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Review Article

Veratrum album in montane grasslands: a model system for implementing biological control in land management practices for high biodiversity habitats

Urs Schaffner[1], David Kleijn[2], Valerie Brown[3]
and Heinz Müller-Schärer[2]
[1]CABI Bioscience Centre Switzerland, 1 Chemin des Grillons,
CH-2800 Delémont, Switzerland
[2]University of Fribourg, Département de Biologie/Ecologie, Pérolles,
CH-1700 Fribourg, Switzerland
[3]Centre for Agri-Environmental Research (CAER),
Department of Agriculture, The University of Reading, Earley Gate,
P.O. Box 236, Reading RG6 6AT, UK

Abstract

Low-input agriculture on montane grasslands as practised until the mid 20th Century, has promoted local biodiversity by creating and maintaining open and semi-open habitats below the timberline. Today, socioeconomic trends lead to management intensification in nearby grasslands and to abandonment of more remote grasslands; either of these trends puts the local biodiversity under pressure. One especially time-consuming and costly activity in montane alpine grasslands is weed control. In Europe, broadcast application of chemical control is not recommended or not even allowed because the available herbicides are unselective, and treatment of individual plants, either chemically or mechanically, is extremely labour-intensive. Stakeholders are therefore urged to develop new control concepts that are economically affordable and highly selective. The implementation of biological control into existing management schemes may provide an appropriate strategy for management of the most problematic montane grassland weeds. In order to develop effective biological weed management strategies, it is necessary to (a) identify life cycle transitions of the weed that are both amenable to manipulation and influential on population growth; and (b) combine control due to natural antagonists and limiting resources. *Veratrum album* is an important weed on grazed montane grasslands, because it exhibits acute toxicity to mammals and locally displaces fodder plants. This paper reviews the available information on the ecology of *V. album* and its natural antagonists, and explores prospects for its biological control. It is suggested that this species and its antagonists provide a promising model system for exploring the possibilities of implementing biological weed management within existing and future management schemes of montane grasslands.

Introduction

In Europe, low-input agriculture as practised until the mid 20th Century promoted local biodiversity, in lowland and montane areas, by creating and maintaining open and semi-open habitats below the timberline. Subsequent intensification of lowland agriculture has put this diversity in jeopardy (Nösberger *et al.*, 1994). While the number of species in unforested areas at low altitudes has already declined substantially, grasslands in the montane zone are still characterized by high plant and animal diversity (Haslett, 1997). In fact, montane grassland habitats have become the last refugia for many lowland species in Central Europe and elsewhere. These grasslands may therefore act as significant propagule sources for the recolonization of lowland habitats, should these be taken out of intensive cultivation for economic or nature conservation reasons.

Nevertheless, even montane habitats are suffering from changing management and populations of certain specialist species are disappearing (Fischer & Stöcklin, 1997). In particular, increases in the level of nitrogen input, and altered grazing and/or mowing regimes, have had significant negative effects on the diversity of the remaining montane grasslands (Baumberger *et al.*, 1996). In addition, the direct impacts associated with the development of tourism in mountain areas have been an important cause for the decline in the number of species-rich habitats.

Socioeconomic trends have also led to an intensification of grassland management near the farm and extensified land use of marginal grasslands further away, a trend which is likely to continue (Ammon & Müller-Schärer, 1999). More intensive management usually translates into enhanced fertilizer and herbicide inputs, which have strong and long-lasting effects on species composition and interactions in high-altitude habitats (Hegg *et al.*, 1992). Increased inputs result in the domination of a small number of tall, often fast-growing and competitive species that exclude a larger number of species of low stature. This commonly results in an overall reduction in local species richness and increased weed pressure (Bignal & McCracken, 1996; Kleijn & Snoeijing, 1997). A few herbicides are effective against perennial weeds under high altitude conditions; but, unfortunately, most are unselective (e.g. Troxler & Rouel, 1987; Dorée 1988) and will therefore also harm beneficial and rare plant species and their associated herbivores.

Two of the key factors determining the economic viability of an agricultural system are the labour required and the labour costs. As costs rose over recent decades, maintenance of more marginal grasslands became increasingly unprofitable (high costs, low returns). This has led to the abandonment of small mountain farms and to reduced grazing on the less productive grasslands, or even the complete withdrawal of livestock. Either of these options will induce vegetation change towards later successional plant communities, which generally have a much lower species richness than the traditionally managed montane grasslands (Stampfli & Zeiter, 2000). Therefore, developments that reduce the amount of labour needed to maintain marginal grasslands will contribute to the conservation of these very species-rich habitats.

Weed control in alpine grasslands is an especially time-consuming activity. All alpine weed species are perennials with thick persistent roots or rhizomes that store large reserves (e.g. *Cirsium* spp., *Rumex* spp., *Senecio alpinus* (L.) Scop. (Asteraceae), *Veratrum album* L. (Liliales, Melanthiaceae)). Their regrowth potential makes them hard to control. Broadcast application of herbicides on alpine pastures is not allowed in most European countries, but some countries allow treatment of individual plants (e.g. Switzerland, Germany). Recently, efforts have been undertaken to completely ban herbicides from alpine pastures, e.g. through mutual agreements between local farmers and large food retailers for organic production. Current mechanical weed control methods (mowing, digging out the roots/rhizomes or weed wiping) are either not effective or too labour-intensive. Furthermore, grazing can only be implemented as a management technique when the weed species is non-toxic to the grazing animal. Stakeholders are therefore urged to develop new control concepts which are economically affordable and highly selective. In pastures, especially of alpine regions, generally only a single species may cause a problem in a given location (Schroeder, 1984; Ammon & Müller-Schärer, 1999). In order to protect the many desirable species in the pastures and their biodiversity value, a highly specific control is required.

Biological control, namely the use of natural antagonists to reduce weed densities below an economic and/or ecological threshold, may provide an appropriate strategy for management of the most problematic montane grassland weeds. This approach is promising because (a) usually only one or a few weeds cause the majority of the problems; (b) biological control, when applied with caution, does not have negative side effects on the environment; and (c) the competitive effect of the surrounding vegetation can enhance the effects of antagonists on the target weed. In particular, the system management or classical approach of biological control (Müller-Schärer & Frantzen, 1996), which uses a small inoculum source of a native antagonist or of a specialist natural enemy from other parts of the weed's native distribution area, respectively, seem appropriate. This approach may be combined with other non-chemical control measures to result in an effective and economic way of reducing weed abundance in montane grasslands, while minimizing the detrimental effects on nontarget flora and invertebrates.

For the successful implementation of biological management strategies, a detailed knowledge of the biology and population dynamics of the target weed species and its natural antagonists is needed. On the basis of this information, a protocol can be developed which integrates such non-chemical weed management practices into current land management schemes. This will provide a cost-effective means to conserve the diversity of alpine grasslands.

Veratrum album is an important weed on grazed montane grasslands. This species, which exhibits acute toxicity to mammals, may reach high densities (more than 10 plants/m^2) and displace fodder plants. It attains pest status in grasslands above 500 m asl (above sea level) in France, Italy, Germany, Austria and Switzerland (unpublished report for FAO). For these reasons, two symposia (5th Meeting of the FAO Working Group for Mountain Pastures, Yugoslavia, 1988; Symposium of the European Grassland Federation on 'Grassland renovation and weed control in Europe', Austria, 1991) and numerous publications have focused on the chemical and mechanical control of *V. album* (Troxler & Rouel, 1987; Dorée, 1988; Milevoj, 1988; Jeangros & Troxler, 1991).

This paper reviews the available information on the ecology of *V. album* and its natural antagonists and explores prospects for its biological control. It is suggested that this species and its antagonists provide a promising model system for exploring the possibilities of implementing biological weed management within existing and future management schemes of montane grasslands.

The Ecology of *Veratrum album*

Distribution

Veratrum album, a long-lived perennial hemicryptophytic herb, is one of several very similar species in the genus *Veratrum*. The genus is distributed over the entire Northern Hemisphere. The subdivision of the genus into species is difficult and subject to considerable debate amongst taxonomists. As a consequence, the number of *Veratrum* species occurring worldwide varies from 30 (Gleason & Cronquist, 1991) to 48 (Hess *et al.*, 1967). Approximately 14 species are known from China alone. Lower numbers are found in western Asia, Europe (two species) and North America (approximately ten species). In Eurasia, the only unequivocal taxonomic classification of the genus is the subdivision into two sections *Alboveratrum* (e.g. *V. album*) and *Fuscoveratrum* (e.g. *Veratrum nigrum* L.). *Veratrum album* is often separated into two subspecies, *V. album* ssp. *album* (central- and south-European distribution) and *V. album* ssp. *lobelianum* (Euro-Siberian distribution) (Hess *et al.*, 1967; Lauber & Wagner, 1996). However, as most available literature ignores this distinction, this paper addresses *V. album* in its wider context. The distribution of *V. album* ranges from coastal Alaska and Japan in the east through China and Siberia, the Caucasus and the Alps to south-western Europe, where it reaches its western border in Portugal

(Hultén & Fries, 1986). In Central Europe, its distribution is restricted to above *ca.* 800 m asl while at higher latitudes the species seems to occur also at sea level. The species shows a strong preference for moist growth conditions. From Switzerland westwards, it occurs primarily on north-facing slopes; in the drier areas of Spain and Portugal, it is further restricted to streambeds or along fens and lakes (U. Treier, pers. comm.).

The generative reproduction cycle

Veratrum album plants flower infrequently and irregularly. In general, mature plants flower once every 4-8 years. Despite this low flowering frequency, in larger populations it is possible that a substantial proportion of plants flower each year. However, this does not appear to be the case, as flowering seems to be triggered, at least in part, by climatic conditions. Long periods, in which only isolated individuals within populations flower, are interspersed by years in which a large proportion of most populations over extended geographical areas flower. Whether seeds are produced only during mass flowering years or also in low numbers by isolated plants during the intervening years between will be determined largely by the pollination system of the species. Unfortunately, the pollination system of *V. album*, or any other *Veratrum* species, is unknown (Mulligan & Munro, 1987). Flower morphology shows adaptations to cross pollination. Flowers are protandrous: at flower opening, the anthers are ripe and ready to shed their pollen, while the stigmas are not yet fully mature. After the pollen is shed, the stigmas mature fully. Nectar is produced during the entire period at the base of petals, and the greenish-white flowers emit a strong smell. Flies (Diptera) were the only insects observed on flowers over a two-year study period (D. Kleijn, pers. obs.) and frequently had their heads and thoraxes covered by yellow pollen.

If cross pollination is indeed obligate, seed production may be even more limited to mass flowering years than the flowering pattern suggests. Indeed, in the closely related species, *Veratrum viride* Ait, Taylor (1956) reported that a year of massive seed production is usually followed by five or more years of very scant seed production. Nevertheless, *V. album* has been observed to re-colonize sites by seeds approximately five years after most adult plants had been killed chemically (Kees, 1987). This suggests that, despite the longevity of the rhizomes and the irregular seed production, seeds do play a prominent role in the population dynamics of *V. album.*

Veratrum album seedlings consist of a single linear, grass-like cotyledon which is approximately 5 cm long. Apparently, no real leaf is produced in the first year. In subsequent years, juveniles remain extremely small. Thus, the period when, due to their small size, trampling or grazing by livestock have lethal consequences for seedlings and juveniles may be relatively long in this species.

The vegetative reproduction cycle

Veratrum album is also capable of vegetative reproduction. Vegetative reproduction is, however, closely linked to flowering events. When a plant does not flower, a preformed apical crown bud grows out from the rhizome in spring to form a shoot consisting of only leaves and leaf sheaths. At the end of the growing season, the shoot dies with the next year's apical bud already distinguishable at the base of the senescing shoot. Alternatively, when a plant flowers, the apical meristem dies off and one to three lateral crown buds take over the next year's vegetative growth. Dorée (1988) determined the number of lateral buds on 100 rhizomes in two populations and found 57% and 35% bearing one bud, 40% and 60% bearing two buds, and 3% and 5% bearing three buds for the two populations, respectively. As the older parts of the original rhizome inevitably rot away with time, about a decade after the plant has flowered, instead of one single plant, one to three genetically identical individuals may grow in close proximity although physically completely separated. As a significant proportion of plants in each population flower only every 4-8 years, this process may be slow, but nevertheless results in a substantial increase in population size.

Factors affecting distribution and abundance

Veratrum album is generally absent in Europe below altitudes of 800 m asl. Its distribution may be explained by the germination requirements of the seeds. Although little is known about the requirements of *V. album*, the North American species, *Veratrum californicum* Durand, *Veratrum eschscholtzii* A. Gray (= *Veratrum viride* ssp. *eschscholtzii*), *Veratrum fimbriatum* A. Gray and *V. viride*, have been investigated in detail by Taylor (1956). He observed that the seeds of the alpine species, *V. eschscholtzii*, *V. viride* and *V. californicum*, all require long periods of stratification (4-4.5 months for the first two, and 3 months for the latter species, at 1.7-4.4°C). In contrast, seeds of *V. fimbriatum*, a species growing at sea level, germinated optimally after 2-2.5 months at 4.4-7.2°C, and germination was possible without a cold period. Assuming a similar germination strategy of *V. album* to the ones of the North American alpine species, its seeds might only meet the stratification requirements in Central Europe above *ca.* 800 m asl.

Taylor (1956) further observed that seedlings of both *V. fimbriatum* and *V. eschscholtzii* were sensitive to sunlight, and, unless shaded, quickly turned yellow with their apices dying back early in the season. This may therefore explain why *V. album* densities in grasslands are usually highest near forest edges and around solitary trees (D. Kleijn, pers. obs.).

Veratrum album is commonly found in four major habitats in montane areas in Central Europe: the dwarf scrub zone above the timberline, forests, pastures and moist hay meadows. The population structure differs markedly in these different habitats. A preliminary study showed that in pastures the average plant size was over three times higher than in hay meadows (Table 1). The percentage of flowering plants and biomass per area were both significantly higher in pastures. However, the number of plants per area does not differ between the two habitats. This agrees with other studies showing that selective grazing of palatable plants leads to dominance of unpalatable, chemically-defended plant species (Fernández *et al.*, 1992; Augustine & McNaughton, 1998). However, the differences described above cannot be unequivocally attributed to the effects of selective grazing by cattle, as the habitats differed also in abiotic conditions, especially the soil water table which was higher in the hay meadows than in the pastures. Experiments are currently underway to disentangle the effects of grazing and habitat conditions.

Table 1. Performance variates of *Veratrum album* in four Swiss populations in pastures and hay meadows, respectively. In each population, a quadrat of 5 × 10 m was sampled. Data were analysed by one-way ANOVA, biomass data were ln-transformed, and percentage data angular-transformed prior to analysis

	Mean shoot size	No. plants (/50 m^2)	% flowering plants	Total biomass (g/m^2)
Mown	3.1	92	0.33	4.9
Grazed	11.4	94	4.30	21.82
F	10.91	0.01	8.80	15.49
P	0.016	0.925	0.025	0.008

Current Management of *Veratrum album*

Mowing the shoots of *V. album* is one way of controlling the species that farmers have practised for centuries. Such control practice has clear effects on individual plant performance, but apparently little effect on population densities. Plants subjected to mowing for seven consecutive years were, on average, 43% the size of the control plants (Schaffner *et al.*, 1995). Interestingly, the distribution of dry weight between rhizomes, roots, leaves and leaf sheaths ('stem') was the same for mown and control plants. As mown plants do not flower, spread through seeds will be greatly limited in mown populations. Over the seven-year period, only three plants died, demonstrating that mowing, at least in the short term, does not enhance mortality. Other studies support the finding that mowing does not result in significant changes in plant densities, although it does reduce plant height and size (Dorée, 1988; B. Jeangros & J. Troxler, pers. comm.), or may have a significant impact on fecundity. The resilience of *V. album* to complete defoliation for large parts of the growing season (as mown plants do not form a new shoot during that season) is probably due to the capacity of the rhizomes and roots to store considerable reserves (Schaffner *et al.*, 1995).

Reserve levels in rhizomes of hemicryptophytic species fluctuate seasonally (e.g. Koridon, 1968; Rosnitschek-Schimmel, 1985; Schaffner *et al.*, 1995). In spring or early summer, as the shoots emerge from the ground, the rhizome reserves reach a seasonal low. As the shoots become larger, more and more reserves are transported back to the rhizomes, so that reserve levels rise steadily through the summer to reach a peak at the end of the growing season, when resources are re-translocated from senescing shoots to roots and rhizomes. Reserve levels remain high throughout the winter until the following spring when they are used to initiate shoot growth. Therefore, the efficiency of mowing, as a control measure, may be considerably improved by optimal timing. Experiments so far have taken place when the growing season was well underway and plants had, therefore, already been able to translocate resources back to the rhizome, thereby minimizing the long-term effect of the treatment.

In the past two decades, a number of studies have tested the efficacy of herbicides for controlling *V. album* (Kees, 1987; Troxler & Rouel, 1987; Dorée, 1988). In general, most herbicides performed poorly and efficacy was never 100%. However, a number of herbicides consistently achieved reductions in plant densities of over 70%. Whole field applications were no more effective than individual plant applications and also had detrimental effects on other species and therefore are usually not recommended (Troxler & Rouel, 1987). The most effective herbicides, for spot treatment, are glyphosate and a mixture of the phenoxyacetic acid derivatives MCPP and 2,4-D.

Effects of *Veratrum album* on Local Biodiversity

The distribution and occurrence of *V. album* in species-rich montane areas is of considerable ecological significance, because of its potential impact on local biodiversity of plants and its associated fauna. *Veratrum album* is an uncharacteristically tall species in otherwise unproductive montane grasslands. Especially in pastures, probably due to its clonal mode of reproduction, it often grows in dense patches, thereby dominating the vegetation. Such dominant species often have a pronounced effect on the species richness of the vegetation (Bobbink & Willems, 1987). We undertook preliminary investigations to determine whether *V. album* had adverse effects on the species richness of the surrounding vegetation. In two populations near Les Verrières (Neuchâtel) and Jaun (Fribourg), respectively, twenty 1-m long transects consisting of ten 10 × 10 cm subplots were established. Each transect started in the centre of a *V. album* patch and extended into open grassland. Species numbers were determined in each subplot. Subsequently, analysis showed that the species richness in and approximately 10 cm beyond patches of *V. album* shoots was significantly lower than that in the open grassland (Figure 1). Thus, at a small scale, *V. album* appears to affect adversely the species richness in montane grasslands, probably as a result of other species being outshaded by the tall *V. album* shoots. It is not clear, however, whether *V. album* also induces reductions in species richness on a larger scale. Bearing in mind the clonal growth habit of the species, it is likely that local biodiversity will be gradually eroded. This, together with the likelihood of satellite populations being initiated by seed, could lead to an increasing impact on, and fragmentation of, areas of uninvaded montane grassland.

The effect of *V. album* on grassland biodiversity may, however, not always be negative. In intensively grazed montane grasslands of the Caucasus region in Georgia, *V. album* was shown to provide safe sites for other plants and their associated fauna, and thereby to contribute to the maintenance of high levels of species biodiversity in these habitats (Callaway *et al.*, 2000).

Antagonists of *Veratrum* Species

Herbivores and pathogens associated with *Veratrum album* in Europe

Vertebrates

Damage by mammals of *V. album* plants was rarely observed in Switzerland (Schaffner, 1994). The overall lack of vertebrate feeding on *V. album* is probably caused by the presence of highly toxic alkaloids; for example, the LD_{50} dose of the ester germerine for rats is 3.7 mg/kg body weight (Haas, 1938). Furthermore, the alkaloids have a teratogenic effect on embryos and foetuses of cattle, sheep and goats (Binns *et al.*, 1972).

Cattle are usually repelled by *V. album*, but have been observed to feed upon it, especially later in the season when the surrounding vegetation has been heavily grazed. At this time, the concentration of alkaloids in the leaves is at its lowest level, which may also contribute to the observed herbivory late in the season (Schaffner, 1994). Wildlife (chamois and probably deer) sometimes nibble on the upper parts of young leaves. Feeding damage by rodents on the underground parts has never been observed.

Invertebrates

The invertebrate herbivore community in Europe is well documented from host records in the literature and a monographic study carried out in Switzerland (Schaffner, 1994). These sources show that at least 27 insect species feed on *V. album* in Europe (Table 2). The insect orders most frequently represented are Lepidoptera and Thysanoptera.

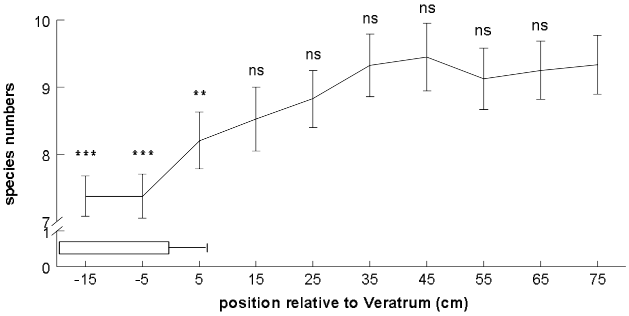

Figure 1. The species numbers (± *s.e.*) of alpine pasture vegetation in relation to the distance from patches of *Veratrum album* shoots. After ANOVA, subplot means were compared with that of the reference plot at 75 cm using the Dunn-Šidák method. ns: not significant, ** $P<0.01$, *** $P<0.001$. The bar in the lower left corner indicates the mean patch size (+ *s.e.*).

Approximately 80% of the herbivore community in Europe consists of broadly polyphagous species that feed on plant species in more than two families. The remaining species appear to be monophagous. In no-choice feeding tests, *Rhadinoceraea nodicornis* Konow (Hym., Tenthredinidae), *Thrips herricki* Bagnall (Thysanop., Thripidae) and *Aphis veratri* Walker (Homoptera, Aphididae) accepted the congeneric *V. nigrum*, but not plants in other genera. No feeding tests were conducted with the mining Diptera. Since in the field they were only recorded from *V. album* (V. Tschirnhaus, pers. comm), it is likely that the larval host ranges are also restricted to the genus *Veratrum*. With the low percentage of endophagous and specialized herbivores, the arthropod community of *V. album* in Central Europe has characteristics of young herbivore communities on introduced plant species (Strong *et al*., 1984).

Table 2. Phytophagous arthropods associated with *Veratrum album* in Europe. Data on field study and literature records from Schaffner (1994). Plant parts affected: L = leaves; St = stems; F = fruit; Fl = flowers; R = rhizomes and roots. Monophagous = restricted to genus *Veratrum*; polyphagous = feeding on two or more plant families.

Order	Family	Insect species	Literature	Field study	Plant part	Degree of host specificity
Coleoptera	Curculionidae	*Otiorhynchus corvus* Boheman	+			polyphagous
Lepidoptera	Noctuidae	*Xestia baja* Denis & Schiffermüller		+	L	polyphagous
		Cerastis rubricosa F.		+	L	polyphagous
		noctuid sp. 3		+	F	
	Geometridae	*Eupithecia veratraria* H.Sch.	+	+	F, Fl	polyphagous
		E. fenestrata Mill.	+	+	F	
		E. castigata Hübner		+	Fl	polyphagous
		E. satyrata Hübner		+	Fl	polyphagous
		geometrid sp. 5		+	Fl	
	Tortricidae	*Clepsis rogana* Guenée	+	+	L	polyphagous
		C. steineriana Hübner	+			
		C. rolandriana L.	+			
Hymenoptera	Tenthredinidae	*Rhadinoceraea nodicornis* Konow	+	+	L	monophagous
		Aglaostigma alboplagiatum Lacourt	+	+	L	polyphagous
Diptera	Agromyzidae	*Liriomyza wachtlii* Groschke	+	+	F, L	monophagous
	Scatophagidae	*Delina veratri* Hd.	+	+	L	monophagous
	Lonchaeidae	*Earomyia* sp.		+	St	monophagous
Orthoptera	Acrididae	*Omocestus viridulus* L.		+	L	polyphagous
		Miramella alpina Kollar		+	L	polyphagous
	Tettigoniidae	*Metrioptera roeseli* Hagenbach		+	L	polyphagous
Homoptera	Aphididae	*Aphis veratri* Walker	+	+	L	monophagous
		A. fabae Scopoli	+	+	L	polyphagous
		aphidid sp. 3		+	L	
Thysanoptera	Thripidae	*Thrips herricki* Bagnall	+	+	L	monophagous
		T. brevicornis Priesner	+			polyphagous
		T. trybomi Karny	+			polyphagous
		Taeniothrips picipes Zetterstedt	+			polyphagous
	Aeolothripidae	*Aeolothrips intermedius* Bagnall	+			polyphagous

Veratrum album is frequently visited by ants tending aphids. Hence, externally feeding herbivores may be exposed to a high predation pressure by ants and other predatory groups. The only specialist species with free-living larvae is the sawfly, *R. nodicornis*, which is well protected against predators by sequestering the alkaloids of *V. album* in the larval haemolymph (Schaffner *et al.*, 1994). Among the arthropod herbivores, grasshoppers removed more leaf biomass than all other arthropods together. In the field, some plants were found to be almost completely defoliated by grasshoppers (U. Schaffner, pers. obs.). It is interesting to note that individuals of *Miramella alpina* Kollar (Orth., Acrididae) died within a few days when fed exclusively with *V. album*. However, when *V. album* was offered in a mixed diet, the grasshoppers readily fed on this toxic plant and increased weight as quickly as those fed with a mixed diet without *V. album* (U. Schaffner, unpubl. data). Disturbed adults emit orally a droplet that possibly contains metabolites of plants recently ingested. This suggests that the aposematically coloured *M. alpina* gains protection from predators by including toxic plants, such as *V. album*, in its diet. Nevertheless, feeding bioassays revealed that *M. alpina* clearly preferred old over young *V. album* leaves, which may be due to the considerably higher alkaloid concentration in younger leaves, rendering them more toxic than older leaves (U. Schaffner, unpubl. data).

A second group of invertebrate herbivores that occasionally has a severe impact on *V. album* plants is molluscs. In Switzerland, the following species have been recorded to feed readily on *V. album*, particularly at wet sites: *Arion hortensis* Ferussac, *Arion rufus* L., *Helicella itala* L., *Trichia plebeia* Draparnaud, *Trichia montana* Studer, *Trichia villosa* Studer, *Arianta arbustorum* L. and *Cepaea hortensis* Mueller. These are likely to be most prevalent in damp situations with good ground cover.

Pathogens

Two rust fungi have been isolated from *V. album*, *Uromyces veratri* (DC.) Schröt. and *Puccinia veratri* Duby (Table 3). While for both species the teliospores are exclusively associated with *Veratrum* spp., they have a host switch during the aecial stage (*U. veratri*: *Adenostyles*, *Cacalia*, *Homogyne*, *Tussilago*; *P. veratri*: *Epilobium*) (Gäumann, 1959). *Puccinia veratri* especially may reach very high infestation levels under natural conditions. However, due to the cooler conditions at higher altitudes, the epidemic spread of *P. veratri* is slow. It appears that natural infestation by *P. veratri* during the second half of the growing season does not have a measurable impact on resource acquisition by *V. album*, which is probably because the plant has by then replenished the reserves used in shoot production (Schaffner *et al*., 1995).

Besides the above-mentioned fungi, *Mycocentrospora veratri* (Peck) U. Braun (Hyphomycetes) (Morgan-Jones & Phelps, 1995) causes necrotrophic leaf-spots. Indeed, this is the most common and evident pathogen on *V. album* in Switzerland, although its effects on the fitness of *V. album* are unknown.

Herbivores and pathogens associated with *Veratrum* species outside Europe

Very little information is available on invertebrate herbivores and pathogens associated with *V. album* in Asia. An interesting exception concerns the flea beetle *Neocrepidodera* sp. (Col., Chrysomelidae), which has been recorded from *V. album* in Russia (Medvedev & Roginskaya, 1988). Larvae of these flea beetles develop in roots and are usually specialist feeders on a restricted number of closely related plant species.

The arthropod community associated with other species in the genus *Veratrum* is also poorly known. In North America, three congenerics of the sawfly *Rhadinoceraea nodicornis*, *Rhadinoceraea aldrichi* MacGillivray, *Rhadinoceraea insularis* Kincaid and *Rhadinoceraea nubilipennis* Norton (Smith & McDearman, 1990), feed on *Veratrum* spp. Smith & McDearman (1990) suggested that the alkaloid phytochemistry of the plant tribe Veratrae, which includes *Zygadenus* and *Veratrum*, may be involved with sawfly speciation in *Rhadinoceraea.* The fact that *R. nodicornis* sequesters the *Veratrum* alkaloids (Schaffner *et al.*, 1994) indicates that there is indeed a strong relationship between this sawfly genus and its hostplants.

A study carried out with *V. californicum* in California revealed more arthropod species per stem on wetter compared with drier sites. However, the number of individuals per stem was higher on drier sites. The latter was due to a lepidopteran species that occurred in high densities, sometimes defoliating *V. californicum* plants, on drier sites (Friedlander *et al*., 1999).

In North America, the ectophagous nematodes, *Pararotylenchus spiralis* Baldwin & Bell, 1981 and *Pararotylenchus sphaerocephalus* Baldwin & Bell, 1981 (Tylenchida, Hoplolaimidae), were found in the soil around *V. californicum* and *Veratrum* sp. These species are considered to have a broad host range (Baldwin & Bell, 1981), and thus may not be specifically associated with *Veratrum* spp.

Numerous pathogens have been isolated from *Veratrum* spp. in different parts of the world (Table 3). However, no information is available on their effect on *Veratrum* plants.

Table 3. Plant pathogens associated with *Veratrum* spp. in different parts of the world. References for North America from Conners (1967) and USDA (1960), for Korea from Shin (1997), and for Europe from Gäumann (1959).

Family	Pathogen species	Host Plant	Reported from
Uredinales	*Uromyces veratri* (DC.) Schröt.	*V. album*	Europe
	Puccinia veratri Duby	*V. album, V. viride*	Europe, Canada
Ascomycetes	*Phyllachora melanoplaca* (Desm.) Sacc.	*V. viride*	USA
Coelomycetes	*Phyllosticta melanoplaca* Thüm.	*V. viride*	Canada
	Colletotrichum liliacearum Ferraris	*V. viride*	USA
	Cylindrosporium veratrinum Sacc. & G. Winter	*V. viride*	USA
Hyphomycetes	*Cercosporella terminalis* Peck	*V. viride*	USA
	Pseudocercosporella sublineolata (Thüm.) U. Braun	*V. patulum*	Korea
	Mycocentrospora (*Cercosporella*) *veratri* (Peck) U. Braun	*V. album*	Europe, Canada
Agonomycetes	*Sclerotium durum* Pers.	*V. viride*	Alaska
Discomycetes	*Helotium* spp.	*V. viride*	Alaska
	Patinella aloysii-sabaudiae Sacc.	*V. viride*	Alaska

Plant structures and developmental stages attacked by antagonists

During a field survey in Switzerland, the majority of herbivores were found to attack *V. album* relatively late in the season, usually at the time when most of the leaves were unfolded (Schaffner, 1994). This is particularly true for the most damaging groups, i.e. the grasshoppers and molluscs. Only the noctuid moth, *Xestia baja* Denis & Schiffermüller, attacked the developing leaf cones, thereby simultaneously feeding on and damaging several leaves.

Young plants revealed much less feeding damage than old plants. Furthermore, grasshoppers and molluscs were observed much more frequently on taller plants. Only the sawfly, *Rhadinoceraea nodicornis*, was repeatedly observed to feed on young plants.

In Europe, insects seem to attack exclusively the above-ground parts of *V. album*. During the field study in Switzerland, no trace of feeding damage to the rhizome was observed (in a sample of 1500 rhizomes that was dug up and inspected). *Otiorhynchus corvus* Boheman (Col., Curculionidae) found on *V. album* in Slovakia may be an exception, but the report does not specify whether larvae were found attacking the roots, or whether adults were observed feeding on the leaves (Holecova *et al.*, 1997).

Discussion: The Way Forward?

In order to develop effective biological management strategies in weed control, it is necessary to: (a) identify life cycle transitions of the weed that are both amenable to manipulation and influential on population growth; and (b) combine top-down control due to damage inflicted by natural antagonists, with bottom-up control due to a reduced growth rate caused by limiting resources. Modelling plant population dynamics may help to identify a weed's most vulnerable life stage and predict the effect of biological control organisms on the population growth rate of the target weed (Müller-Schärer, 1988; McEvoy & Coombs, 1999).

Little quantitative information is available on the various life cycle transitions of *V. album* and their relationship to its population growth rate. The survival rate of established plants is known to be very high; even repeated disturbances, such as the complete removal of all above-ground tissue, hardly affects the mortality in a population. It is therefore likely that factors inflicting direct stress on the below-ground organs will have the greatest potential to increase the mortality of established plants in a population.

Clonal growth of established plants is probably only of minor importance in population build-up. Rapid increase in population size, on both a local and spatial scale, is likely to depend primarily on seeds. However, no quantitative data are available on the size and persistence of the soil seed-bank, the germination rate and the seedling survival rate, or how these are affected by biotic or abiotic factors, such as vegetation cover, nutrient availability and disturbance. Habitat-specific life cycle transitions may influence the choice of the appropriate management strategy. For example, in nutrient-rich habitats, characterized by a high vegetation cover, seedling recruitment may be microsite limited rather than seed limited. On the other hand, established plants in nutrient-poor habitats may produce relatively few seeds, but the transition to successful seedling establishment may be enhanced due to a higher number of available microsites. Trampling by cattle is likely to kill seedlings, but may at the same time create gaps in the vegetation that actually favour seed germination and survival of seedlings. Hence, quantification of the influence of the various life cycle transitions on the population dynamics of *V. album*, and how these transitions depend on environmental conditions and management activities, is a prerequisite for developing an effective biological management strategy for *V. album.*

The next critical question is to assess which of the sensitive *V. album* life cycle transitions are amenable for manipulation, either by bottom-up or top-down effects. *Veratrum album* plants growing on nutrient-rich pastures have a larger overall size, size of inflorescence and ultimately seed output per flowering year than plants growing on nutrient-poor soil above the timberline. An overall reduction of nutrients in overused montane soils is a key for restoration of biodiversity, but this may not be achieved in the short or medium term; effects of fertilization remain apparent in upland habitats for 50 years and longer (Hegg *et al.*, 1992). Nevertheless, if weeds differ in their resource requirements from the surrounding vegetation, there may be opportunities for competitive control of weed populations by appropriate control of nutrient ratios in the soil (Tilman *et al.*, 1999). In the case of *V. album*, it may be of particular interest to elucidate nutrient factors that affect seedling establishment more severely than that of the surrounding vegetation.

Top-down control of established plants by natural antagonists seems to be rare in the extreme west of *V. album's* distribution. There is no evidence that even the highest densities of native pathogens or herbivores observed in Central Europe inflict an increased rate of mortality. Complete removal of the above-ground biomass one month after spring growth for several consecutive years reduced the seed output, but hardly affected population size.

Current evidence suggests that the storage organs are the critical plant parts that need to be attacked in order to increase the mortality rate of established plants. As described above, the herbivore community associated with *V. album* in Europe does not appear to exploit the available below-ground feeding niches. Except for the record of the weevil, *Otiorhynchus corvus*, on *V. album* in Slovakia, no root- or rhizome-feeding insects are reported from the west of the species distribution.

Within *V. album* plants, alkaloid concentrations are highest in the below-ground organs. This raises the question: why does a plant invest energy in defending organs that are not attacked? A plausible explanation is that rhizome- and root-feeding species are missing in the west of the species distribution, but are present in the centre. The record of the flea beetle, *Neocrepidodera* sp., on *V. album* in Russia (Medvedev & Roginskaya, 1988) suggests that this plant niche is indeed occupied in Asia. Flea beetles have been repeatedly used in biological weed control. Some of the greatest successes in control of terrestrial weeds are attributed to members of this insect group, such as control of tansy ragwort, *Senecio jacobaea*, by *Longitarsus jacobaeae* Waterhouse (Col., Chrysomelidae) in Oregon (McEvoy *et al.*, 1991), or leafy spurge, *Euphorbia* sp., by *Aphthona lacertosa* (Rosenhauer) and *Aphthona nigriscutis* Foudras (Chrysomelidae) in the northwestern USA and Canada. Provided that *Necrepidodera* sp. occurring in Russia is restricted to the genus *Veratrum*, it may provide an interesting candidate for attacking the unexploited below-ground niches in Europe. It is likely that intensive surveys in eastern Asia will yield more specialist root feeders, which could be considered as biological control agents.

A generally neglected area of weed population management is the effect of natural enemies on seedling survival. Often, a large number of seedlings die due to pathogen or herbivore attack within the first days or weeks after germination (Gange *et al.*, 1991). No information is available on pathogens or herbivores attacking *V. album* seedlings, nor is the ontogeny of alkaloid synthesis known. Indeed, there may be a short span in the seedling's development when defence levels are low. Such a period may be highly susceptible to attack by polyphagous antagonists, such as ectophagous nematodes or slugs, as has been shown for other toxic plant species (Weeks & Bush, 1974; Gange *et al*., 1991; Hanley *et al*., 1995).

In summary, various aspects of the *V. album* population dynamics need further investigation, before a sensible manipulation of bottom-up and top-down effects can be implemented in management practices of montane grasslands. In particular, detailed plant population viability analyses are required in order to determine the susceptibility of the various plant development stages of *V. album* to control measures. If native antagonists cannot exert the required pressure on the plant's sensitive developmental stages even when enhanced by specific manipulation of the system, field surveys towards the centre of origin of the genus *Veratrum* will be necessary to identify natural antagonists that have impact on the plant developmental stages. Experimental investigations on individual and combined effects of land management and biological control measures are then needed to develop a protocol for a low-impact management strategy for this weed. We suggest that Integrated Weed Management Systems will provide (a) long-term control of weeds through rapid reduction of population densities to acceptable levels, followed by maintenance of populations at these low densities; and (b) prevention of invasion and/or spread of low-density populations that would create future problems. Research is needed to test the practicality, effectiveness and ecological sustainability of such systems in the longer term.

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