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Chemistry of *Cirsium* and *Carduus*: A role in ecological risk assessment for biological control of weeds?

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Abstract

Prediction of host plant range and ecological impact of exotic phytophagous insects, such as insects for classical biological control of weeds, represents a major challenge. Recently, the flowerhead weevil (*Rhinocyllus conicus* Fröl.), introduced from Europe into North America to control exotic thistles (*Carduus* spp.), has become invasive. It feeds heavily on some, but not all species of native North American thistles (*Cirsium* spp.). We hypothesized that such non-target use among native plants could be better predicted by knowledge of characteristic chemical profiles of secondary compounds to supplement the results of host specificity testing. To evaluate this hypothesis, we reviewed the literature on the chemistry of *Cirsium* and *Carduus* thistles. We asked what compounds are known to be present, what is known about their biological activity, and whether such information on chemical profiles would have better predicted realized host range and ecological effects of *R. conicus* in North America. We found an extensive, but incomplete literature on the chemistry of true thistles. Two main patterns emerged. First, consistent chemical similarities and interesting differences occur among species of thistles. Second, variation occurs in biologically active groups of characteristic compounds, specifically flavonoids, sterols, alkaloids and phenolic acids, that are known to influence host plant acceptance, selection, and feeding by phytophagous insects. Surprisingly, sesquiterpene lactones, which are characteristic in closely related Asteraceae, have not been extensively reported for *Cirsium* or *Carduus*. The minimal evidence on sesquiterpene lactones may reflect extraction methods vs. true absence. In summary, our review suggests further research on thistle chemistry in insect feeding is warranted. Also, since the exotic Canada thistle (*Cirsium arvense*) is an invasive thistle of current concern in North America, such research on mechanisms underlying host range expansion by exotic insects would be useful.

Keywords: *Carduus*, chemical mediation, *Cirsium*, flavonoids, host range expansion, insect host preference, insect herbivory, secondary metabolites, sterols

1. Introduction

Invasive exotic species, such as Eurasian thistles, present a major threat to sustained productivity and biodiversity in the United States (Vitousek et al., 1997; Simberloff, 1997; National Invasive Species Council, 2001; Pimentel et al., 2000). Consequently, such exotic weeds often are targeted for classical biological control, i.e. the importation, release, and redistribution of exotic insects from the region of the weed's origin to limit the plant's invasiveness (DeBach and Rosen, 1991; OTA, 1995; Delfosse, 2000). However, the release of exotic insects entails a risk to native plants and communities (Howarth, 1991; Simberloff and Stiling, 1996; Louda et al., 1997, 1998; Stiling and Simberloff, 1999). Prediction of both the risk and the ecological impact of exotic insects poses a critical challenge (Louda, 1999a; Strong and Pemberton, 2000; Louda et al., 2003a, 2003b).

The extraordinary diversity of plant secondary metabolites (see, for example, Rosenthal and Berenbaum, 1991 & Walton and Brown, 1999), combined with the known influence of some of these chemicals upon insects (e.g. Carde and Bell, 1995), suggests that comparative chemistry may contribute to improving prediction of the host use and impact of introduced herbivorous insects. However, the role of chemical composition and variation in predicting the interactions between insect biological control agents and their targeted, exotic host plants relative to potential non-targeted, less preferred (secondary) native host species has yet to be explored.

In this study, we reviewed the literature on the reported chemical profiles in the two main genera of true thistles (*Cirsium*, *Carduus*) in order to determine whether such information would improve the likelihood of predicting relative host plant use and non-target effects. In the specific case of the Eurasian biological control weevil (*Rhinocyllus conicus* Frölich), introduced for exotic thistle control, about one-third of the native North American thistle species are now reported as host plants (Goeden and Ricker, 1986a, 1986b, 1987a, 1987b; Turner et al., 1987; Louda et al., 1997, 1998). Populations of some species are being severely impacted (Louda et al., 1997, 1998; Louda, 1999a; Louda and Arnett, 2000). Thus, an additional aim of this review was to collate the information that may aid in the further development of screening protocols in similar cases, such as the biological control efforts now targeting the invasive Eurasian *Cirsium arvense* (Canada thistle) in North America.

It seems paradoxical that despite 50 years of studies showing chemical variation among plants as a significant factor in the preference and performance of insects on plants (e.g. Dethier, 1947; Ehrlich and Raven, 1964; Singer, 1971; Futuyma, 1983; Price, 1984; Spencer, 1988; Roitberg and Isman, 1992; Rosenthal and Berenbaum, 1991; Bernays and Chapman, 1994; Carde and Bell, 1995), there is still little evidence on the role of chemical variation in host range expansion. Un-

answered questions include the degree to which chemical profile matters (Courtney and Kibota, 1990), the amount of chemical differentiation necessary to retard range expansion, and the precision of laboratory bioassays of insect preference in prediction of ecological effects on secondary hosts by a biological control insect (Arnett and Louda, 2002; Louda et al., 2003a, 2003b).

Phylogenetic relationships, geographic distribution, and host chemistry have been hypothesized to be determinants of the evolution and ecology of insect host preference, host range, and host shifts (Becerra, 1997). Becerra and Venable (1999) recently argued that host chemistry was the most significant of these factors. They found that host shifts by *Blepharida* spp. beetles were best explained by chemical similarities among host plants, independent of either molecular phylogeny or geographic distribution (Becerra, 1997; Becerra and Venable, 1999). Such findings suggest the hypothesis that knowledge of chemical profiles among potential host plant species could improve the prediction of the ultimate host range and, so, the assessment of the potential for significant non-target effects among native plants that are identified as secondary hosts in host specificity testing of insects for weed biocontrol. To date, host chemistry has not been evaluated explicitly in such ecological risk assessments of host range for biocontrol insects.

The specific case history that stimulated our interest in this hypothesis is the current interaction of the Eurasian flower head weevil, *Rhinocyllus conicus*, with non-targeted native North American *Cirsium* spp. This weevil, which was introduced to control naturalized exotic *Carduus* spp. such as musk thistle (*Carduus nutans*), uses the flower heads of more than 33% of the 90⁺ native North American thistles (*Cirsium* spp.) examined thus far (Goeden and Ricker, 1986a, 1986b, 1987a, 1987b; Turner et al., 1987; Palmisano and Fox, 1997; Louda et al., 1997, 1998; Louda, 1998, 1999b; Herr, 2000). However, preference and relative use vary among thistle species. Reductions in seed production by *R. conicus* are greater for some species than others (Zwölfer and Harris, 1984; Turner et al., 1987; Louda et al., 1997, 1998; Louda, 1998, 1999b; Herr, 2000; Louda and Arnett, 2000; Gassmann and Louda, 2001). The weevil is severely reducing seed production in half of the native thistle species studied intensively in natural areas and national parks in the Great Plains and Rocky Mountains (Louda et al., 1997, 1998, 1999a). The population density of Platte thistle (*Cirsium canescens* Nutt.), the most intensively studied native species (Louda and Potvin, 1995), has declined significantly since *R. conicus* invaded the native prairie sites, with less evidence of feeding impact on the numbers of the co-occurring wavyleaf thistle, *C. undulatum* (Louda, 1998, 1999a; Louda and Arnett, 2000).

Better understanding of the potential role of chemical mediation in the varied non-target effects observed has important implications, both for our basic understanding of host range expansion and for the evaluation of insects for biological control of weeds. If evolution of chemical mediation of host range and preferences is important (Becerra and Venable, 1999), then three conditions must be met. These are: (1) insect preference among available host plant species must exist; (2) characteristic chemical profiles must vary; and (3) insect behavioral responses must reflect that chemical variation. We found support for each of these conditions in the literature.

First, the existence of insect preference hierarchies is well substantiated, including for *R. conicus* (Zwölfer and Harris, 1984). The voluminous literature demonstrates the existence of consistent host plant preferences of phytophagous insects among plant species (see, for example, Spencer, 1988 & Carde and Bell, 1995), including for *R. conicus* in Europe (Zwölfer, 1965; Zwölfer and Harris, 1984; Gassmann and Louda, 2001) and in North America (e.g. Turner et al., 1987; Louda and Arnett, 2000; Arnett and Louda, 2002).

Second, abundant evidence documents both differences and similarities in secondary plant metabolites among closely related plants (e.g. Wagner, 1977; Hegnauer, 1989; Harborne, 1990, 1991; Rosenthal and Berenbaum, 1991). No recent study, however, has compiled the evidence available on chemical profiles of true thistles. Our preliminary observations suggested that variation in characteristic profiles of biologically active compounds of *Carduus* and *Cirsium* could be important in the *R. conicus* case. For example, some of the flavonoids, such as apigenin, overlap between the preferred coevolved weed, *Carduus nutans*, and newly acquired native North American host plants, such as *Cirsium canescens* and *C. undulatum*. Yet, other flavonoids, such as chrysoeriol vs. luteolin, differentiate exotic *Carduus* spp. from native prairie *Cirsium* spp. (see below). These observations suggested a new synthesis of the information available on chemical profiles of thistles is needed to assess the hypothesis of chemical mediation in non-target thistle plant use by *R. conicus* in North America.

Third, a large body of evidence shows that insect acceptance, preference, and proximate host choice often are related to chemical profile (e.g. Spencer, 1988; Bernays and Chapman, 1994; Carde and Bell, 1995; Becerra and Venable, 1999; Simmonds, 2001). However, the potential contribution of overlap and non-overlap in chemical profiles to host preference and observed variation in feeding and oviposition by thistle-feeding species, such as *R. conicus*, is unknown.

Thus, four fundamental questions guided our review. First, what is known about the chemical profiles of two of the main genera of true thistles (*Cirsium* and *Carduus*: Family Asteraceae, Tribe Carduinae, Subtribe Carduineae) that are respectively native and non-native in North America? Second, what is the evidence that these plant secondary metabolites are biologically active, providing a potential mechanism for mediation of differential feeding and oviposition by thistle-adapted insects among potentially acceptable hosts in the field? Third, to what extent would knowledge of the chemical profile and biological activity of *Cirsium* and *Carduus* have enhanced our ability to predict whether rare North American *Cirsium* spp. were vulnerable to potential ecological impacts by the alien Eurasian biological control insect, *R. conicus*? Finally, could similar information be used in contemporary efforts for biological control in management of other invasive Eurasian species, such as Canada thistle (*Cirsium arvense*)?

In this review we follow Harborne (1999) and define secondary metabolites as substances that do not appear to have primary metabolic functions (photosynthesis, respiration, and carbon fixation) and which vary in their distribution in the plant kingdom. For a compound to be classified as biologically active, there must be evidence that it can be taken up by an organism and that this uptake has some effect (Berenbaum, 1995). Documented functions of some secondary metabo-

lites include: UV protection, defense against pathogens, and hormonal regulation (see Rosenthal and Berenbaum, 1991; Harborne et al., 1999; Walton and Brown, 1999). Mixtures of compounds also can act synergistically to affect insect behavior (e.g. Berenbaum and Zangerl, 1988; Macedo and Langenheim, 1989; Desrochers and Bohm, 1993; Espinosa-Garcia and Langenheim, 1991; Cates, 1996; Harborne, 1999).

2. Chemistry and biological activity of compounds from *Cirsium* and *Carduus*

We found information on secondary chemistry from 92 species of *Cirsium* and 12 species of *Carduus*. The compounds reported include: flavonoids, sterols and triterpenes, alkaloids, polyacetylenes, acetylenes and hydrocarbons, sesquiterpene lactones, phenolic acids, lignans, and a few other compounds (Figure 1). These

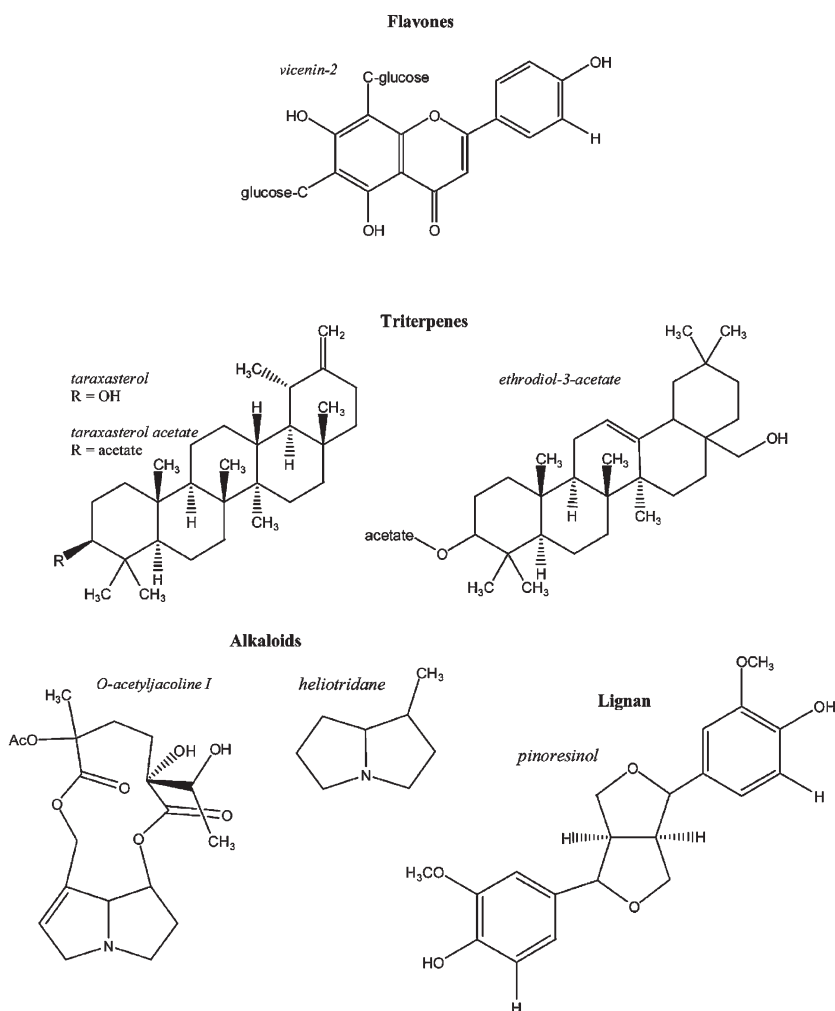


Figure 1. Selected compounds reported to show insect bioactivity.

data are reviewed by chemical family, first for flavonoids as the group for which the most data exist (Tables 1 & 2), and then for the other compounds reported (Tables 3 & 4).

2.1. Flavonoids

2.1.1. Chemistry

The best-known group of secondary metabolites in *Cirsium* and *Carduus* are flavonoids (Tables 1 & 2). However, in a recent review of flavonoids and their importance in feeding and oviposition of insects, Simmonds (2001) pointed out that, in spite of extensive research on flavonoids, little information exists on their chemical ecology. Most of the research on flavonoids has focused on chemotaxonomic, rather than ecological, questions, including for the Asteraceae (Bohm, 1998). By 1994, the total number of flavonoids known was over 4000 (Harborne, 1999). Derived from the acetate/malonate pathway for the A ring and the shikimate pathway for the B and C rings, these compounds can be found in almost all the plants' organs, including stems, leaves, and flowers (Strack, 1997). Most flavonoids consist of three six-carbon rings, with one containing a carbonyl group and each ring having different alcohol, methyl ether, or glycosidic (sugar) substituents. The different moieties affect the activity of the flavonoid (Hedin and Waage, 1986; El-Lakany et al., 1997; below). Since *Cirsium* and *Carduus* spp. flavonoids differ widely in their sugars (Tables 1 & 2), the variation represents a potential mechanism for host recognition and differences in host preference.

2.1.2. Biological activity

The reported biological activity of flavonoids toward insects ranges from feeding deterrents for generalized phytophagous insects (e.g. Hedin and Waage, 1986; Harborne, 1990) to feeding stimulants and oviposition inducers, such as luteolin, for more specialized insects (e.g. Feeny et al., 1988; Harborne, 1991; Haribal and Renwick, 1996). In a review of the role of flavonoids in insect-plant interactions, Simmonds (2001) found clear evidence flavonoids can affect insect feeding and oviposition, and she documented variability in flavonoid activity: among insect species, stages of insect maturity, and extract concentrations. For example, Feeny et al. (1988) found luteolin 7-O-(6''-O-malonyl)- β -D-glucoside, in combination with trans-chlorogenic acid from wild carrot (*Daucus carota*), stimulated oviposition by the black swallowtail butterfly (*Papilio polyxenes*). However, individually the compounds had no effect. Also, Zielske et al. (1972) found that a derivative of luteolin, 7- α -L-rhamnosyl-6-methoxyluteolin, from alligator weed (*Alternanthera phylloxeroides*) was at least partially responsible for the feeding preference of *Agasicles* spp. leaf beetles. Quercetin, a common flavonoid extracted from cotton (*Gossypium hirsutum*) and also found in *Cirsium* and *Carduus* spp., stimulated feeding by the boll weevil, *Anthonomus grandis* (Hedin et al., 1968). Haribal and Renwick (1996) found that, out of six glycosidic quercetin compounds in *Asclepias curassavica*, only two were active as oviposition stimulants for the monarch butterfly, *Danaus plexippus*. Interestingly, the only difference among the six compounds was the constituent sugar (Haribal and

Table 1. Flavonoids reported in *Cirsium* spp. by compound ^a

Compound	Species	Biological activity	References
acacetin/apigenin 4'-methylether	<i>C. arvense</i> , <i>C. japonicum</i>	aldose reductase inhibitor, iodothyronine, deiodinase, histamine release from peritoneal mast cells	1
acacetin-7-O-diglycoside	<i>C. subnitveum</i>	?	2
acacetin rhamnoglucoside	<i>C. purpuratum</i> , <i>C. spinosum</i>	?	3,4
apigenin ^a	<i>C. arvense</i> , <i>C. carolinianum</i> , <i>C. japonicum</i> , <i>C. magofukui</i> , <i>C. nipponicum</i> , <i>C. oleraceum</i> , <i>C. purpuratum</i> , <i>C. rhinoceros</i> , <i>C. sieboldii</i> , <i>C. syriacum</i> , <i>C. vallis-demonii</i> , <i>Cirsium</i> spp. (62) ¹¹	anti-inflammatory, anti-spasmodic, insect attractant as a UV-pigment, antibacterial	5-20
apigenin-5-O-glucoside	<i>C. magofukui</i> , <i>C. sieboldii</i>	?	19
apigenin-7-O-diglycoside	<i>C. syriacum</i> , <i>C. vulgare</i>	?	13, 21
apigenin-7-glycoside	<i>C. arvense</i> , <i>C. nipponicum</i> , <i>C. oleraceum</i> , <i>C. syriacum</i>	?	12, 13, 16,
apigenin-7-glycoside	<i>C. chikushiense</i>	?	19
apigenin-7-O-diglycoside	<i>C. canescens</i> , <i>C. flodmanii</i> , <i>C. pulcherrimum</i>	?	2
apigenin-6,8-C-diglycoside	<i>C. canescens</i> , <i>C. flodmanii</i> , <i>C. ochrocentrum</i> , <i>C. subnitveum</i> , <i>C. undulatum</i>	?	2
6-methoxy apigenin-7-O-diglycoside	<i>C. canescens</i>	?	2
6-methoxy apigenin-8-C-glycoside	<i>C. drummondii</i>	?	2
apigenin-7-rhamnoglucoside	<i>C. arvense</i>	?	14
C-glycosylapigenin	<i>C. gratiosum</i>	?	19
chrysoerial-7-O-diglycoside, 6-methoxy chrysoerial-7-O-diglycoside	<i>C. canescens</i>	?	2
chrysoerial-7-O-diglycoside	<i>C. flodmanii</i> , <i>C. pulcherrimum</i> , <i>C. subnitveum</i> , <i>C. undulatum</i>	?	2
monoglycoside	<i>C. chikushiense</i> , <i>C. undulatum</i>	?	2, 19
cirsilol	<i>C. lineare</i> (aerial leaf surface)	arachidonate 5-lipoxygenase inhibitor	1
cirsilimeol-4'-glucoside, cirsilol-4'-glucoside	<i>C. lineare</i>	?	23

(continued on next page)

Table 1. (continued)

Compound	Species	Biological activity	References
cirsimaritin	<i>C. amplexifolium</i> , <i>C. arvense</i> , <i>C. kamtschaticum</i> , <i>C. pendulum</i> , <i>C. rhothophyllum</i> , <i>C. tanakae</i> ssp. <i>aomorense</i>	?	3, 19, 23-26
cirsimaritin-4'-O-glucoside	<i>C. aomorense</i> , <i>C. japonicum</i> var. <i>ussuriense</i> , <i>C. rhothophyllum</i> , <i>C. tanakae</i>	?	27, 29
cirsimaritin-4'-O-rutinoside	<i>C. brevistylum</i>	?	29
cirsitakaoside, cirsitakaogenin	<i>C. japonicum</i> var. <i>takaense</i>	?	30
cynroside	<i>Cirsium</i> spp. (17)	?	10
diosmetin-7-O-diglycoside	<i>C. ochrocentrum</i> , <i>C. scariosum</i> , <i>C. undulatum</i>	?	2
genkwanin-4'-O-glucoside	<i>C. vulgare</i>	?	21
hispidulin (<i>scutellarein</i> 6- methyl ether)	<i>C. carolinianum</i> , <i>C. oligophyllum</i>	cytotoxic	20, 31, 32
hispidulin triacetate	<i>C. carolinianum</i>	?	20
hispidulin-7-O- α -L- rhamnopyranosyl-(1 \rightarrow 2)- α -D- glucopyranoside	<i>C. japonicum</i> var. <i>ussuriense</i> , <i>C. rhinoceros</i>	cardiovascular contractibility	8, 33
hispidulin-4'-glucoside,	<i>C. oligophyllum</i>	?	31
hispidulin-7,4'-diglycoside			
hispidulin-7-O- neohesperidoside	<i>C. japonicum</i> var. <i>ussuriense</i>	?	27
kaempferol			
kaempferol-7-O-methyl ether,	<i>C. arvense</i> , <i>C. syriacum</i> , <i>C. vallis-demonii</i>	?	13, 15
kaempferol-3-O-rhamnoside	<i>C. vallis-demonii</i>	?	11
kaempferol-3-O-galactose			
kaempferol-3-O- arabinosylgalactose	<i>C. babanum</i> , <i>C. arvense</i>	?	19, 26
kaempferol-3-O-glucoside	<i>C. babanum</i> , <i>C. vulgare</i>	?	19, 21, 26
isokaempferide	<i>C. vulgare</i>	?	21, 26
3-O-methylkaempferol	<i>C. arvense</i>	?	6, 7, 34
astragalol (<i>kaempferol</i> -3-O- glucopyranoside)	<i>C. arvense</i>	?	35
		?	6, 7

Table 1. (continued)

Compound	Species	Biological activity	References
linarin (<i>acacetin-7-rutinoside</i>)	<i>C. albenscens</i> , <i>C. arisanense</i> , <i>C. arvense</i> , <i>C. babanum</i> , <i>C. gratioisum</i> , <i>C. foliosum</i> , <i>C. hosogawa</i> , <i>C. japonicum</i> , <i>C. japonicum var. australe</i> , <i>C. japonicum var. ussuriense</i> , <i>C. kagamontanum</i> , <i>C. kamtschaticum</i> , <i>C. kawakamii</i> <i>var. variegatum</i> , <i>C. microspicatum var. microspicatum</i> , <i>C. microspicatum var. kiotense</i> , <i>C. nipponicum var. incomptum</i> , <i>C. oleraceum</i> , <i>C. pectinellum</i> , <i>C. purpuratum</i> , <i>C. rhinoceros</i> , <i>C. senjoense</i> , <i>C. spicatum</i> , <i>C. spinosum</i> , <i>C. subcoriaceum</i> , <i>C. tioganum var. coloradense</i> , <i>C. yezeense</i> , <i>Cirsium spp.</i> (46) ¹¹ <i>C. foliosum</i> , <i>C. tioganum var. coloradense</i> <i>C. arvense</i> , <i>C. echinus</i> , <i>C. hosogawa</i> , <i>C. oleraceum</i> , <i>C. rhinoceros</i> , <i>C. syriacum</i> , <i>C. vallis-demonii</i> , <i>Cirsium spp.</i> (44) ¹¹	analgesic, anti-inflammatory	2, 8, 10, 19, 22, 23, 27, 28, 35-42
6-methoxy linarin		?	2
luteolin ^a		enzyme inhibitor (α -glucosidase & α -amylase) larval growth inhibitor, antibacterial insect attractant as UV-pigment	8-11, 13, 16-18, 41, 43-45
luteolin-7-O-diglycoside	<i>C. pulcherrimum</i> , <i>C. tovedyi</i>	?	2
luteolin-4'-O- β -glucoside	<i>C. helenioides</i>	?	46
luteolin-7-O-glucoside ^a	<i>C. amplexifolium</i> , <i>C. buergeri</i> , <i>C. chikushiense</i> , <i>C. gyojanum</i> , <i>C. hosogawa</i> , <i>C. kawakamii</i> , <i>C. lucens</i> , <i>C. matusmurae</i> , <i>C. matusmurae var. pubescens</i> , <i>C. nipponicum var. yoshinoi</i> , <i>C. suffultum</i> , <i>C. wallichii</i> , <i>C. yakusimense</i>	insect attractant as UV-pigment	3, 17-19, 23, 41, 47-49
luteolin-7-glucuronide	<i>C. sieboldii</i>	?	23, 49
luteolin-5-O-glucoside	<i>C. magofukai</i> , <i>C. sieboldii</i>	?	19
luteolin-7-O- β -glucopyranoside	<i>C. helenioides</i> , <i>C. oleraceum</i> , <i>C. palustre</i>	?	22, 46, 50, 51
narnigenin	<i>C. vallis-demonii</i> antibacterial 11, 16	?	31
nepetin, nepetin-4'-glucoside	<i>C. oligophyllum</i>	?	26
pectolinaringen	<i>C. arvense</i>	?	8
pectolinaringenin-7-O-D- β -glucopyranoside	<i>C. rhinoceros</i>	?	
pectolinaringenin-7-O- α -L-rhamnopyranosyl	<i>C. nipponicum</i>	?	50

Table 1. (continued)

Compound	Species	Biological activity	References
pectolinarin (pectolinarigenin-7- rutinoside)	<i>C. arisanense</i> , <i>C. babanum</i> , <i>C. bitchuense</i> , <i>C. brevicaulis</i> , <i>C. brevistylum</i> , <i>C. dipsacolepis</i> , <i>C. ferum</i> , <i>C. gratiosum</i> , <i>C. indudatum</i> , <i>C. japonicum</i> , <i>C. japonicum</i> var. <i>takaense</i> , <i>C. kagamontanum</i> , <i>C. kamtschaticum</i> , <i>C. microspicatum</i> var. <i>kiotoense</i> , <i>C. microspicatum</i> var. <i>microspicatum</i> , <i>C. nipponicum</i> var. <i>incomptum</i> , <i>C. oleraceum</i> , <i>C. otajae</i> , <i>C. pectinellum</i> , <i>C. purpuratum</i> , <i>C. rhinoceros</i> , <i>C. senjense</i> , <i>C. spicatum</i> , <i>C. spinosum</i> , <i>C. subcorticium</i> , <i>C. tioganium</i> var. <i>coloradoense</i> , <i>C. yezonense</i> , <i>C. yoshiizawae</i> , <i>Cirsium</i> spp. (19) ¹¹ <i>C. oleraceum</i> , <i>C. vallis-demonii</i>	analgesic, anti-inflammatory	2-4, 8, 10, 19, 22, 23, 28-30, 35, 36, 40, 42, 48, 52, 53
quercetin ^a	<i>C. babanum</i>	antioxidant, larval growth inhibitor, oviposition stimulator, antibacterial ?	35, 45, 54, 55 19
quercetin-3-O- arabinylo-galactose	<i>C. arvensis</i>	?	26
quercetin-3-O-digalactoside	<i>C. foliosum</i> , <i>C. scariosum</i> , <i>C. tioganium</i> , var. <i>coloradense</i> , <i>C. pulcherrimum</i> , <i>C. subnitivum</i> , <i>C. toedjji</i> , <i>C. undulatum</i> <i>C. arvensis</i>	?	2
quercetin-3-O-β-D- galactopyranoside	<i>C. babanum</i> , <i>C. vulgare</i>	antibacterial antibacterial	18, 19, 21 18, 21
quercetin-3-O-galactoside	<i>C. vulgare</i>	?	6, 34
quercetin-3-O-β-D- glucopyranoside	<i>C. arvensis</i>	?	11
quercetin-7-O-methyl ether, quercetin-3-O- rhamnoglucoside	<i>C. vallis-demonii</i> <i>C. arvensis</i>	?	26
3-O-methylquercetin	<i>C. oleraceum</i>	?	35
rutin ^a (<i>quercetin</i> -3-O- <i>rutinoside</i>)	<i>C. arvensis</i> var. <i>setosum</i> , <i>C. echinus</i>	larval growth inhibitor, antibacterial	2, 3, 16, 23, 43, 45
rhoifolin	<i>C. bitchuense</i>	?	23, 49
skutellarein ^a	<i>C. oleraceum</i>	larval growth inhibitor	9, 45
syringin	<i>C. arvensis</i>	?	7

Table 1. (continued)

Compound	Species	Biological activity	References
5,7,4'-trihydroxy-6-methoxyflavone-7-O- α -L-rhamnopyranosyl-(1 \rightarrow 2)- β -D-glucopyranoside	<i>C. japonicum</i>	?	39
vicenin-2 ^a	<i>C. gratiotum</i> , <i>C. oligophyllum</i>	oviposition stimulant	19, 31, 56, 57
tricin-5-O-glucoside	<i>C. arvensis</i>	?	26

Key for Table 1 References — 1. Harborne, Baxter, Moss, 1999; 2. Gardner, 1974; 3. Morita et al., 1964; 4. Nakaoki and Morita, 1959; 5. Simmonds and Grayer, 1999; 6. Syrchina et al., 1998; 7. Syrchina et al., 2000; 8. Lee et al., 1994; 9. Tarle et al., 1984; 10. Glyzinm et al., 1977; 11. Statti et al., 1997; 12. Kaneta et al., 1978; 13. Khafagy et al., 1981; 14. Shelyuto et al., 1970; 15. Shelyuto et al., 1975; 16. Hedin and Waage, 1986; 17. Harborne, 1967; 18. Harborne, 1977; 19. Iwashima et al., 1995; 20. Bohlmann and Abraham, 1981; 21. McGowan and Wallace, 1972; 22. Shelyuto et al., 1971; 23. Morita et al., 1973; 24. Ramasubramanian et al., 1988; 25. Yun and Chang, 1978; 26. Wallace, 1974; 27. Park et al., 1995a; 28. Park et al., 1995b; 29. Wallace and Bohm, 1971; 30. Lin et al., 1978; 31. Iwashima et al., 1999; 32. Ulubelen and Oksuz, 1982; 33. Lim et al., 1997; 34. Syrchina et al., 1999; 35. Shelyuto et al., 1978; 36. Gardner, 1973; 37. Rendyuk et al., 1977a; 38. Rendyuk et al., 1977b; 39. Miyaichi et al., 1995; 40. Martinez-Vazquez et al., 1998; 41. Wu et al., 1981; 42. Morita and Lin, 1976; 43. Rasulov et al., 1989; 44. Kim et al., 2000; 45. Elliger et al., 1980; 46. Ogurtsova and Syuzeva, 1974; 47. Lin, 1975; 48. Nakaoki and Morita, 1960; 49. Morita et al., 1965; 50. Shelyuto et al., 1972a; 51. Shelyuto et al., 1972b; 52. Do et al., 1994; 53. Lin et al., 1975; 54. Williamson et al., 1999; 55. Haribal and Renwick, 1995; 56. Ohsugi et al., 1985; 57. Nishida et al., 1987.

^aShown biological activity in insects.

Table 2. Flavonoids reported in *Carduus* spp. by compound^a

Compound	Species	Biological activity	References
apigenin ^a	<i>C. assoi</i> , <i>C. nutans</i> , <i>C. pycnocephalus</i> , <i>C. tenuiflorus</i>	anti-inflammatory, anti-spasmodic, antibacterial, insect attractant UV-pigment	1-10
apigenin-7-O-glucoside	<i>C. pycnocephalus</i> , <i>C. nutans</i>	?	7,10
apigenin-7-O-neohesperidoside	<i>C. nutans</i>	?	9
chrysoeriol-7-O-b-D-(6-O-acetyl glucopyranosyl)(1→3)-β-D-glucopyranoside	<i>C. pycnocephalus</i>	antimicrobial	11
diosmetin	<i>C. pycnocephalus</i>	antimicrobial	11, 12
hispidulin (<i>scutellarein 6-methyl ether</i>)	<i>C. assoi</i>	cytotoxic	13
hispidulin-7-O-β-D-glucopyranoside	<i>C. assoi</i>	?	5
isorhamnetin	<i>C. nutans</i>	?	8
kaempferol	<i>C. assoi</i> , <i>C. getulus</i> , <i>C. nutans</i> , <i>C. tenuiflorus</i> , <i>C. pycnocephalus</i>	?	5, 7, 9
kaempferol-3,4'-dimethyl ether-7-O-glucoside	<i>C. pycnocephalus</i>	?	7
kaempferol-3-O-glucoside-7-O-rhamnoside	<i>C. nutans</i>	?	9
kaempferol-3-O-β-D-glucopyranoside	<i>C. assoi</i>	?	5
kaempferol-3-O-α-L-rhamnofuranoside	<i>C. nutans</i>	?	8
kaempferol-3-O-α-L-rhamnoside	<i>C. pycnocephalus</i>	?	12
kaempferol-7-O-rhamnoside	<i>C. nutans</i>	?	9
kaempferol-3-O-α-L-rhamnopyranose	<i>C. assoi</i> , <i>C. tenuiflorus</i>	?	5,6
kaempferol-3-methyl ether-7-O-glucoside	<i>C. getulus</i>	?	14
luteolin ^a	<i>C. acanthoides</i> , <i>C. assoi</i> , <i>C. getulus</i> , <i>C. nutans</i>	enzyme inhibitor(α-glucosidase and α-amylase) larval growth inhibitor, antibacterial, insect attractant as UV-pigment	2-5, 10, 15
luteolin-7-O-galactoside	<i>C. acanthoides</i> , <i>C. nutans</i>		10
luteolin-7-O-digalactoside	<i>C. acanthoides</i>		10
luteolin-7-O-glucoside ^a	<i>C. acanthoides</i> , <i>C. nutans</i>		10
luteolin-7-O-diglucoside	<i>C. nutans</i>		10
luteolin-7-O-rutinoside	<i>C. nutans</i>		10
luteolin-3-O-α-L-rhamnopyranoside	<i>C. assoi</i>		5
luteolin-4-methyl ether-7-O-glucoside	<i>C. getulus</i>		14
narnigenin	<i>C. tenuiflorus</i>	antibacterial	2, 6

(continued on next page)

Table 2. (continued)

Compound	Species	Biological activity	References
quercetina	<i>C. getulus</i>	antioxidant, larval growth inhibitor, oviposition stimulator, antibacterial	2, 15, 16, 17
quercetin 3,3-dimethyl ether	<i>C. getulus</i>	cytotoxic	14
rutin ^a (<i>quercetin-3-O-rutinoside</i>)	<i>C. nutans</i>	larval growth inhibitor, antibacterial	2, 8
tilianin	<i>C. nutans</i>		8
tricin	<i>C. assoi</i>		5

Key for Table 2 References – 1, Simmonds and Grayer, 1999; 2, Hedin and Waage, 1986; 3, Harborne, 1967; 4, Harborne, 1977; 5, Fernandez et al., 1991; 6, Cardona et al., 1992b; 7, Amer et al., 1985; 8, Kaloshina and Mazulin, 1988; 9, Abdallah et al., 1989; 10, Bain and Desrochers, 1988; 11, El-Lakany et al., 1997; 12, El-Lakany et al., 1995; 13, Ulubelen and Oksuz, 1982; 14, Abdel-Salam et al., 1982; 15, Elliger et al., 1980; 16, Williamson et al., 1999; 17, Haribal and Renwick, 1996.

^a Shown biological activity in insects.

Renwick, 1996). Vicenin-2, rutin, narirutin and hesperidin (together, but not individually) were strong oviposition stimulants for *Papilio xuthus* (Ohsugi et al., 1985; Nishida et al., 1990). Both vicenin-2 and rutin have been found in some *Cirsium* and *Carduus* species (below).

2.1.3. Occurrence and activity in *Cirsium* and *Carduus*

We found 78 flavonoids reported from *Cirsium* spp. and 31 from *Carduus* spp. (Tables 1 & 2). Three of the six flavonoid groups were reported: flavonols, flavones, and one isoflavone. The compounds most often reported for both *Carduus* and *Cirsium* (Tables 1 & 2) were: apigenin, cirsimaritin, kaempferol, linarin, luteolin, pectolarin, and quercetin (with various glycosides attached). Ten flavonoid groups were shared between *Cirsium* and *Carduus*. *Cirsium* spp. had 11 groups of flavonoids reported that were not found in *Carduus* spp., while two flavonoids were reported only from *Carduus* spp.

Linarin and pectolarin, known to have anti-inflammatory properties (Table 1), are common in *Cirsium* spp. but have not been studied for their biological activity towards insects. Other less common compounds with known biological activity included: diosmetin, vicenin-2, skutellarein, and rutin (Tables 1 & 2). Antimicrobial activity was identified in diosmetin (Haribal and Renwick, 1996). Vicenin-2 was isolated from *Cirsium oligophyllum* (Iwashina et al., 1995, 1999). Rutin was found in *Cirsium echinus*, *C. arvense* var. *setosum*, and *C. undulatum*, (Morita et al., 1964, 1973; Gardner, 1973; Elliger et al., 1980; Rasulov et al., 1989) and *Carduus nutans* (Hedin and Waage, 1986; Kaloshina and Mazulin, 1988). The literature suggests both a high frequency of occurrence in flavonoids, and both overlap and variation in these compounds among *Cirsium* and *Carduus* species.

Table 3. Other reported secondary metabolites in *Cirsium* spp. by compound^a

Compound	Species	Biological activity	References
Sterols and triterpenes			
acetyl-lupeol, acetyl- α -amyirin, acetyl- α -amyirin, acetyl- β -amyirin	<i>C. vallis-demonii</i>	?	1
Δ -5-avenasterol, brassicasterol	<i>C. vulgare</i>	?	2
β -amyirin	<i>C. oleraceum</i> , <i>C. hypoleucum</i>	?	3,4
β -amyirin acetate	<i>C. carolinianum</i> , <i>C. hypoleucum</i>	?	4
campesterol	<i>C. vallis demonii</i> , <i>C. vulgare</i>	?	2,5
lupeol	<i>C. canum</i> , <i>C. hypoleucum</i> , <i>C. oleraceum</i> , <i>C. vallis demonii</i>	?	3-5
lupeol acetate	<i>C. canum</i> , <i>C. carolinianum</i> , <i>C. hypoleucum</i>	?	4
β -sitosterola	<i>C. eclinus</i> , <i>C. syriacum</i> , <i>C. oleraceum</i> , <i>C. vallis demonii</i> , <i>C. vulgare</i>	Disrupts ecdysteroid biosynthesis molting hormone in <i>Plodia interpunctella</i> (Lepidoptera). Stimulated feeding of pea weevil; phagostimulant for black vine weevil, obscure root weevil, and alfalfa weevil	2, 3, 5-8
β -sitosterol glucoside	<i>C. syriacum</i> , <i>C. vallis-demonii</i>		1, 6
stigmasterol	<i>C. oleraceum</i> , <i>C. vallis demonii</i> , <i>C. vulgare</i>		2, 3, 5
squalene	<i>C. hypoleucum</i>	antifungal	4
taraxasterol ^a	<i>C. ardense</i> , <i>C. oleraceum</i> , <i>C. setosum</i> , <i>C. texanum</i> , <i>C. vallis demonii</i>	molting inhibitor	3, 5, 10-13
ψ -taraxasterol	<i>C. canum</i> , <i>C. oleraceum</i>		3, 4
ψ -taraxasterol acetate	<i>C. ardense</i> , <i>C. canum</i> , <i>C. carolinianum</i> , <i>C. hypoleucum</i>		4, 14
Polyacetylenes and hydrocarbons			
acetylenic alcohol, aplotaxene, triolacetylene (ciryneol)	<i>Cirsium</i> spp., <i>C. japonicum</i>	teliospore germination stimulation	15-19
aplotaxene epoxide	<i>C. hypoleucum</i>	?	20

(continued on next page)

Table 3. (continued)

Compound	Species	Biological activity	References
Tridecylpolyacetylenes, aplotaxene, 1-pentadecene, 1-heptadecene 1,8,11-heptadecatriene	<i>C. arvense</i>	teliospore germination stimulation (<i>Puccinia punctiformis</i>)	4, 21
aplotaxene, dihydroaplotaxene, tetrahydroaplotaxene, <i>n</i> -dodecane, 2-methyl dodecane, <i>n</i> -tridecane, 2-methyltetradecane, <i>n</i> -pentadecane, 3-methylpentadecane, <i>n</i> -hexadecane, 2-methylhexadecane, <i>n</i> -heptadecane, <i>n</i> -octadecane, <i>n</i> -nonadecane, <i>n</i> -eicosane, 1-dodecene, 1-tetradecene, 1-pentadecene, 1-hexadecene, 1-heptadecene, 1-octadecene	<i>C. dipsacolepis</i>	?	22
Aliphatic aldehydes			
7-octenal, (2E)-2,8-nonadienal, (2E)-2,9-decadienal, (2E)-2,10-undecadienal, ((2E,4E)-2,4,10-undecatrienal, (2E,4E)-, (2Z,4Z)-, and (2E,4Z)-2,4,11-dodecatrienal vinylpentaacetylene	<i>C. dipsacolepis</i>	?	22
4,6-tetradecadiene-8,10,12-triyn-1-ol	<i>C. acule</i> , <i>C. arvense</i> , <i>C. candolleianum</i> , <i>C. canum</i> , <i>C. carnolicum</i> , <i>C. decussatum</i> , <i>C. eriophorum</i> , <i>C. erisithales</i> , <i>C. ferox</i> , <i>C. helenioides</i> , <i>C. horridulum</i> , <i>C. hypoleucum</i> , <i>C. montanum</i> , <i>C. occidentale</i> , <i>C. oleyaceum</i> , <i>C. palustre</i> , <i>C. panmonicum</i> , <i>C. syriacum</i> , <i>C. tuberosum</i> , <i>C. vulgare</i>	?	4, 23
1,11-tridecadiene-3,5,7,9-tetraene	<i>C. helenioides</i> , <i>C. montanum</i> , <i>C. oleyaceum</i> , <i>C. palustre</i> , <i>C. vulgare</i>	?	23
	<i>C. acule</i> , <i>C. candolleianum</i> , <i>C. canum</i> , <i>C. decussatum</i> , <i>C. erisithales</i> , <i>C. horridulum</i> , <i>C. hypoleucum</i> , <i>C. montanum</i> , <i>C. occidentale</i> , <i>C. oleyaceum</i> , <i>C. palustre</i> , <i>C. panmonicum</i> , <i>C. syriacum</i> , <i>C. tuberosum</i> , <i>C. vulgare</i>	?	4, 23
1,8,11,14-heptadecatetraene	<i>C. canum</i> , <i>C. hypoleucum</i>	?	4

Table 3. (continued)

Compound	Species	Biological activity	References
Alkaloids			
O-acetyljacoline (I) ^a (a pyrrolizidine)	<i>C. wallichii</i>	possible attractant for male ithomine and danaïne butterflies	24, 25
circumamide	<i>C. brevicaulis</i>	antimicrobial	26
heliotridane ^a (a pyrrolizidine)	<i>C. steigerum</i>	possible attractant for male ithomine and danaïne butterflies	25, 27
Phenolic acids^a			
p-coumaric acid, caffeic acid, ferulic acid, p-hydroxybenzoic acid, protocatechuic acid, vanillic acid	<i>C. vulgare</i>	insect antifeedants 28–34	
Guanolides (sesquiterpene lactones)			
dehydrocostus lactone, azuleno[4,5-b]furan-2(3H)-one, decalhydro-6,9-bis(methylene)	<i>C. carolinianum</i>	?	4
Other compounds			
fumaric acid	<i>C. arisanense</i>	?	35
cyperenyl acetate and cyperenal (sesquiterpenes)	<i>C. dipsacolepis</i>	?	36
vernopolanthofuran	<i>C. hypoleucum</i>	?	4
2,4-tetradecadieneamide, N-(2-methyl propyl)	<i>C. canum</i>	?	4

Key to Table 3 References — 1, Statti et al., 1997; 2, Nolasco et al., 1987; 3, Krzysztofik and Ludwiczak, 1970; 4, Bohlmann and Abraham, 1981; 5, Aquino et al., 1987; 6, Khaifay et al., 1981; 7, Rasulov et al., 1989; 8, Svoboda and Lusby, 1994; 9, Shanks and Doss, 1987; 10, Dutta et al., 1972; 11, Dominguez et al., 1974; 12, Synchrona et al., 1998; 13, Abdel-Salam et al., 1982; 14, Tulloch and Hoffman, 1982; 15, Yano, 1977; 16, Yano, 1980; 17, Takaishi et al., 1991a; 18, Baek et al., 1995; 19, French et al., 1988; 20, French et al., 1994; 21, Binder and French, 1994; 22, Takano and Kawaminami, 1988; 23, Bohlmann et al., 1973; 24, Negi et al., 1989; 25, Pliske et al., 1976; 26, Sawaguchi et al., 1994; 27, Ismailov, 1958; 28, McGowan and Wallace, 1972; 29, Woodhead and Cooper-Driver, 1979; 30, Woodhead et al., 1980; 31, Gross, 1981; 32, Lege et al., 1995; 33, Fischer et al., 1990; 34, Classen et al., 1990; 35, Lin et al., 1975; 36, Takano and Kawaminami, 1988.

^aShown biological activity in insects.

Table 4. Other reported secondary metabolites in *Carduus* spp. by compound^a

Compound	Species	Biological activity	References
Sterols and triterpenes			
erythrodil 3-acetate ^a	<i>C. getulus</i>	molting inhibitor	1-2
lupeol	<i>C. pycnocephalus</i>	?	3
β-sitosterol ^a	<i>C. acanthoides</i> , <i>C. getulus</i> , <i>C. pycnocephalus</i> , <i>C. nutans</i>	Disrupts ecdysteroid biosynthesis molting hormone in <i>Plodia interpunctella</i> Stimulated feeding of pea weevil; phagostimulant for black vine weevil, obscure root weevil, and alfalfa weevil	1-7
β-sitosterol glucoside	<i>C. pycnocephalus</i>	?	3
sitosterol-3-O-xyloside	<i>C. nutans</i>	?	7
taraxasterol acetate, ^a taraxasterol ^a	<i>C. getulus</i> , <i>C. nutans</i>	molting inhibitor	1, 2, 7
Δ-5-avenasterol, brassicasterol, campesterol, stigmasterol	<i>C. acanthoides</i>	?	4
Polyacetylenes and hydrocarbons			
vinylpentaacetylene	<i>C. argyroa</i> , <i>C. collinus</i> , <i>C. glaucus</i> , <i>C. leucophyllus</i> , <i>C. nigrescens</i> , <i>C. nutans</i> , <i>C. personata</i> , <i>C. pycnocephalus</i>	?	8
4,6-tetradecadiene-8,10,12-triyn-1-ol	<i>C. leucophyllus</i>	?	8
1,11-tridecadiene-3,5,7,9-tetrayne	<i>C. nigrescens</i> , <i>C. personata</i>	?	8
2,6,8,14-tetradecatetraene-4-yne-10,11,12,13-methylene	<i>C. argyroa</i> , <i>C. collinus</i>	?	8
Alkaloids			
acanthoidine, acanthoine, ruscopine	<i>C. acanthoides</i>	(acanthoidine only)	hypotensive (dog and human) 9-11
Coumarins			
6-prenyloxy-7-methoxycoumarin, isoescopoletin, isofraxidin	<i>C. tenuiflorus</i>	?	12
Lignans			
1-hydroxypinoresinol, pinoresinol, ^a syringaresinol	<i>C. assoi</i> , <i>C. tenuiflorus</i>	(pinoresinol only) Toxicity to 4th instar milkweed bug larvae and blood sucking bug. Pinoresinol has antimolting activity	13, 14
2-hydroxyolivil, laricinresinol, prinsepiol	<i>C. assoi</i>	?	15

Key to Table 4 References — **1**, Abdel-Salam et al., 1982; **2**, Abdel-Salam et al., 1983; **3**, El-Lakany et al., 1995; **4**, Nolasco et al., 1987; **5**, Svoboda and Lusby, 1994; **6**, Shanks and Doss, 1987; **7**, Abdallah et al., 1989; **8**, Harborne et al., 1999; **9**, Frydman and Deulofeu, 1962; **10**, Boidadzhiev, 1964; **11**, Cabral et al., 1999; **12**, Cabral et al., 2000; **13**, Fernandez et al., 1991; **14**, Bohlmann et al., 1973; **15**, Cardona et al., 1992b.

^aShown biological activity in insects.

2.2. Sterols and triterpenes

2.2.1. Chemistry

The second most common secondary metabolites in *Cirsium* and *Carduus* species were sterols and triterpenes (Tables 3 & 4). Little is known, however, about their activity with respect to insect specialists on these genera. Sterols and triterpenoids are classes of terpenoids (isoprenoids). Terpenoids are derived from isopentenyl and dimethylallyl pyrophosphates (Bramley, 1997), and the sterols are derived from triterpenoids (C₃₀), the largest class (Harborne, 1999). Triterpenoids are generally classified as membrane constituents, occurring mostly in leaf glandular trichomes, bud exudates, and bark resins (Harborne, 1999). Glandular trichomes or resin ducts often are found on the involucre bracts of *Cirsium* spp. (Great Plains Flora Association, 1986; Bremer, 1994; personal observation).

2.2.2. Biological activity

Most research on the effects of plant sterols and triterpenes on insects are related to their effect on hormonal activity, often with the aim of employing them as insecticides (Prestwich, 1986). Sterols have an antagonistic effect on the ability of larvae to molt (Alder, 1995; Luu and Werner, 1996; Dugassa-Gobena et al., 1998), since insect metabolism is vulnerable to dietary sterols (Feldlaufer and Svoboda, 1988; Darvas, 1991; Svoboda, 1992). On the other hand, some insects incorporate ingested sterols into their metabolism, relying upon them for their molting hormones (Svoboda et al., 1991, 1994). For example, a lepidopteran (*Plo-dia interpunctella*) used synthetic β -sitosterol, a compound found in *Cirsium* and *Carduus* spp., as a dietary source to produce cholesterol (Svoboda and Lusby, 1994), essential to the production of ecdysteroid molting hormones (Svoboda et al., 1991). Additionally, β -sitosterol stimulated feeding by several weevils, such as the pea leaf weevil (*Sitona lineatus*), black vine weevil (*Oiorhynchus sulcatus*), obscure root weevil (*Sciopithes obscurus*), and alfalfa weevil (*Hypera postica*) (Shanks and Doss, 1987).

2.2.3. Occurrence and activity in *Cirsium* and *Carduus*

The sterol, β -sitosterol, which can affect insect molting (above), was reported from five of the 92 *Cirsium* spp. studied (*C. echinus*, *C. oleraceum*, *C. syriacum*, *C. vallis demonii*, *C. vulgare*), as well as four of the 12 *Carduus* spp. (*C. acanthoides*, *C. getulus*, *C. pycnocephalus*, *C. nutans*) (Tables 3 & 4). The triterpenes, taraxasterol acetate, taraxasterol and erythrodiol-3-acetate, extracted from *Carduus getulus* inhibited molting of the cotton leafworm (*Spodoptera littoralis*) (Abdel-Salam et al., 1982). Taraxasterol acetate and taraxasterol also were found in eight *Cirsium* spp. (*C. arvense*, *C. canum*, *C. carolinianum*, *C. hypoleucum*, *C. oleraceum*, *C. setosum*, *C. texanum*, *C. vallis demonii*) (Table 3), as well as two *Carduus* spp. (*Carduus getulus*, *C. nutans*) (Table 4). Tulloch and Hoffman (1982) found ψ -taraxasterol acetate (and other uncommon compounds) in the epicuticular wax of *Cirsium arvense*. Although other sterols and triterpenes are reported from *Cirsium* and *Carduus* spp. (Tables 3 & 4), their biological activity has not been evaluated.

2.3. Polyacetylenes, acetylenes and other hydrocarbons

2.3.1. Chemistry

These groups of compounds are grouped, based on the similarity of their structure, long hydrocarbon chains. Polyacetylenes and acetylenes are characteristic of the Asteraceae (Bohlmann et al., 1973; Baek et al., 1995; Harborne et al., 1999). Polyacetylenes are fatty acid derivatives that are generally stored in secretory plant cells, called laticifers (Mauseth, 1988; Ellis, 1997), that secrete latex. Viscous exudates, such as latex, usually contain secondary metabolites (Mauseth, 1988). Most true thistles have clear latex that exudes upon damage from most organs of the plant. Aphid clusters have been observed on some *Cirsium* spp. around exuded droplets likely to be latex (Bremer, 1994; personal observation). The chemical profile of these exudates of thistles does not appear to have been characterized. However, polyacetylenes are reported to be common and characteristic in thistle roots (below).

2.3.2. Biological activity

Polyacetylenes from the Asteraceae have been reported to have major antifeedant properties, including against root-feeding insects of thistles (e.g. Yano, 1977; Bohlmann and Abraham, 1981; Aquino et al., 1987; Negi et al., 1989; Takaishi et al., 1990, 1991a, 1991b; Binder et al., 1992; Binder and French, 1994; Shen and Mu, 1990; Stevens et al., 1990; Christensen, 1992; Sawaguchi et al., 1994). Polyacetylenes from leaves of rabbitbrush, *Chrysothamnus nauseosus*, had antifeedant properties against the Colorado potato beetle, *Leptinotarsa decemlineata* (Rose et al., 1980). All four polyacetylenes found inhibited feeding by third instar larvae of *L. decemlineata*. Phenylheptatriyne (PHT) from Asteraceae also had antifeedant effects on the moth, *Euxoa mossoria* (McLachlan et al., 1982). In addition, both synthetic polyacetylenes and those extracted from various Asteraceae species had insecticidal properties on mosquito larvae (Arnason et al., 1981; Wat et al., 1981; Towers et al., 1984; Wang et al., 1990; Guillet et al., 1997; Wan et al., 2000). Alternately, however, some polyacetylenes were reported to stimulate feeding by insect specialists on Asteraceae, such as the leaf beetle *Chrysolina aurichalcea* (Matsuda et al., 1982).

2.3.3. Occurrence and activity in *Cirsium* and *Carduus*

Almost all of the polyacetylenes and hydrocarbons reported from *Cirsium* and *Carduus* (Tables 3 & 4) were from roots rather than above-ground organs (Table 3). The one exception was a heptadecatetraene, which was isolated from the aerial parts of *Cirsium hypoleucum* and *C. canum* (Bohlmann and Abraham, 1981). In the extensive study of the roots of *Cirsium dipsacolepis*, eight aliphatic aldehydes and 24 hydrocarbons were isolated, but their biological activity is unknown (Takano and Kawaminami, 1988; Table 3). Takano and Kawaminami (1988) found that almost 80% of the volatile oils extracted from the roots of *Cirsium dipsacolepis* were made up of aplotaxene and four derivatives of aplotaxene. In an extensive review of naturally occurring acetylenes, Bohlmann et al., (1973) found four main compounds in many *Cirsium* and *Carduus* spp. (Tables 3 & 4). None of these four have

been investigated for their biological activity. Most of the literature on the biological activity of polyacetylenes in thistles concerns their effect on Canada thistle rust (*Puccinia punctiformis*), a root-borne thistle fungus. Polyacetylenes and hydrocarbons from *Cirsium* spp. roots influenced fungal colonization. These compounds included: acetylenic alcohol, aplotaxene, triolacetylene, aplotaxene epoxide, tridecylpolyacetylene, 1-pentadecene, 1-heptadecene, and 1,8,11-heptadecatriene (Table 3). Polyacetylenes from Canada thistle (*Cirsium arvense*) stimulated germination of *P. punctiformis* teliospores (Whitehead et al., 1982; French, 1990; Shen and Mu, 1990; Christensen, 1992; Eskelesen and Crabtree, 1995). Furthermore, some evidence suggests polyacetylenes can influence interactions among plant hosts. For example, Eskelesen and Crabtree (1995) found that polyacetylenes in *Cirsium arvense* acted as allelopathic compounds against neighboring plants. Research is needed to determine if polyacetylenes occur in foliage or flower heads of *Cirsium* or *Carduus* spp., where an effect on host choice by non-rootfeeding thistle insects might occur.

2.4. Alkaloids

2.4.1. Chemistry

Alkaloids (>12 000 structures) have been detected in about 15% of all plants, bacteria, fungi, and animals (Wink, 1997). Alkaloids are a heterogeneous group of nitrogen-containing compounds, specifically those that are not otherwise recognizable as peptides, nonprotein-amino acids, amines, cyanogenic glycosides, glucosinolates, cofactors, phytohormones or primary metabolites, such as purines or pyrimidines (Wink, 1997). Alkaloids are derived from amino acids joined with moieties derived from other pathways, such as terpenoids. Most alkaloids are synthesized in the cytoplasm and stored in plant cell vacuoles, although some are sequestered into latex (Wink, 1997). Alkaloids sometimes are more concentrated in epidermal tissues than in the mesophyll (Wink, 1986), and they usually are associated with organs essential for plant survival: flowers, seeds, and roots (Wink, 1997).

2.4.2. Biological activity

Alkaloids function as chemical defenses against herbivores and microbes and as allelopathic compounds against plant competitors (Harborne, 1993). Typically alkaloids are deterrents to feeding by generalist insects, but attractants for more specialized insects. For example, quinolizidine alkaloids in *Genista mospessulana* are thought to maintain exclusive host use by *Uresiphita reversalis* (Lepidoptera: Pyralidae) (Montlor et al., 1990). Also, pyrrolizidine alkaloids of *Heliotropium indicum* are powerful attractants for male *Ithomiine* and *Danaine* butterflies to their host plant (Pliske et al., 1976).

2.4.3. Occurrence and activity in *Cirsium* and *Carduus*

Six alkaloids are reported from *Cirsium* (Table 3) or *Carduus* spp. (Table 4). Two are pyrrolizidine alkaloids (Figure 1): O-acetyljacoline (I) from *Cirsium wallichii* (Negi et al., 1989) and heliotridane from *Cirsium steigerum* (Ismailov, 1958). Both

of these were among the attractant compounds for male Ithomiine and Danaine butterflies (Pliske et al., 1976). One other alkaloid (1-*N*-(*p*-coumaroyl) pipercolic acid), reported in *Cirsium brevicaule*, showed antibacterial activity against the bacteria: *Staphylococcus typhimurium*, *Pseudomonas aeruginosa*, and *P. vulgaris* (Sawaguchi et al., 1994). Other alkaloids reported from *Carduus acanthoides* (acanthoine, acanthoidine, ruscopine) were found primarily in the roots; these compounds showed hypotensive effects on dogs and humans (Frydman and Deulofeu, 1962; Harborne et al., 1999). We found no direct tests of the effect of any of the alkaloids found in thistles on insect host choice.

2.5. Sesquiterpene lactones

2.5.1. Chemistry

Over 3000 structures are known for this subset of terpenoids (Harborne, 1999). Sesquiterpenoids make up hundreds of groups with similar backbones, and the sesquiterpene lactones contain four major groups of these backbones. These compounds have been studied as chemosystematic markers, but not for true thistles. These groups of terpenoids, derived from the isopentyl and dimethylallyl diphosphates, are characterized by a 15-carbon skeleton containing a lactone ring (Gershenzon and Croteau, 1991; Bramley, 1997). Sesquiterpene lactones are often associated with specialized secretory structures, such as glands or glandular trichomes (Loomis and Croteau, 1973; Kelsey and Shafizadeh, 1980; Rossiter et al., 1986; Bramley, 1997), similar to those observed on some thistle flower heads.

2.5.2. Biological activity

Reported biological activity of the sesquiterpene lactones from the Asteraceae is significant (Rodriguez et al., 1976; Picman, 1986; Rosenthal and Berenbaum, 1991). These compounds influence many organisms, including insects (e.g. Mabry and Gill, 1977; Kelsey and Shafizadeh, 1980; Harmatha and Nawrot, 1984; Rees and Harborne, 1985; Picman, 1986; Rossiter et al., 1986; Arnason et al., 1987; Harborne, 1990; Callaway et al., 1999). Insect responses are widely variable and complicated. Cnicin (a guaianolide) is a bitter antifeedant for generalist insects (Landau et al., 1994; Harborne et al., 1999), but an oviposition and development stimulant for specialist insects on *Centaurea* spp. (Landau et al., 1994). Glaucolide A deterred feeding by larvae of six lepidopterans: southern armyworm, fall armyworm, yellow woolly bear, cabbage looper, and yellow striped armyworm (Burnett and Jones, 1974). Nawrot et al. (1983) found a deterrent effect of eight sesquiterpene lactones from *Laserpitium siler*, *L. archangelica*, and *Laser trilobum* against three generalist beetles: *Sitophilus granaries*, *Tribolium confusum*, and *Trogoderma granarium*. Sesquiterpene lactones and lignan lactones from three other Asteraceae (*Eupatorium cannabinum*, *Homogyne alpine*, *Petasites albus*) reduced feeding by these insects (Harmatha and Nawrot, 1984). Sesquiterpene lactones (lactucin, lactupicrin and 8-deoxylactucin) in the milky latex of chicory, *Cichorium intybus*, displayed a marked deterrence of feeding by the polyphagous acridid grasshopper, *Schistocerca gregaria* (Rees and Harborne, 1985).

2.5.3. Occurrence and activity in *Cirsium* and *Carduus*

The sesquiterpene lactones from the thistle tribe (Cardueae) have not been analyzed intensively for true thistles (Subtribe Carduineae). However, they have been for the related knapweeds (Subtribe Centaurineae), likely because of their role in folk medicines and their potential insecticidal properties (Rodriguez et al., 1976; Picman et al., 1978; Rees and Harborne, 1985; Picman, 1986). The sesquiterpene lactones found in knapweeds belong to three subgroups: elemanolides, germacranolides, and guainolides. A small fraction of the common compounds reported in *Centaurea* spp. include: acroptilin, cnicin, and cynaropicrin (e.g. Ok-suz and Putun, 1983; Locken and Kelsey, 1987; Benayache et al., 1992; Youssef and Frahm, 1994; Harborne et al., 1999). Cnicin, extracted from *Centaurea maculosa* and *C. vallesiaca*, when sprayed on artificial diets stimulated oviposition by the specialist lepidopteran insects: *Stenoides straminea*, *Agapeta zoegana* (Cochylidae), *Pterolonche inspersa* (Pterolonchidae) (Locken and Kelsey, 1987). However, larvae of a generalist lepidopteran (*Spodoptera littoralis*) did not survive on the cnicin-treated diets. In Nebraska, thistles are hosts to species of moth larvae in the genus *Homoeosoma* spp. (e.g. *H. impressale* on *Cirsium canescens* and *C. undulatum*: Louda, 1998). Although these species have not been tested, the related *Homoeosoma electellum* (sunflower moth) from *Helianthus annuus* has been. The exudates from glandular trichomes in sunflower, *H. annuus*, contained more than five sesquiterpene lactones; these decreased feeding by *H. electellum* significantly, although the effect decreased as larva developed (Rossiter et al., 1986). In fact, *H. electellum* experienced higher mortality, retarded growth, and an extended development period in the presence of sesquiterpene lactones from the glandular trichomes (Rossiter et al., 1986).

Surprisingly, given the prevalence and activity of these compounds in other composites, including close relatives, we found only one report of sesquiterpene lactones in *Cirsium* spp.

Two guaianolides, dehydrocostus lactone and azuleno[4,5-b]furan-2-(3H)-one, decahydro-6,9-bis(methylene), were isolated from the roots of *Cirsium carolinianum* (Bohlmann and Abraham, 1981). The only other reports we found for a *Carduus* species (Andronesco et al., 1984; Kataria, 1995; Bicchi and Rubiolo, 1996) was for a plant species (*C. benedictus*) that has since been reclassified into the genus *Cnicus*, a genus more closely related to *Centaurea* than to *Carduus* (Dittrich, 1977; Bremer, 1994).

2.6. Phenolic acids

2.6.1. Chemistry

The term "phenolic acids" describes a variety of organic compounds bearing one or more phenolic hydroxyl group and a carboxyl function (Gross, 1981). The total number of phenolics, including flavonoids, is over 8000 (Harborne, 1999). Like flavonoids and other phenolic compounds, they originate in the shikimate pathway (Harborne, 1999). Most phenolics are found in conjunction with sugars in water-soluble forms in the vacuole. Some commonly occurring phenolic acids, like hydroxybenzoic acid, can be found in almost any part of a plant (Harborne, 1999).

2.6.2. Biological activity

Phenolic acids can affect insect behavior (Gross, 1981). For example, reduced feeding by various grasshoppers and by a planthopper, *Peregrinus maidis*, was correlated with high concentrations (dry weight) of total phenolic acids (Woodhead et al., 1980). Also, ferulic acid was shown to be involved in maize resistance to the weevil *Sitophilus zeamais* (Classen et al., 1990). More than half of the common phenolic acids that were tested reduced feeding of the Mexican bean beetle (Coccinellidae) when sprayed on to leaves of its preferred host, the common bean *Phaseolus vulgaris* (Fischer et al., 1990). Additionally, high levels of phenolic acid content in the older leaves (0.3–1.0%) of *Sorghum bicolor* significantly reduced feeding by *Locusta migratoria* (Woodhead and Cooper-Driver, 1979). Lege et al. (1995) suggested that resistance in cotton (*Gossypium hirsutum*) to spider mite (*Tetranychus urticae*) might be attributed to high levels of the condensed tannins and phenolic acids.

2.6.3. Occurrence and activity in *Cirsium* and *Carduus*

Phenolic acids found in cotton also have been found in *Cirsium* spp. (Table 3). *Cirsium vulgare*, for example, contains many of the compounds tested from cotton: *p*-coumaric, caffeic, ferulic, *p*-hydroxybenzoic, protocatechuic and vanillic acids (McGowan and Wallace, 1972). This group could influence host choice behavior; higher oviposition rates by *R. conicus*, for example, are correlated with feeding on leaf material prior to flower presentation (Louda, unpublished data). However, the importance of this group of compounds in host preference and acceptance by thistle insects is unknown.

2.7. Lignans

2.7.1. Chemistry

Lignans, a distinct class of phenolics, are phenylpropanoid dimers (Figure 1) that are derived from coniferyl alcohol (Strack, 1997; Walton and Brown, 1999). Lignans are common constituents of wood and bark, i.e. secondary growth cells (Harborne, 1999).

2.7.2. Biological activity

Lignans have the ability to bind to estrogen receptors in humans (Williamson et al., 1999), so they are considered phytoestrogens. Lignans and related compounds, reported active in preventing breast and prostate cancer and delaying menopause, are found in many plants common in human diets (Mazur and Adlercreutz, 1998; Gordaliza et al., 2000; Thompson, 2000). We found reports of antimicrobial, antifungal, and antifeedant effects of lignans (Strack, 1997). A lignan, [+]-epimagnolin A, extracted from the buds of *Magnolia fargesii* inhibited growth of *Drosophila melanogaster* larvae (Miyazawa et al., 1994). In another study, the lignan podophyllotoxin given orally or applied topically to a beetle, *Rhodnius prolixus*, inhibited molting (Cabral et al., 2000). The lignanamide demethylgrossamide, found in a methanolic extraction of *Xylopiya aethiopica* seeds, exhibited potent deterrence of feeding by the subterranean termite, *Reticulitermes speratus*, at 5000 ppm (Lajide et

al., 1995). Lignans (gomisin B, gomisin N) in the fruits of *Schisandra chinensis* were insecticidal for *Drosophila melanogaster* (Miyazawa et al., 1998).

2.7.3. Occurrence and activity of lignans in *Cirsium* and *Carduus*

No lignans were reported in *Cirsium* spp. (Table 3), but five were reported in *Carduus* spp. (Table 4). Pinoresinol, found in *Carduus assoi* and *C. tenuiflorus* (Fernandez et al., 1991; Cardona et al., 1992a; Cabral et al., 1999), is the only lignan known from thistles for which effects on insects have been reported. Pinoresinol, also common in spruce and pine trees (Strack, 1997), exhibits anti-molting activity (58% molting inhibition) to the 4th instar milkweed bug larvae, *Oncopeltus fasciatus*, and the blood-sucking bug, *Rhodnius prolixus* (Cabral et al., 1999, 2000). Effects reported were dose-dependent: an effect was seen with an oral dose of 100 µg/ml. Also, pinoresinol has similar structure to [+]epimagnolin A (Figure 1), which was reported to inhibit fly growth (above). The biological activity of the other lignans reported in *Carduus assoi* and *C. tenuiflorus* (Table 4) is unknown.

2.8. Other compounds

Two sesquiterpenes, cyperenyl acetate and cyperenal, were isolated from the roots of *Cirsium dipsacolepis* (Takano and Kawaminami, 1988). An unsaturated dibasic acid, fumaric acid, was isolated from leaves of *Cirsium arisanense* (Lin et al., 1975). These are unique compounds and their biological activity has not been studied.

3. Discussion

If, as hypothesized, host chemistry dominates the factors influencing field host preference (Becerra, 1997; Becerra and Venable, 1999), then studies of chemical ecology as part of the screening of biological control candidates could be an important new tool in risk assessment. Among the thistle species for which chemical data exist (Tables 1–4), we found both important similarities and striking differences in the known chemical profiles between *Carduus*, a predominantly Eurasian genus, and *Cirsium*, the Palearctic genus that contains North American thistles, and among *Cirsium* spp. (Tables 5–7). These findings are consistent with the hypothesis that comparative analyses of secondary metabolites, with specific information on biological activity, potentially could provide added predictive power for potential host choice and use by exotic insects in biological control of weeds. The evidence compiled here provides an initial framework for such screening in future thistle control projects, such as in contemporary efforts to find host-specific biological control agents for the Eurasian *Cirsium arvense* (Canada thistle) in North America.

3.1. Comprehensiveness of the data

We were surprised to find that only a small proportion of *Cirsium* spp. and *Carduus* spp. has been studied for their chemistry and biological activity. In the genus

Table 5. Flavonoid groups in *Cirsium* and *Carduus* spp^{a,b}

	<i>Cirsium</i>	No. of derivatives	No. of spp.	<i>Carduus</i>	No. of derivatives	No. of spp.
<i>Cirsium</i> only						
acacetin	+	3	5	-		
cirsiliol	+	3	1	-		
cirsimaritin	+	3	10	-		
genkwanin	+	1	1	-		
linarin	+	n/a	26	-		
nepetin	+	2	1	-		
pectolinarin	+	4	29	-		
rhoifolin	+	n/a	1	-		
skutellarin ^c	+	n/a	1	-		
syringin	+	n/a	1	-		
vicenin-2 ^c	+	n/a	2	-		
<i>Cirsium</i> and <i>Carduus</i>						
apigenin ^c	+	11	22	+	3	4
chrysoeriol	+	4	6	+	1	1
diosmetin	+	1	3	+	1	1
hispidulin	+	5	5	+	2	1
kaempferol	+	9	5	+	9	5
luteolin ^c	+	7	25	+	8	4
narnigenin	+	n/a	1	+	n/a	1
quercetin ^c	+	11	13	+	2	1
rutin ^c	+	n/a	2	+	n/a	1
tricin	+	1	1	+	1	1
<i>Carduus</i> only						
isorhamnetin	-			+	1	1
tilianin	-			+	1	1
total number of derivatives		65	n/a		29	n/a
total number of species studied		n/a	97 ^d		n/a	12

^a Totals include the number of times that compound appeared in any of the species discussed in this review.

^b See Tables 1 and 2 for references.

^c At least one derivative has insect bioactivity.

^d North American native species totaled 13 out of the 92 *Cirsium* studied.

Carduus, we found evidence in the literature for compounds from only 12 species (Tables 2 & 4) out of about 90+ species of *Carduus* worldwide (Bremer, 1994). No *Carduus* species are native to North America. The low proportion (13%) of worldwide *Carduus* species that have been analyzed for their chemical profile is surprising. Two species, *Carduus acanthoides* and *C. nutans*, are considered major weeds worldwide (Frick, 1978; Delfosse, 2000; USDA Plant Database, 2002). Four of the 12 *Carduus* spp. studied chemically have been inadvertently introduced and naturalized in North America: *Carduus acanthoides*, *C. nutans*, *C. pycnocephalus*, and *C. tenuiflorus* (Tables 2 & 4).

Table 6. Species groups with shared chemical profiles by reported insect biologically active compounds^a**Flavonoids**

Apigenin	Luteolin
<i>Cirsium arvense</i> ^c	<i>Cirsium amplexifolium</i>
<i>Cir. canescens</i> ^b	<i>Cir. arvense</i>
<i>Cir. carolinianum</i>	<i>Cir. buergeri</i>
<i>Cir. chikushiense</i>	<i>Cir. chikushiense</i>
<i>Cir. drummondii</i> ^b	<i>Cir. echinus</i>
<i>Cir. gratiosum</i>	<i>Cir. gyojanum</i>
<i>Cir. japonicum</i>	<i>Cir. helenoides</i>
<i>Cir. magofukui</i>	<i>Cir. hosogawa</i>
<i>Cir. nipponicum</i>	<i>Cir. kawakamii</i>
<i>Cir. oleraceum</i>	<i>Cir. lucens</i>
<i>C. ochrocentrum</i> ^b	<i>Cir. magofukui</i>
<i>Cir. purpuratum</i>	<i>Cir. matusmurae</i>
<i>Cir. rhinoceros</i>	<i>Cir. matusmurae</i> var. <i>pubescens</i>
<i>Cir. sieboldii</i>	<i>Cir. nipponicum</i> var. <i>yoshinoi</i>
<i>Cir. syriacum</i>	<i>Cir. oleraceum</i>
<i>Cir. vallis-demonii</i>	<i>Cir. palustre</i>
<i>Cir. vulgare</i>	<i>Cir. pulcherrimum</i> ^b
<i>Carduus assoic</i>	<i>Cir. rhinoceros</i>
<i>Car. nutans</i> ^c	<i>Cir. seiboldi</i>
<i>Car. pyncnocephalus</i> ^c	<i>Cir. suffultum</i>
<i>Car. tenuiflorus</i> ^c	<i>Cir. syriacum</i>
	<i>Cir. tweedyi</i> ^b
	<i>Cir. vallis-demonii</i>
Vicenin-2	<i>Cir. wallichii</i>
<i>Cirsium gratiosum</i>	<i>Cir. yakusimense</i>
<i>Cir. oligophyllum</i>	<i>Carduus acanthoides</i> ^c
	<i>Car. assoi</i> ^c
Rutin	<i>Car. gelulus</i> ^c
<i>Cirsium gratiosum</i>	<i>Car. nutans</i> ^c
<i>Cir. arvense</i> var. <i>setosum</i>	
<i>Carduus nutans</i> ^c	Skutellarein
	<i>Cirsium oleraceum</i>
Quercetin	
<i>Cirsium arvense</i> ^c	<i>Cirsium subniveum</i> ^b
<i>Cir. babanum</i>	<i>Cir. tioganum</i> var. <i>coloradense</i> ^b
<i>Cir. foliosum</i> ^b	<i>Cir. tweedyi</i> ^b
<i>Cir. oleraceum</i>	<i>Cir. undulatum</i> ^b
<i>Cir. pulcherrimum</i> ^b	<i>Cir. vallis-demonii</i>
<i>Cir. scariosum</i> ^b	<i>Cir. vulgare</i> , <i>Carduus getulus</i> ^c

(continued on next page)

In the genus *Cirsium*, we found evidence in the literature for compounds from 106 species worldwide (Tables 1 & 3), even though at least 250 species of *Cirsium* have been described (Bremer, 1994). Only 16 of the 104 species (15.4%) examined to date occur in North America, and only six of those 16 (37.5%) are native to North America. Yet, at least 94 native *Cirsium* species and 125 accepted native taxa occur among the 100 species and 131 accepted taxa currently listed for the USA

Table 6. (continued)**Other Secondary Metabolites:****Sterols and triterpenes:**

b-sitosterol	taraxasterol	taraxasterol acetate
<i>Cirsium echinus</i>	<i>Cirsium arvensec</i>	<i>Cirsium canum</i>
<i>Cir. syriacum</i>	<i>Cir. oleraceum</i>	<i>Cir. carolinum</i>
<i>Cir. oleraceum</i>	<i>Cir. setosum</i>	<i>Cir. hypoleucum</i>
<i>Cir. vallis demonii</i>	<i>Cir. texanum</i> ^b	<i>Carduus getulus</i> ^c
<i>Cir. vulgare</i> ^c	<i>Cir. vallis demonii</i>	<i>Car. nutans</i> ^c
<i>Carduus acanthoides</i> ^c	<i>Carduus getulus</i> ^c	erythrodiol 3-acetate
<i>Car. getulus</i> ^c	<i>Car. nutans</i> ^c	<i>Carduus getulus</i> ^c
<i>Car. nutans</i> ^c		
<i>Car. pycnocephalus</i>		

Alkaloids:

O-acetylajacoline (I)	heliotridane
<i>Cirsium wallichii</i>	<i>Cirsium steigerum</i>

Phenolic acids:

p-coumaric, caffeic, ferulic, vanillic, p-hydroxybenzoic, protocatechuic
Cirsium vulgare^c

Lignans:

pinoresinol
Carduus assoi^c
Car. tenuiflorus^c

^a References in Tables 1–4.

^b Native North American species.

^c Introduced North American species (*Carduus* is not native to North America).

(USDA Plant Database, 2002). Therefore, only 13.8% of the native *Cirsium* spp., 10.4% of the accepted native taxa, and 16% of all species including exotics in the USA have been examined for their chemistry. Interestingly, the two native North American species for which the most compounds have been identified, *Cirsium canescens* and *C. undulatum*, are the same two species for which the most field evidence exists on non-target host selection by *Rhinocyllus conicus* (Rees, 1977, 1978; Louda et al., 1997; Louda, 1998, 1999b; Louda and Arnett, 2000).

3.2. Missing data for sesquiterpene lactones?

We were surprised by the scarcity of reports of sesquiterpene lactones in the 104 species of *Cirsium* and *Carduus* examined to date. We found only one report of these compounds for *Cirsium* or *Carduus* (Bohlmann and Abraham, 1981). Yet, these compounds often are common in the Asteraceae, including in close relatives of true thistles. For example, sesquiterpene lactones are common secondary metabolites in *Centaurea* and *Cnicus*, which are very close relatives (e.g. Bremer, 1994). Furthermore, these compounds significantly influence insect activity (above). There are two possible explanations for the apparent scarcity of

Table 7. Flavonoids reported in *Cirsium* and *Carduus* species in *Rhinocyllus* case study^a

Flavonoid	European hosts			North American hosts		
	<i>Carduus nutans</i> (1)	<i>Carduus acanthoides</i> (2)	<i>Cirsium vulgare</i> (3)	High <i>Rhinocyllus</i> use	No <i>Rhinocyllus</i> use (6)	
				<i>Cirsium undulatum</i> (4)	<i>Cirsium canescense</i> (5)	<i>Cirsium tioganum</i> var. <i>coloradense</i> (7)
apigenin	X					
apigenin-6-8-C-diglycoside				X	X	
apigenin-7-O-diglucoside			X		X	
6-methoxy apigenin-7-O-diglucoside					X	
apigenin-7-O-glucoside	X					
apigenin-7-O-neohesperidoside	X			X	X	
chrysoerial-7-O-diglycoside					X	
6-methoxy chrysoerial-7-O-diglucoside				X		
chrysoerial-7-O-monoglycoside				X		
diosmetin-7-O-diglucoside						
genkwanin-4'-O-glucoside			X			
isorhamnetin	X					
kaempferol	X					
kaempferol-3-O-arabinosylgalactose			X			
kaempferol-3-O-glucoside			X			
kaempferol-3-O-glucoside-7-O-rhamnoside	X					
kaempferol-3-O- α -L-rhamnofuranoside	X					
kaempferol-7-O-rhamnoside	X					
linarin			?	?	?	X
6-methoxy linarin						X
luteolin	X	X	?	?	?	
luteolin-7-O-galactoside	X	X				
luteolin-7-O-digalactoside		X				
luteolin-7-O-glucoside	X	X				
luteolin-7-O-diglucoside	X					
luteolin-7-O-rutinoside	X					
pectolinarin			?	?	?	X
quercetin	?	?			?	
quercetin-3-O-diglycoside				X		X
quercetin-3-O-galactose			X			
quercetin-3-O-glucose			X			
rutin	X		X	?	?	
tilianin	X					

(continued on next page)

Table 7. (continued)**Key to Table 7 References** (Numbers in parentheses):

1: Bain and Desrochers, 1988; Kaloshina and Mazulin, 1988; Abdellah et al., 1989

2: Frydman and Deulofeu, 1962; Nolasco et al., 1987; Bain and Desrochers, 1988

3: McGowan and Wallace, 1972; Wallace, 1974; Iwashina et al., 1995

4, 5: Gardner, 1974

6: Turner et al., 1987; Goeden and Ricker, 1987a

7: Gardner, 1973.

? = Literature suggests compound suspected to be found, but has not been found.

^a Shown biological activity in insects.

sesquiterpene lactones reported from thistles. Either few of these compounds are present, or they have been missed in the general isolation protocols and not targeted for isolation with specifically suited procedures. Flavonoid analysis, the most common analysis reported here, relies mostly on polar and cellulose-based chromatography. The nonpolar sesquiterpene lactones are unlikely to be retained on this medium, and so are likely to have been discarded. We suggest that the prevalence of sesquiterpene lactones in other tribes of the Asteraceae (Hegnauer, 1977, 1989; Herz, 1977; Heywood et al., 1977; Seaman, 1982), the evidence of biological activity (above), and their presence in closely related species argue for direct studies of the presence or absence of sesquiterpene lactones in *Cirsium* and *Carduus*. Since specific methods for isolation of sesquiterpene lactones are well known (e.g. Bohlmann et al., 1984; Fernandez et al., 1989, 1995; Bicchi and Rubiolo, 1996), and since sesquiterpene lactones would be strong candidates to mediate host recognition and feeding by more specialized insects, we conclude that this lack of evidence presents an important opportunity for research.

3.3. Potentially relevant variation in flavonoids

Although the connection between plant flavonoid profile and insect behavior has been investigated, more research is needed (Rees and Harborne, 1985; Bohm, 1998; Simmonds, 2001). The evidence available strongly suggests that flavonoids could be important in thistle-insect interactions. Flavonoid occurrence and variation in thistles were well documented (Tables 1 & 2). Flavonoids were the most commonly reported compounds in thistles, providing 51.4% of the 212 total com-

pounds reported from *Cirsium* and *Carduus* spp. For the flavonoids that have been recovered from these genera thus far, 71% of them were from *Cirsium* spp., compared to 28% from *Carduus* spp. To date, 44% of the flavonoid compounds reported from these genera have been tested for some form of biological activity, but only 13% for insect activity.

The similarities and differences in the flavonoid constituents of *Cirsium* and *Carduus* spp. may offer a useful starting point in searching for a chemical contribution to differential host preference. A group of flavonoid compounds were reported only from *Cirsium* spp., including pectolinarin, linarin, cirsimaritin, and acacetin. Alternatively, at least 12 flavonoid compounds were reported for both *Cirsium* and *Carduus* spp., including apigenin, chrysoeriol, diosmetin, hispidulin, kaempferol, luteolin, narnigenin, quercetin, rutin, and triclin (Table 5). Of the flavonoid compounds found, at least six are known to be biologically active towards insects: skutelarein, vicenin-2, apigenin, luteolin, quercetin, and rutin. Yet, flavonoid composition varied among species. Using such contrasts, one can infer that some of these compounds could be important in insect host choice (Table 6).

Variation in extraction protocols reported in the literature also suggests further investigation into flavonoid content is needed. For example, rutin (*quercetin-3-O-rutinoside*) may be found in other thistle species with additional effort. The inability of rutin to dissolve in non-polar solvents is due to its high polarity as a flavonol diglycoside. Thus, rutin is only partially soluble in alcoholic solvents, used to extract flavonoids. Rutin, therefore, often may be discarded with the extracted plant material before the diagnostic chromatography is begun (personal observation). Another possibility is that aglycosidic flavonoids that occur as plant exudates can be extracted by a quick second dip into a non-polar solvent, such as acetone, and so may be discarded with the waxes and lipids (Bohm, 1998).

Many flavonoids have long been known as either antifeedants or stimulants on larvae and adults of various insects (Tables 1 & 2). This knowledge has stimulated the investigation of the relationship between host plant flavonoid profile and insect behavior (Rees and Harborne, 1985; Bohm, 1998; Simmonds, 2001). For species of *Cirsium* and *Carduus*, the two main classes of flavonoids reported to exhibit biological activity towards insects are flavones and flavonols. These two groups of flavonoids are structurally similar, differing in only one alcohol group. Given the variation among flavonoids, which has proven to be distinctive among taxa (Bohm, 1998), and given their reported biological activity towards insects, analysis of flavonoid variation may provide an efficient initial approach to characterize profiles of thistle species relevant to their interactions with insects. Examination of the effect of mixtures of these compounds could also be productive, since a small difference of one or two compounds in a profile can make a marked difference in insect response (Berenbaum et al., 1991; Harborne, 1999), especially in relation to environmental variation (Louda and Rodman, 1983; Macedo and Langenheim, 1989; Louda and Collinge, 1992; Desrochers and Bohm, 1993; Cates, 1996).

3.4. Latex and exudates from *Cirsium* spp.

The literature revealed groups of biologically active compounds associated with plant exudates from resin ducts, glandular trichomes, laticifers, and buds (Loomis and Croteau, 1973; Kelsey and Shafizadeh, 1980; Rossiter et al., 1986; Mauseth, 1988; Bramley, 1997; Wink, 1997; Ellis, 1997; Harborne, 1999). Many *Cirsium* species have glands on the involucre bracts (Great Plains Flora Association, 1986; Bremer, 1994). Also, many insects, including *Rhinocyllus conicus*, must feed on their host plants, prior to oviposition. Further, both vulnerable native thistle species in sand prairie (*Cirsium canescens*, *C. undulatum*) produce exudates from glandular ridges on bracts of their flower heads (personal observation). Together these observations suggest that characterization of the exudates of thistles would be productive.

3.5. Methodological observations

It became apparent that one of the main constraints on the current interpretation of the data available (Tables 1–4), similar to most meta-analyses, was that extraction and identification methods differed vastly among studies. Thus, articles that reported only a few compounds may not have screened the plant as intensively as those that reported more. Also the scarcity of sesquiterpene lactones in the literature on thistles may reflect methodological constraints (above). The implication for future work is that the plants of interest, such as invasive exotic weeds and potential non-target native host plants, need to be analyzed using a standardized protocol for extractions and chromatographic separations to determine comprehensively whether specific groups of potentially biologically active compounds are present. A primary goal should be to assure that all separations, from non-polar to polar compounds, be equally analyzed. The continuing improvement in equipment and techniques for spectroscopic characterization suggests that structures may be more easily and accurately determined now (Eisner and Meinwald, 1995; Bohm, 1998) than traditionally (Mabry et al., 1970). Furthermore, determination of mixtures of compounds is becoming increasingly efficient.

3.6. Application to *Rhinocyllus conicus* non-target host plant use

The case that stimulated our question and literature survey was the report of varying use of non-target native North American thistles by the musk thistle biological control weevil *R. conicus*. In fact, the *R. conicus* case history provides a unique opportunity, given the field data now available on non-target host selection, to examine the potential for a role of chemical profile in host range expansion. Doing so should help improve the prediction of ecological impacts by exotic phytophagous insects in new environments. So, within the constraints of the data available, we compared known chemical profiles among three thistles that coevolved with *R. conicus* and three that did not (Table 7). The three coevolved Eurasian species were the two main *Carduus* spp. targeted for biological control, *C. nutans* and *C. acanthoides* (Frick, 1978), and the weevil's predominant host plant

in maritime France, *Cirsium vulgare* (Zwölfer and Preiss, 1983; Briese, 1996). These three coevolved species varied in reported levels of *R. conicus* use. For example, Turner et al. (1987) found naturalized *Cirsium vulgare* (a European species) was heavily used in California: a rate of 0.03–0.24 adults, emerging from 17% of the heads sampled. The three native North American species, in order of their documented use by *R. conicus* were: *C. canescens*, *C. undulatum*, and *C. tiogianum var. coloradense* (Turner et al., 1987; Goeden and Ricker, 1987a; Louda et al., 1997; Louda, 1998, 1999b; Louda and Arnett, 2000). The use by *R. conicus* of *Cirsium canescens* is high and higher than that of *C. undulatum* in native sand prairie of central USA (Louda et al., 1997, 1998; Louda, 1998, 1999b; Louda and Arnett, 2000). In California, *Cirsium tiogianum var. coloradense*, however, had a very low *Rhinocyllus conicus* use rate: 0.1 heads per plant, in one of four populations studied (Turner et al., 1987), and Goeden and Ricker (1987b) did not find *R. conicus* on the *C. tiogianum var. coloradense* plants they sampled.

Variation in flavonoids among these six taxa was species-specific (Table 7), reflecting the usefulness of flavonoids as a chemosystematic trait for analysis of evolutionary lineages (Bohm, 1998). The characterization and identification of flavonoids for the *Cirsium* spp., including the native North American thistles on which we have extensive field data (Platte [*Cirsium canescens*] and wavyleaf [*C. undulatum*] thistles), emerged from chemosystematic work (McGowan and Wallace, 1972; Gardner, 1973, 1974; Wallace, 1974; Iwashina et al., 1995). Such variation also provides a potential basis for host recognition, preference, and variation in insect performance (Harborne, 1999; Simmonds, 2001). The flavonoid profiles of the two main *Carduus* species (*Carduus nutans*, *C. acanthoides*) naturalized in the North America have also been determined (Frydman and Deulofeu, 1962; Nolasco et al., 1987; Abdallah et al., 1989; Bain and Desrochers, 1988; Kaloshina and Mazulin, 1988).

Interestingly, the two native *Cirsium* spp. and the two invasive *Carduus* spp. have both overlapping and distinctive flavonoids (Table 7). The data for *C. vulgare* and *C. tiogianum var. coloradense* showed different profiles than those of *C. canescens* and *C. undulatum* (Table 7). The European *Cirsium* spp. did not have kaempferol or luteolin reported, although these two compounds have been found in many other *Cirsium* spp. (Table 5). Nor were pectolinarin and linarin reported. In our contrast, only *Cirsium tiogianum var. coloradense* had these compounds, although they were very common in other *Cirsium* spp. None of the four reported flavonoids in *Cirsium tiogianum var. coloradense*, the under-utilized North American species, were reported from the three coevolved European host plants (Table 7). Also, the more heavily damaged native species, Platte thistle (*C. canescens*), overlaps *Carduus nutans* for more flavonoids than does the other co-occurring native species, wavyleaf thistle (*C. undulatum*). Thus, the patterns of chemical variation are consistent with the prediction of higher use of *C. canescens* than of *C. undulatum*, as observed (Louda, 1998, 1999a; Louda and Arnett, 2000).

Sterols also varied among species. Sterols in *Carduus nutans* and *C. acanthoides* were not found in *Cirsium undulatum*, *C. canescens*, *C. tiogianum var. coloradense*, or *C. vulgare* (Abdallah et al., 1989; Nolasco et al., 1987). This variation may contrib-

ute to *Rhinocyllus conicus* general preference for *Carduus* over *Cirsium* spp. *Carduus acanthoides* also contained the alkaloids, acanthoidine, acanthoine and ruscopine, none of which have not been reported for the North American hosts and which could also play a role in host preference (Frydman and Deulofeu, 1962; Boidadzhiev, 1964).

Characterization of the chemical profile of the rare, federally listed Pitcher's thistle, *Cirsium pitcheri*, a close relative of Platte thistle, *Cirsium canescens* (Loveless and Hamrick, 1988) is not available. However, such data would provide information that would improve further the evaluation of the potential threat to the populations of this threatened rare species, should *R. conicus* disperse into its protected habitat (Louda et al., 2003c).

Given the reports to date, further analysis of chemical variation in vegetative tissues vs. in flowers is warranted to supplement what is known for these species to address the issue of host recognition, acceptance, and choice. Observations show that *R. conicus* often chooses potential host plants before flowering (anthesis) is initiated. Also, higher oviposition rates were correlated with feeding on leaf material (Louda and colleagues, unpublished data). Thus, we hypothesize that phagostimulatory and discriminatory compounds for *R. conicus* are likely to be within cell walls of the vegetative tissues. Candidate compound groups include flavonoids, sterols, triterpenes, lignans, and potentially sesquiterpene lactones, rather than the volatile components of flowers, for example. Also, based on the data reported in the literature, polyacetylenes, phenolic acids and alkaloids, most of which are reported primarily from the root systems, are less likely mediators of weevil host plant choice than flavonoids in this case. The probability that lignans play an important role in *R. conicus* host preference is not well supported by the present literature. More likely candidate compounds for phagostimulatory and discriminatory mediation of *R. conicus* host plant acceptance and preference appear to be flavonoids and sterols in the above-ground vegetative tissues.

Further information on chemical profiles and their variation should improve our understanding of mechanisms and vulnerabilities among closely related plant species to utilization by relatively stenophagous phytophagous insects, such as *R. conicus*, that are used in biological control of weeds. Thus, the *Rhinocyllus conicus* case history, along with the existing chemical and biological activity literature, suggests further examination of the role of flavonoids in host acceptance and preference of thistle-feeding insects is warranted. Their evaluation could contribute to improving prediction of potential ecological impacts of phytophagous insects in new environments.

4. Conclusion

From the literature on the chemistry of the main genera of the true thistles (*Cirsium*, *Carduus*), it is clear that multiple secondary metabolites are shared by species in these genera (Tables 1-4). Compounds that have already been shown to have biological activity towards insects are present in either *Cirsium* spp., or *Car-*

duus spp., or both. Some of the compounds have a potential role in mediating the outcome of insect–plant interactions in the new environment in North America in the *Rhinocyllus* case study (Tables 5–7). In screening potential biological control agents for potential host range expansion, our review suggests secondary host plant chemistry provides a currently unexplored avenue for more precise evaluation of likely host range. Additionally, our findings are consistent with the suggestions of Becerra and Venable (1999) that host chemistry may be more important to beetle host preference than close phylogenetic relationship or geographic region of origin. Since the aim of screening tests for biological control agents is to predict the risk of host range expansion and ecological impact in the new region, and since current host specificity testing can fall short of doing so (Arnett and Louda, 2002), additional chemical data should be useful (Harborne, 1991; Simmonds, 2001). Our review suggests that consideration of contemporary chemical profiles to supplement host specificity tests based on phylogenetic relationships will contribute to a clearer prediction of potential host plant use and ecological impacts.

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