawaii may provide insights into future global patterns of species distributions under a scenario of global warming.

Many of the European species that have naturalized above 2000 m in the Hawaiian Islands (Appendix) have already been studied as weeds in other parts of the world. This presents immediate opportunities for comparative studies of behavior. For example, *Verbascum thapsus* populations at extreme high and low elevations in Hawaii exhibit high rates of fasciation (Fig. 6), but this morphological shift was not reported



Fig. 6. *Verbascum thapsus* growing near 2100 m on the slope of Mauna Kea, Hawaii. Unusual-shaped, fasciated inflorescences like this one occur at frequencies up to 60% in some populations in Hawaii.

from mainland temperate areas where this plant has invaded (Gross and Werner, 1978; Reinartz, 1984; Naber and Aarssen, 1998). Plants with the fasciated morphology appear to produce three times more seeds than normal plants (C.C. Daehler, unpublished data), and this could conceivably contribute to the unusually high densities of *V. thapsus* observed in Hawaii. A comparative approach that examines the behavior of species in their native ranges and in invaded regions shows great promise in addressing a diversity of theoretical and applied questions about the population ecology and evolution of invaders (Reinhart et al., 2003; DeWalt et al., 2004; Jakobs et al., 2004; Maron et al., 2004; Vilà et al., 2005).

With increasing availability of fine-scale climatic data linked with geographic information systems (GIS), there is significant interest in building and testing more sophisticated models that forecast an invader's eventual range, based on its distribution elsewhere (Sutherst and Maywald, 1991; Sutherst et al., 2000; Peterson and Vieglais, 2001; Peterson, 2003). The extreme range of climatic conditions (temperature, rainfall, solar radiation, etc.) occurring across tropical mountain transects provides an ideal system for testing predictions of European species' invaded range, based on climatic tolerances in their native ranges or elsewhere. If the

models prove to be sufficiently accurate, then they will have many applications. On the other hand, if major discrepancies are found between an invader's predicted range and its actual range in Hawaii, then hypotheses explaining the discrepancies can be developed and tested, yielding new insights into factors controlling the environmental range of temperate invaders.

Hawaii is well known for its spectacular plant invasions, but the best-known cases are tropical or subtropical plants at lower elevations (e.g. *Lantana camara*, *Miconia calvescens*, *Psidium cattleianum*). Nevertheless, as documented in this review, temperate invaders dominate in Hawaii's upper-montane habitats, presenting various opportunities for comparative work by temperate plant researchers.

Acknowledgements

I thank Hansjörg Dietz for organizing the workshop on mountain invasions, further stimulating my interest in this topic. I also thank Gabi Jakobs for motivating discussions on studying invasions across elevation gradients. This manuscript was improved by comments from Lloyd Loope, Hansjörg Dietz, and two anonymous reviewers.

Appendix

Naturalized plants occurring above 2000 m elevation in the Hawaiian Islands. Date indicates first record of naturalization, 'Low elev' is the lowest record when available, 'High elev' is the highest record; Geography: 1 = temperate, 2 = tropical, 3 = unassigned; Notes: R = rare occurrence, D = disruptive in native communities, forming dense stands that appear to inhibit recruitment of natives; additional specialized impacts: (1) alters vegetation structure, (2) alters ecosystem processes by promoting fire, (3) smothering growth.

Species	Family	Date	Low elev (m)	High elev (m)	Geography	Notes
<i>Achillea millefolium</i>	Asteraceae	1911	1200	3000	1	
<i>Ageratina adenophora</i>	Asteraceae	< 1885	600	2440	2	D
<i>Agrostis capillaris</i>	Poaceae	1939	600	2000	1	R
<i>Agrostis stolonifera</i>	Poaceae	1912	640	2318	1	D
<i>Aira caryophylla</i>	Poaceae	1916	1050	2440	1	
<i>Amaranthus retroflexus</i>	Amaranthaceae	1977		2150	1	R
<i>Amsinckia intermedia</i>	Boraginaceae	1944		3000	1	R
<i>Anagallis arvensis</i>	Primulaceae	1895	0	2450	1	
<i>Anthoxanthum odoratum</i>	Poaceae	1907	840	3050	1	D
<i>Arenaria serpyllifolia</i>	Caryophyllaceae	1935	0	3000	1	
<i>Atriplex suberecta</i>	Chenopodiaceae	1923	0	2150	2	
<i>Avena sativa</i>	Poaceae	< 1871	60	2074	1	
<i>Axonopus fissifolius</i>	Poaceae	1912	160	2250	2	
<i>Bidens alba</i>	Asteraceae	1958	0	2285	2	
<i>Bidens pilosa</i>	Asteraceae	< 1845	0	2590	2	
<i>Brassica juncea</i>	Brassicaceae	1942		2500	1	
<i>Bromus catharticus</i>	Poaceae	1909	300	3040	1	
<i>Bromus hordeaceus</i>	Poaceae	1909	610	2290	1	

Appendix (continued)

<i>Bromus rigidus</i>	Poaceae	1910	550	2270	1	
<i>Bromus rubens</i>	Poaceae	1937	450	2000	1	
<i>Bromus tectorum</i>	Poaceae	1871	1250	3040	1	
<i>Carduus pycnocephalus</i>	Asteraceae	1986	1340	2130	1	
<i>Castilleja arvensis</i>	Scrophulariaceae	1968	60	2100	2	
<i>Centaurium erythraea</i>	Gentianaceae	1909	10	2960	1	
<i>Cerastium fontanum</i>	Caryophyllaceae	<1871	0	3900	1	
<i>Chenopodium album</i>	Chenopodiaceae	1986	70	2060	1	R
<i>Chenopodium ambrosioides</i>	Chenopodiaceae	<1871	600	2450	2	
<i>Chenopodium carinatum</i>	Chenopodiaceae	1922	0	2200	2	
<i>Chenopodium murale</i>	Chenopodiaceae	1864	0	2750	1	
<i>Chloris virgata</i>	Poaceae	1903	0	2135	2	
<i>Collomia linearis</i>	Polemoniaceae	1986		2700	1	R
<i>Coronopus didymus</i>	Brassicaceae	1864	0	3040	1	
<i>Cortaderia jubata</i>	Poaceae	1989	600	2200	3	D
<i>Cotoneaster pannosus</i>	Rosaceae	1994	747	2377	1	D
<i>Crassula argentea</i>	Crassulaceae	1975		2135	2	R
<i>Crepis capillaris</i>	Asteraceae	1934	1140	2260	1	
<i>Cynodon dactylon</i>	Poaceae	1835	0	2680	2	
<i>Dactylis glomerata</i>	Poaceae	1909	100	3040	1	D
<i>Delairea odorata</i>	Asteraceae	1910	500	2500	2	D(3)
<i>Descurainia sophia</i>	Brassicaceae	1963		2070	1	R
<i>Emex spinosa</i>	Polygonaceae	1928	150	2000	1	
<i>Epilobium billardierianum</i>	Onagraceae	1909	800	3200	1	
<i>Eragrostis brownii</i>	Poaceae	1916	1130	2590	2	
<i>Eragrostis pilosa</i>	Poaceae	1932	1980	2500	3	
<i>Erodium cicutarium</i>	Geraniaceae	<1871	0	3100	1	
<i>Eschscholzia californica</i>	Papaveraceae	1968		2270	1	
<i>Eucalyptus globulus</i>	Myrtaceae	1910	1950	2590	1	D(1)
<i>Euchiton japonicus</i>	Asteraceae	1909	600	2800	1	
<i>Euphorbia peplus</i>	Euphorbiaceae	1851	300	2300	1	
<i>Fallopia convolvulus</i>	Polygonaceae	1981		2070	1	R
<i>Festuca rubra</i>	Poaceae	1929	820	2285	1	
<i>Foeniculum vulgare</i>	Apiaceae	1910		2130	1	
<i>Gamochaeta purpurea</i>	Asteraceae	<1871	0	2100	1	
<i>Gastridium ventricosum</i>	Poaceae	1909	550	2000	1	
<i>Geranium dissectum</i>	Geraniaceae	1910	915	2150	1	
<i>Geranium homeanum</i>	Geraniaceae	1909	1130	2150	1	
<i>Geranium pusillum</i>	Geraniaceae	1909		2000	1	R
<i>Geranium retrorsum</i>	Geraniaceae	<1871	915	2070	1	
<i>Gilia capitata</i>	Polemoniaceae	1929	2400	2562	1	R
<i>Glyceria fluitans</i>	Poaceae	1916	1230	3300	1	R
<i>Helichrysum foetidum</i>	Asteraceae	1949	730	2300	2	
<i>Heterotheca grandiflora</i>	Asteraceae	1909	10	2270	1	D
<i>Holcus lanatus</i>	Poaceae	1909	760	3250	1	D
<i>Hordeum brachyantherum</i>	Poaceae	1909	30	2440	1	R
<i>Hordeum vulgare</i>	Poaceae	1927	40	2500	1	
<i>Hydrocotyle bowlesioides</i>	Apiaceae	1943	10	2030	2	
<i>Hypochoeris glabra</i>	Asteraceae	1915	600	2800	1	
<i>Hypochoeris radicata</i>	Asteraceae	1909	1100	3040	1	
<i>Ilex aquifolium</i>	Aquifoliaceae	1981	1860	2600	1	
<i>Juncus bufonius</i>	Juncaceae	1910	1000	2380	1	
<i>Juncus effusus</i>	Juncaceae	1900	1000	2000	1	
<i>Juncus ensifolius</i>	Juncaceae	1911		2017	1	

Appendix (continued)

<i>Juncus tenuis</i>	Juncaceae	1915	700	2440	3	
<i>Koeleria macrantha</i>	Poaceae	1909	1370	2830	1	
<i>Kyllinga brevifolia</i>	Cyperaceae	1864	20	2165	2	D
<i>Lamium amplexicaule</i>	Lamiaceae	1982		2140	1	R
<i>Lapsana communis</i>	Asteraceae	1909	950	3230	1	
<i>Lepidium bonariense</i>	Brassicaceae	1975		2000	3	R
<i>Lepidium virginicum</i>	Brassicaceae	< 1871	0	3040	1	
<i>Leucanthemum vulgare</i>	Asteraceae	1911	900	2520	1	
<i>Lobularia maritima</i>	Brassicaceae	1940	0	2000	1	
<i>Lolium perenne</i>	Poaceae	1909	850	2440	1	
<i>Lotus subbiflorus</i>	Fabaceae	1926	640	2440	1	
<i>Lupinus arboreus</i>	Fabaceae	1990		2160	1	R
<i>Madia sativa</i>	Asteraceae	1927		2500	1	R
<i>Malva parviflora</i>	Malvaceae	1826	0	2270	2	
<i>Medicago lupulina</i>	Fabaceae	1909	5	2840	1	
<i>Medicago sativa</i>	Fabaceae	1929	3	2680	1	
<i>Melilotus indica</i>	Fabaceae	1909	2	2855	1	
<i>Melinis repens</i>	Poaceae	1903	0	2330	2	D(2)
<i>Modiola caroliniana</i>	Malvaceae	1909	850	2100	2	
<i>Oenothera affinis</i>	Onagraceae	1915	1100	2050	3	
<i>Oenothera stricta</i>	Onagraceae	1919	1200	3040	3	
<i>Opuntia ficus-indica</i>	Cactaceae	< 1809	0	2075	2	
<i>Orthocarpus purpurascens</i>	Scrophulariaceae	1945		2050	1	R
<i>Oxalis corniculata</i>	Oxalidaceae	< 1809	0	2300	3	
<i>Parentucellia viscosa</i>	Scrophulariaceae	1971	1450	2450	1	
<i>Paspalum dilatatum</i>	Poaceae	1911	40	2290	2	
<i>Passiflora tarminiana [mollissima]</i>	Passifloraceae	1926	850	2225	2	D(3)
<i>Pennisetum clandestinum</i>	Poaceae	1938	0	2000	2	D(2,3)
<i>Pennisetum polystachion</i>	Poaceae	1923	30	2140	2	
<i>Pennisetum setaceum</i>	Poaceae	1914	40	2745	2	D(2)
<i>Phalaris minor</i>	Poaceae	1903		2200	1	
<i>Physalis peruviana</i>	Solanaceae	1825	450	2135	3	
<i>Pinus patula</i>	Pinaceae	1944	2100	2500	1	D(1)
<i>Pinus pinaster</i>	Pinaceae	1976	2100	2500	1	D(1)
<i>Pinus radiata</i>	Pinaceae	Unknown	1200	2200	1	D(1)
<i>Plantago lanceolata</i>	Plantaginaceae	1895	0	3110	1	
<i>Poa annua</i>	Poaceae	< 1871	0	2440	1	
<i>Poa pratensis</i>	Poaceae	1911	1220	4025	1	
<i>Polycarpon tetraphyllum</i>	Caryophyllaceae	1909	0	3040	1	
<i>Polygonum aviculare</i>	Polygonaceae	1932	1000	2080	1	
<i>Polypogon interruptus</i>	Poaceae	1910	0	2000	1	
<i>Prunella vulgaris</i>	Lamiaceae	1909	820	2590	1	
<i>Rhamnus californica</i>	Rhamnaceae	1940	1500	2000	1	
<i>Rubus argutus</i>	Rosaceae	1904	200	2300	1	D
<i>Rumex acetosella</i>	Polygonaceae	1895	1115	3040	1	
<i>Rytidosperma pilosum</i>	Poaceae	1932	1980	2500	3	
<i>Rytidosperma semiannulare</i>	Poaceae	1937	1066	2375	1	R
<i>Senecio sylvaticus</i>	Asteraceae	1910	1270	3200	1	
<i>Sherardia arvensis</i>	Rubiaceae	1909	600	2270	1	
<i>Sida rhombifolia</i>	Malvaceae	< 1871	0	2135	2	
<i>Silene gallica</i>	Caryophyllaceae	1864	60	3040	1	
<i>Sisymbrium altissimum</i>	Brassicaceae	1943	15	3050	1	
<i>Solanum pseudocapsicum</i>	Solanaceae	< 1871	600	2100	2	
<i>Solanum tuberosum</i>	Solanaceae	1927		2740	3	R

Appendix (continued)

<i>Sonchus asper</i>	Asteraceae	1975		3040	1	
<i>Sonchus oleraceus</i>	Asteraceae	< 1871	5	2440	1	
<i>Sporobolus africanus</i>	Poaceae	1909	150	2440	2	
<i>Stachys arvensis</i>	Lamiaceae	1864	2	2400	1	
<i>Stellaria media</i>	Caryophyllaceae	1930	50	3950	1	
<i>Stipa cernua</i>	Poaceae	1957	1830	2140	1	
<i>Taraxacum officinale</i>	Asteraceae	1909	10	3040	1	
<i>Trifolium arvense</i>	Fabaceae	1932	850	3040	1	
<i>Trifolium dubium</i>	Fabaceae	1915	910	2200	1	
<i>Trifolium pratense</i>	Fabaceae	1932	820	2070	1	
<i>Trifolium repens</i>	Fabaceae	1909	720	3040	1	
<i>Ulex europaeus</i>	Fabaceae	1910	760	2230	1	D
<i>Urtica urens</i>	Urticaceae	1909	790	2290	1	
<i>Verbascum blattaria</i>	Scrophulariaceae	1955		2000	1	R
<i>Verbascum thapsus</i>	Scrophulariaceae	1932	5	3965	1	D
<i>Verbascum virgatum</i>	Scrophulariaceae	1943		3000	1	
<i>Verbena litoralis</i>	Verbenaceae	1837	10	2280	2	
<i>Verbesina encelioides</i>	Asteraceae	< 1871	0	2805	1	
<i>Veronica arvensis</i>	Scrophulariaceae	1909	400	2560	1	
<i>Veronica plebeia</i>	Scrophulariaceae	1909	860	2520	3	
<i>Veronica serpyllifolia</i>	Scrophulariaceae	1926	820	3060	1	
<i>Vicia sativa</i>	Fabaceae	1909	860	3040	1	
<i>Vulpia bromoides</i>	Poaceae	1905	185	2710	1	
<i>Vulpia myuros</i>	Poaceae	1911	580	3040	1	
<i>Wahlenbergia gracilis</i>	Campanulaceae	1928	0	2850	1	

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