Candidates for the biological control of teasel, *Dipsacus* spp.

René Sforza[1]

Summary

Dipsacus fullonum L., wild teasel, and *D. laciniatus* L., cut-leaf teasel (Dipsacaceae), native to Eurasia, were introduced into North America in the 1700s. Primarily cultivated for its seedheads, *D. fullonum* escaped from cultivation and colonized waterways, waste ground, fallow fields and pastures, outcompeting native plants. This study reports on foreign exploration for biological control agents against teasel in its native range. Countries from France to Russia were surveyed, with a particular emphasis on insects feeding either on rosettes or seedheads. Two potential candidates were collected, namely the checkerspot butterfly, *Euphydryas aurinia* (Lepidoptera: Nymphalidae), and the leaf beetle, *Galeruca pomonae* (Coleoptera: Chrysomelidae). This is the first report of these two insect species feeding on teasel. Both were collected in the same locations in northern Turkey, and may feed concurrently on the same plants. *Galeruca pomonae* was also collected from south-eastern Russia. Preliminary host-choice and no-choice test experiments showed that *G. pomonae* can complete its entire development on teasel but does not feed on carrot, radish, cabbage, or lettuce. *Euphydryas aurinia* populations from Turkey were parasitized by a tachinid fly*, Erycia furibunda*. Ecological considerations and host specificity are discussed for potential biological control programs.

Keywords: Biocontrol, Chrysomelidae, Dipsacaceae, Endothenia, *Euphydryas, Galeruca,* invasion, Nymphalidae, teasel, Tortricidae, weeds.

Introduction

Teasel is an invasive species in North America. Research on herbivores of *Dipsacus fullonum* and closely related species has been conducted since 2000. This paper gives an overview of the current research on selection of natural enemies against teasel and understanding its ecology in its native range. The term "teasel" will be used in this paper and refers to *Dipsacus* species in general.

Taxonomy and distribution in its native range

Dipsacus fullonum L. (syn. *D. sylvestris*, *D. sativus* for the cultivated teasel), the wild teasel, is native in Eurasia, from north-western Africa to the northern middle east. Botanists are not clear about the binomial terminology of wild and cultivated teasel (Werner 1975b). This plant belongs to the Dipsacaceae family (300 species worldwide) divided into three tribes, which comprise only 12 North American species among the genera *Dipsacus*, *Knautia*, *Succisella*, *Cephalaria* and *Scabiosa*, all aliens. Closely related families are Caprifoliaceae (500 spp., mainly in Asia), Valerianaceae (400 spp. worldwide), Morinaceae (15 spp. in Asia) and Adoxaceae (1 spp. in North America) (Verlaque 1985b, Wahlberg 2001). With 75% of the total species, the Mediterranean basin and Middle East are considered the likely centre of origin for Dipsacaceae. The genus *Dipsacus* comprises 19 species worldwide; nine distributed in Eurasia, including *D. fullonum, D. laciniatus, D comosus, D. ferox, D. bulgaricus, D. gmelini*, eight in Asia, and two in Africa (Verlaque 1985a).

Biology and ecology of teasel

This robust monocarpic biennial to perennial herb reproduces by seed, producing over 3,000 seeds per plant. No vegetative reproduction has been observed. Depending on conditions, up to 30–80% of the seeds

[1] USDA-ARS, European Biological Control Laboratory, Campus International de Baillarguet, CS 90013 Montferrier sur Lez, 34988 St Gely du Fesc, France <email: rsforza@ars-ebcl.org>.

will germinate, so each plant can produce many offspring. Seeds also can remain viable for at least two years. Seeds typically do not disperse far; most seedlings will be located around the parent plant (Werner 1975b). Parent plants often provide an optimal nursery site for new teasel plants after the adult dies. Dead adult plants leave a relatively large area of bare ground, formerly occupied by their own basal leaves, which new plants readily occupy. Teasel grows in open sunny habitats producing rosettes with puckered leaves having scalloped edges during its first year of growth, after which a 2 m tall prickly flower stem emerges. It flowers from July to September. Found on a variety of soils, it prefers abundant moisture in poorly drained areas, tolerating spring flooding very well. When established in a new area, a teasel population may remain for decades in the same field or roadsides.

In North America, numerous ecological studies on teasel were undertaken to evaluate rosette development, population growth rates, and the effect of the invasion on plant communities (Caswell & Werner 1978, Werner 1977). Bolting, flowering and the size of the remaining rosette vegetation are highly correlated with the size of the vegetative rosette in the first year. Rosette size gives a better prediction of plant fate than does age (Werner 1975a).

Why is it a problem?

Common teasel and *D. laciniatus*, the cutleaf teasel, were primarily introduced from Europe into North America possibly as early as the 1700s. No hybrids have been described so far. Until the 1950s, cultivated teasel was considered a valuable commercial product in North America for its head, used to “tease” or raise the nap on wool cloth, and as a horticultural plant. It has been cultivated in Europe since Roman times for the same purpose. An interesting historical fact is that the Popes of Avignon (France) awarded prizes to the grower cultivating teasels which were then used in the manufacture of the cloth for their vestments. In North America, in the last 20–30 years, it escaped from cultivation and colonized natural areas extending from central Maine south to south-eastern Virginia and west to Utah in the US, and from Ontario to British Columbia in Canada. Lack of natural enemies allowed teasel to proliferate, and it rapidly became common and abundant, probably aided by construction of the American interstate highway system. Whereas the plant is not a problem on Eurasian agricultural land, it is considered a noxious weed locally in Colorado, New Mexico, Missouri and Iowa. Teasels are invading plains, waste grounds, old fields, and pastures and along ditches and edges of forests. If left unchecked, teasel can quickly form large monocultures excluding all native vegetation. Cut-leaved teasel is considered more aggressive than common teasel and has severely threatened several northern and central Illinois natural areas. Teasel may be resistant to control measures (Glass 1991) and spread over high-quality natural communities, as shown by its threatened displacement of a native plant of sensitive conservation status, *Cirsium vinaceum* (Woot. & Standl) in central New Mexico (Huenneke & Thomson 1995). Huenneke & Thomson report that, in the greenhouse, growth of *C. vinaceum* rosettes was significantly reduced by the presence of *Dipsacus*, but the invader was unaffected by the thistle.

Literature records of pathogens and invertebrates on teasel

There is currently a very short list of natural pathogens and invertebrates reported worldwide attacking teasel.

Pathogens

In the US, an aphid-borne potyvirus is reported from California inducing leaf mottling and malformation on teasel and *Scabiosa atropurpurea* (Stoner 1951). The species *Macrosiphum rosae* (L.) and *Myzus persicae* (Sulz) were reported as vectors. Several ubiquitous American fungi hosted by teasel were listed by the USDA (cited by Werner (1975b)), e.g. *Cercospora elongata* Pk, *Mycosphaerella asterinoides* (Ell & Ev.) Fairm., *Peronospora dipsaci* Sacc. *Phyllactinia corylea* Pers. and *Phymatotrichum omnivorum* (Shear). None of these fungi have been studied in detail for teasel infection, but they cause diseases in crops (fruits, potatoes) and have low potential for biocontrol.

Invertebrates

A non-specific nematode, *Ditylenchus dipsaci*, is reported from Idaho (USA), first collected on *Dipsacus* in 1888 but also proved to infect potatoes (Thorne 1945). In the Old World, several rosette invertebrates are reported to attack teasel but without causing any damage. A fly, *Phytomyza ramosa* Hd. (Agromyzidae), is known to attack teasel in the UK (Topham 1968). In addition, teasel flowerheads support larvae of certain tortricid species, namely *Endothenia gentianaeana* (Hübner) and *Cochylis roseana* (Haworth) (Cheesman 1996). A butterfly, *Euphydryas desfontainii* (Godart), is sometimes reported as feeding on *Dipsacus fullonum* (Wahlberg 2001). The list of insects from flowers is great, including many insect orders, mostly Hymenoptera and Diptera acting as pollinators (Judd 1983). A potential candidate for biocontrol is a lepidopteran larva, identified as *Epiblema* near *pflugiana* (Tortricidae), reared out from immature buds of teasel collected in the northern Caucasus (G. Campobasso, pers. comm.).

Survey and insect collection

Field surveys in 2001 and 2002 were conducted in Turkey, south-east Russia (Kransnodar region), France, Spain and Ukraine to look for insects on different species of teasel. Ukraine and Turkey were intensively surveyed. We focused on the rosette stage for collecting phytophagous insects attacking plants before flowering. The flowerhead stage was also of interest for insects that may reduce the seedbank. In spring, rosettes of different sizes were inspected and dug up. Roots were inspected for the presence of pathogens or root-feeding insects. All insects found on leaves as larval stages were caged into cardboard tubes with fresh teasel leaves until they reached the quarantine greenhouse in Montpellier. From each collection site at different time of the year 10 dried flower heads in which a tortricid larva was present were cut off at 10 cm below the top, then transferred into cardboard tubes for transportation.

Preliminary experiments

Rearing

Insects (*Galeruca* (Chrysomelidae) and *Euphydryas* (Nymphalidae)) of foreign origin were reared out on French teasel rosettes grown from seeds in quarantine in pots of 12 cm diameter with perlite and compost (50/50). From April to August, insects were maintained in Plexiglass cages at 22°C, under natural light, and under an average RH of 60%. Plants were removed when defoliated and replaced with fresh material one to two times per week depending on feeding activity. Fifty 2nd instar larvae of *Galeruca* were isolated in Petri dishes each with a teasel leaf disc, and were measured at each instar. All Petri dishes were sealed with parafilm. Duration between stages was evaluated.

Host specificity

A preliminary choice and no-choice test was undertaken with *Galeruca*. Radish, carrot, lettuce, turnip and cabbage were selected for economic value, and for their similar leaf structure with teasel. A leaf disc of 4-cm in diameter was used for each plant and stored at 22°C, 16/8 (L:D) using artificial fluorescent illumination, and under an average RH of 80%. In the no-choice test, a single disc was placed in a Petri dish with three 2nd instar larvae, which were surveyed for feeding activity every day until they died. In the choice test, several combinations with five plants plus teasel were used. Three leaf discs were put in each Petri dish with three larvae of 2nd instar, and were surveyed under the same conditions as before. There were two to three replicates in each treatment. Three positive controls consisted of teasel leaf discs with three larvae each, kept under the same conditions as test Petri dishes.

Results

Teasel distribution and ecological data

Teasel was common from southern Spain to south-eastern Russia. Teasel was rare in west and central Ukraine; the main populations were near the Carpathian mountains, and in south-eastern Crimea. Teasel is very widely distributed in northern Turkey, from Ankara to the Black Sea, but rare or absent in the rest of the country. In general, the largest populations were found when moisture is maintained at relatively high levels throughout the growing season, along rivers, and in abandoned, moist fields. Elevation of teasel sites ranged from sea level to 1875 m (in northern Turkey).

List and collection sites of insect species on teasel

Table 1 shows all the insects collected from Palaearctic sites. Large numbers of chrysomelid beetles, *Galeruca pomonae*, were collected on *Dipsacus*. The largest populations of *Galeruca* species were found in Turkey and Russia. Tortricid larvae were collected from each country surveyed and from most sites within a country.

Table 1. Insects collected from *Dipsacus* plants in Eurasia in 2001–2002.

Insect family	Species	Collecting area	Part of the plant attacked
Coleoptera			
Chrysomelidae	*Longitarsus luridus* (Scopoli)	Krasnodar region (Russia)	rosette
	L. brisouti Heikertinger	Krasnodar region (Russia)	rosette
	Phyllotreta nigripes (F.)	Krasnodar region (Russia)	rosette
	Chaetocnema tibialis (Illiger)	Krasnodar region (Russia)	rosette
	Galeruca (Circassica) pomonae Scop.	Kastamonu (Turkey)	rosette
	G. pomonae Scop.	Krasnodar region (Russia)	rosette
Lepidoptera			
Nymphalidae	*Euphydryas aurinia* Rottemburg	Kastamonu (Turkey)	rosette
Tortricidae	*Endothenia gentianaena* (Hübner)	France, Ukraine, Russia, Turkey	flowerhead
	Diceratura ostrinana (Guenée)	Southern France	flowerhead
	Not identified	Krasnodar region (Russia)	rosette tip

Damage observed

Galeruca

In the field, larvae of all stages of *Galeruca* fed on the leaf blades and on the tip of the rosettes. In April, feeding activity observed was high, with punctures and holes on all leaves and with development of necrosis around holes. Damage due to feeding activity on a rosette depended on the number of larvae per plant, their stage, and the size of the rosette. In Russia, larvae per rosette ranged from 4 to 33 (average number = 20 for 5 rosettes). This beetle can be very damaging, causing whole mats of rosettes to be defoliated. Both larvae and adults were teasel feeders.

Euphydryas

In the field, late larvae are solitary and damage the rosette by intense feeding on margins of the leaves. In the quarantine laboratory, larvae were gregarious at all stages, and colonized rosette leaves, enclosed in wax webs. In July, they were feeding heavily before entering diapause.

Tortricidae

Endothenia gentianaena was confined to one larva per seedhead, feeding on the pith in the central cavity. We did not observe significant damage to seedheads. Several unidentified species inducing severe damage to the plant were collected (data not shown) in the rosette tips.

Biology and ethology of two selected species

General data on *Euphydryas aurinia*

Euphydryas aurinia was found in northern Turkey, near Kastamonu city (1100 m elevation), in semi-alpine areas. Teasel was the only observed food plant. In April, mature larvae were moving from plant to plant, from rosettes to old teasel stems, probably looking for a secure place to pupate. Large larvae were feeding actively on rosette leaves. In Europe, *E. aurinia* is known for its gregarious larval behaviour in the spring (Porter 1982), but my observations in Turkey indicated that they were more solitary in nature. Insect larvae collected were then reared on French teasel in quarantine. Pupation occurred on the top of cages in mid June. Most of the pupae were parasitized by a single tachinid fly*, Erycia furibunda* Zetterstedt. From pupae, we obtained 40 adults that were kept on *Knautia* flowers. The rearing of *E. aurinia* was continued past the adult stage. The females were given *Dipsacus* plants for oviposition. White eggs, rapidly turning yellow, were laid in clusters on the leaves. The subsequent egg batches were collected and the hatching larvae were reared on teasel but larvae did not survive diapause. Both American and French teasel plants served as food plants and were accepted by insects.

General data on *Galeruca pomonae*

Insects were found from 300 to 1100 m elevation in the field in Turkey and at sea level in Russia. We observed high resistance of larvae to moisture inside the rosettes. In August, a *G. pomonae* female was found buried 10-cm deep into the soil along a *Dipsacus fullonum* root. This behaviour was observed in quarantine; after mating, females were found in the pots, sometimes dead. Egg clusters were collected along the inner edge of the pots. Brown in colour and covered by ornamentation, eggs were stuck to soil particles and in between them. We were not able to obtain a second generation. After collecting 1st instar larvae in April, the first adults emerged in June and survived until August in the quarantine on teasel plants. Females may mate several times before egg laying. Table 2 shows partial life tables for *Galeruca pomonae* originating from Turkey and maintained on teasel leaves.

Host specificity

Figure 1 shows survival of *G. pomonae* on different cultivated plants in no-choice and choice conditions. In all treatments, teasel was the only plant attacked. In no-choice tests, survival never exceeded 16 days (radish), and was less than 10 days for lettuce, cabbage and turnip. For radish, 8 of 9 larvae died before 12 days. In choice tests, larvae seemed to live longer than in no-choice as they were associated with teasel leaf discs. Only teasel discs were eaten. A few tentative feedings were observed on cabbage in the treatment carrot+cabbage+*Dipsacus*, but only on the day before the larvae died. In many treatments, even in no-choice, larvae moulted. Controls were the only treatment in which larvae continued their development until adult emergence. For positive controls, we stopped the experiment at 40 days, when 5 (of 9 in the three replicates) individuals were still alive.

Table 2. Measurements of larvae and pupae and duration of 3rd to pupal instar for *Galeruca pomonae*.

Larval stage	3	4	5	Pupa
Mean length in cm ± SE	4.39 ± 0.53 (N = 49)	6.09 ± 0.59 (N=42)	7.63 ± 0.89 (N=41)	7.52 ± 0.80 (N=40)
Mean duration in days ± SE		7.26 ± 1.16 (N=38)	15.79 ± 1.66 (N=39)	3.50 ± 1.08 (N=39)

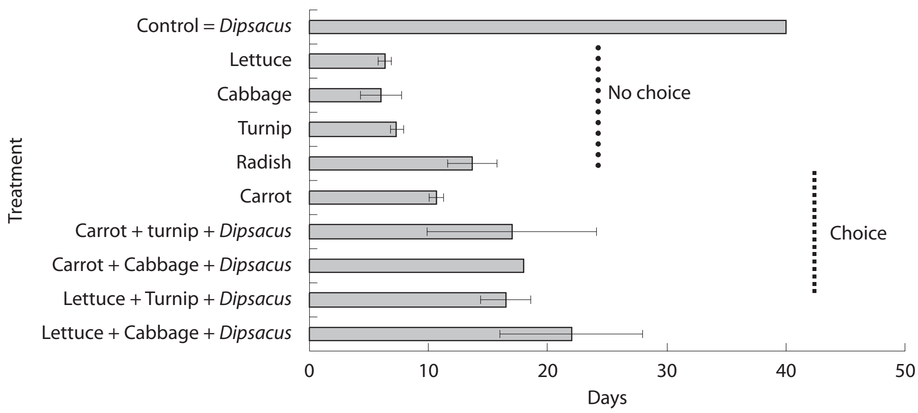

Figure 1. Preliminary choice and no-choice tests with *Galeruca pomonae*.

Conclusions

Evaluation of potential biocontrol agents for further studies

Chrysomelidae

This group is an important source of introduced insects for biological control of weeds in North America (White 1996). Based on the literature, just a few chrysomelid beetles collected in this study were previously reported on *Dipsacus*. Of these, *P. nigripes* and *C. tibialis* were probably accidental feeders (A. Konstantinov, pers. comm.), as they were known from other host plant families. *Longitarsus luridus* is known from other Dipsacaceae, and might be a candidate for further studies. *Galeruca* species might be promising agents for biocontrol of teasel. Our specificity test was only an indicator and showed real association with teasel plant. The short list of test plants does not reflect monophagy of this population of *G. pomonae*, but opens to discussion the role of this species for controlling teasel. It is clear that more Dipsacaceae plants should be included in subsequent host-specificity tests, as well as genera from closely related families, like *Gentiana* sp., *Lonicera* sp., *Plantago* and *Centaurea* sp.

Nymphalidae

Euphydryas aurinia is reported feeding on plant species from three different families: Caprifoliacae, Gentianaceae, and Dipsacaceae (Wahlberg 2001). Within the latter, the genera *Succisa, Scabiosa, Cephalaria and Knautia* are reported as host plants. Our findings show a particular adaptation of *E. aurinia* for Dipsacaceae. It is surprising that *Dipsacus* sp. is not reported as a host plant, as *E. aurinia* is commonly distributed in northern Turkey and is a species widely studied in the Palaearctic region. Nevertheless, this result is confirmed by recent molecular studies reporting that *E. aurinia* is closely related to *E. desfontainii* (both within the named *E. aurinia* clade) feeding on *Dipsacus fullonum*, and on two other plant species belonging to Dipsacaceae (Wahlberg 2001). The importance of certain secondary chemicals known as iridoid glycosides and seco-iridoids to host use by butterflies has been shown (Jensen *et al.* 1975). The *E. aurinia* clade from the Palaearctic mainly utilizes plants in Dipsacaceae containing only seco-iridoids that are also present in Caprifoliaiceae or Gentianaceae on which a few populations of *E. aurinia* feed (Wahlberg 2001).These results have to be compared with Nearctic species in the *Euphydryas* group that are able to exploit a wide range of plants containing both iridoid metabolites, suggesting that *E. aurinia* originating from Eurasia became specialized on Dipsacaceae, which contain only seco-iridoids. In fact, the evolutionary history of host-plant use in the *Euphydryas* group is somewhat linked to the biogeography of the group and suggests promising expectations for a biocontrol program using these species. Special attention should now be devoted to the plant families having only (or mainly) seco-iridoids, such as Dipsacaceae, Gentianaceae, and Oleaceae (Zimmermann *et al.* 2000). On this basis, the choice of host plants for testing specificity will be facilitated by using chemical signatures of selected plants. The main concern will be on the potential split of *E. aurinia* clade onto North American native plants, but it is known that *Euphydryas* species are monophagous or at most oligophagous at the population level (Mazel 1986, Singer 1983), which must be ascertained by host-plant experiments. Potential for biocontrol is also supported by observed mortality occurring when insects are experimentally put on plant species other than the natural one (Mazel 1982). For further collections, we need to consider larval parasitism, as we collected a tachinid fly, previously reported from *E. aurinia* and *E. desfontainii* (Ford and Shaw 1991), and the status of endangered species for the *E. aurinia* clade, which is protected in France.

Tortricidae

As yet, no precise evaluation of seed reduction by these tortricid larvae in *Dipsacus* flowerheads has been made. It is reported for *E. gentianaena* that the mean number of 10 seeds per head is damaged, which is very low compared to teasel seed production (Cheesman 1996). For another tortricid species, *Cochylis roseana,* not found in this study, larvae are held together by solidified, compacted frass, and tend to remain in the teasel heads. The impact should not be negligible as up to 30 individuals may be contained in one single head (Cheesman 1996). Comparing the two microlepidoptera, it seems that *C. roseana*, if specific to teasel, would have more potential than *E. gentianaena* in terms of damage, as many larvae may feed in one flower head instead of a single for *E. Gentianaena*.

Perspectives for further studies

For the Turkish populations of *E. aurinia* and *G. pomonae*, open field tests could take place in the same location, as the insects are sympatric. At the same time, investigations should now focus on French populations of these two groups. Insects of French origin feeding on teasel will be reared and studied outside quarantine, making host-specificity tests easier to undertake. The *Euphydryas aurinia* clade is distributed is southern France, and we will evaluate their specificity for teasel. Concerning chrysomelid beetles, the well-known polyphagy of *Galeruca pomonae* has to be clarified for these Russian and Turkish populations. A recent study reported differentiation between biological and genetic data for characterization of the species status of a weevil, for which morphology was not sufficiently discriminating (Fumanal *et al.* 2002). Other *Galeruca* species might be of interest, as larvae are active leaf feeders. The Lepidoptera is an interesting group to focus on for rosette feeders because, in addition to Nymphalidae, several other species feeding in the rosette tip might have a severe impact on teasel growth as the main shoot is destroyed.

To conclude, surveys on other plant species among the Dipsacaceae, such as *Cephalaria leucantha*, *Knautia arvensis* and *Succisa pratensis*, might provide other potential candidates, as all Dipsacaceae in North America are introduced species.

Acknowledgements

The author thanks his colleagues Tim Widmer (EBCL) and Massimo Cristofaro (BBCA) for fruitful cooperation during foreign exploration, and all the taxonomists involved in these identifications: Ron Beenen (Netherlands) and Alexander Konstantinov (USDA) (Chrysomelidae), Pierre Leraut (MNHN) (Nymphalidae), Christian Cocquempot (INRA) and Benoît Nusillard (EBCL) (Tortricidae), and Michel Martinez (INRA) (Tachinidae), and acknowledges Luc Delaplace and Nicolas Crespy for maintaining insect rearing.

References

Caswell, H. & Werner, P.A. (1978) Transient behavior and life history analysis of teasel (*Dipsacus sylvestris* Huds.). *Ecology* **59**, 53–66.

Cheesman, O.D. (1996) Life histories of *Cochylis roseana* (Haworth) and *Endothenia gentianaeana* (Lepidoptera: Tortricidae) on wild teasel. *The Entomologist* **115**, 65–80.

Ford, T.H. & Shaw, M.R. (1991) Host records of some West Palearctic Tachinidae (Diptera). *Entomologist's Record and Journal of Variation* **103**, 23–38.

Fumanal, B., Martin, J.F., Sobhian, R., Lumaret, J.P. & Bon, M.C. (2002) Host-associated differentiation ot the collar gall weevil *Ceutorhynchus assimilis* (Coleoptera: Curculionidae) and insights in biological control. *Global IOBC International Symposium co-organized with CILBA.* IOBC Bulletin **14**:9:2002.

Glass, W.D. (1991) Vegetation management guideline: cut-leaved teasel (*Dipsacus laciniatus* L.) and common teasel (*Dipsacus sylvestris* Huds.). *Natural areas* **11**, 213–214.

Huenneke, L.F. & Thomson, J.K. (1995) Potential interference between a threatened endemic thistle and an invasive non-native plant. *Conservation Biology* **9**, 416–425.

Jensen, S.R., Nielsen, B.J. & Dalgren, R. (1975) Iridoid compounds, their occurrence and systematic importance in the angiosperms. *Botaniska Notiser* **128**, 148–180.

Judd, W.W. (1983) Insects associated with flowering teasel, *Dipsacus sylvestris*, at Dunville, Ontario. *Proceedings of the Entomological Society of Ontario* **114**, 95–98.

Mazel, R. (1982) Exigences trophiques et évolution dans les genres *Euphydryas* et *Melitaea sensu lato* [Lep. Nymphalidae]. *Annales de la Société entomologique de France* **18**, 211–227.

Mazel, R. (1986) Structure et évolution du peuplement d'*Euphydryas aurinia* Rottemburg (lepidoptera) dans le sud-ouest européen. *Vie et milieu* **36**, 205–225.

Porter, K. (1982) Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. *Oikos* **38**, 308–312.

Singer, M.C. (1983) Determinants of multiple host use by a phytophagous insect population. *Evolution,* **37**, 389–403.

Stoner, W.N. (1951) *Phytopathology* **41**, 91

Thorne, G. (1945) *Ditylenchus destructor*, n.sp., the potato rot nematode, and *Ditylenchus dipsaci* (Kühn, 1857) Filipjev, 1936, the teasel nematode (Nematoda: Tylenchidae). *Proceedings of the helminthological Society of Washington* **12**, 27–34.

Topham, P.N. (1968) The Fuller's teasel. *Proceedings of the botanical Society of British Islands* **7**, 377–381.

Verlaque, R. (1985a) Etude biosystématique et phylogénétique des Dipsacaceae. II. Caractères généraux des Dipsacaceae. *Revue de Cytologie et Biologie végétales – Le Botaniste* **8**, 117–168.

Verlaque, R. (1985b) Etude biosystématique et phylogénétique des Dipsacaceae. III. Tribus des Knautieae et des Dipsaceae. *Revue de Cytologie et Biologie végétales – Le Botaniste* **8**, 171–243.

Wahlberg, N. (2001) The phylogenetics and biochemistry of host plant specialization in melitaeine butterflies (Lepidoptera: Nymphalidae). *Evolution* **55**, 522–537.

Werner, P.A. (1975a) Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia* **20**, 197–201.

Werner, P.A. (1975b) The biology of Canadian weeds. 12. *Dipsacus sylvestris* Huds. *Canadian Journal of Plant Science,* 783–794.

Werner, P.A. (1977) Population growth rates and age *versus* stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). *Ecology* **58**, 1103–1111.

White, R.E. (1996) Leaf beetles as biological control agents against injurious plants in North America. *Chrysomelidae biology*, (eds P.H.A. Jolivet *et al*.), pp. 373–399. SPB Academic Publishing, Amsterdam, The Netherlands.

Zimmermann, M., Wahlberg, N. & Descimon, H. (2000) Phylogeny of *Euphydryas* checkerspot butterflies (Lepidoptera: Nymphalidae) based on mitochondrial DNA sequence data. *Annals of the Entomological Society of America* **93**, 347–355.