

Physiological host range of *Ceratapion basicorne*, a prospective biological control agent of *Centaurea solstitialis* (Asteraceae)

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Abstract

Ceratapion basicorne (Coleoptera: Apionidae) is a weevil native to Europe and western Asia that is being evaluated as a prospective classical biological control agent of *Centaurea solstitialis* (yellow starthistle) in the United States. Host plant specificity of the insect was evaluated in no-choice oviposition experiments. Feeding on leaf tissue by adult females was highly correlated to oviposition rate, both of which occurred primarily on plants in the tribe Cardueae, and especially those in the monophyletic subtribe Centaureinae. The highest rates of larval development occurred on *Ce. solstitialis* and *Centaurea cyanus* (bachelor's button, garden cornflower), and there was significant development on *Centaurea melitensis* (Napa starthistle, tocalote), *Cnicus benedictus* (blessed thistle), *Carthamus tinctorius* (safflower), and *Crupina vulgaris* (common crupina). All the plants that supported some larval development are within a monophyletic clade within the Centaureinae. No native North American plants appear to be at risk of significant damage by this insect. Additional testing of safflower and bachelor's button under choice conditions should complement these results to help determine the degree to which these plants are at risk.

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Keywords: Host plant specificity; Biological control; Weed; Invasive plant; Risk assessment

1. Introduction

1.1. Weed distribution, ecology, and impact

Yellow starthistle (*Centaurea solstitialis* L.) is an invasive alien weed that was accidentally introduced into California over 130 years ago, primarily by importation of contaminated alfalfa seed (Maddox et al., 1985; Gerlach, 1997a,b). The weed infests about eight million hectares in the western US and Canada (Duncan, 2001; Pitcairn et al., 2006). Infestations have been reported in 23 states, with the largest populations in the states of California, Idaho, Oregon, and Washington (Maddox et al., 1985; Sheley et al., 1999). It is considered the most common weed in California, and it is continuing to spread and threaten states to the east (Pitcairn et al., 2006). The weed is designated as noxious in 11 western states and two Canadian provinces (Skinner et al., 2000).

Yellow starthistle is highly invasive in grassland habitats and displaces desirable plants in both natural and grazing areas. Spiny flowerheads interfere with grazing animals and human recreation, and the plants displace desirable vegetation and deplete soil moisture. Consumption of yellow starthistle by horses causes a fatal syndrome known as “chewing disease” or nigropallidal encephalomalacia (Cordy, 1978). Total economic benefits for controlling yellow starthistle in California have been estimated to be between \$40 million and \$1.4 billion, depending on assumptions (Jetter et al., 2003). Environmental benefits due to reduced use of herbicides, increased recreation and increased biodiversity have not been estimated, nor have any benefits to nearby states.

Yellow starthistle is an herbaceous winter annual plant native to southern Europe and the Near East (Maddox, 1981), occurring from Spain to Iran (Wagenitz, 1975; Dostál, 1976; Rechingner, 1980). The geographic center of origin may be in Turkey or Greece, based on the number of subspecies occurring in these regions (Wagenitz, 1975; Dostál, 1976). Although the plants in the western USA are genetically

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diverse, there is no evidence of genetically distinct subpopulations occurring there (Roché, 1965; Sheley et al., 1983a,b; Schumacher et al., 1982; Sun, 1997). The plant is well adapted to a Mediterranean climate (dry summers and wet winters) and can tolerate winter snow. In California, seeds germinate mainly in early winter, rosettes grow slowly until spring, then the plants “bolt” and bloom until they die from desiccation or frost (Pitcairn et al., 1999a; Sheley et al., 1999). Some seeds are released during the summer as individual capitula (flower heads) mature while others are retained until the capitula disintegrate during winter. Seeds falling in summer soon become dormant and require cooler temperatures before germinating, usually soon after the start of winter rains. Seeds buried in soil can remain viable for several years and will germinate after exposure to light when the soil is disturbed (Joley et al., 2003 and Refs. therein).

1.2. Weed management options

Although several herbicides are effective (Sheley et al., 1999; DiTomaso, 2005), conventional herbicide control strategies have often been inadequate because of the large areas infested, the economic and environmental costs of herbicides, or the relatively low monetary return from land used for grazing, rights-of-way, conservation or recreation. Other control strategies such as tillage, mowing, burning, and grazing have been evaluated and can sometimes be effective, but are not practical for managing the weed over large areas of rangeland (DiTomaso et al., 2000; DiTomaso, 2005 and Refs. therein). In the Mediterranean region, where it originates, yellow starthistle generally occurs in low densities and appears to be under natural control (Uygur et al., 2004). Research to discover, evaluate, and introduce classical biological control agents began in the 1960s (Maddox, 1981; Rosenthal et al., 1992; Turner et al., 1995; Sheley et al., 1999). Some biological control agents have been previously introduced, with the establishment of six exotic insect species, all of which attack flowerheads and destroy developing seeds (Turner et al., 1995; Balciunas and Villegas, 2001). A few indigenous invertebrates and diseases have been described on yellow starthistle in California (Pitcairn et al., 1999a,b). Of these, only a few attack plants later than the seedling stage, and these have little effect (Klisiewicz, 1986), but some can cause significant mortality among very young seedlings (Woods et al., 2000). The rust pathogen, *Puccinia jaceae* var. *solstitialis*, was introduced in California in 2003 (Woods et al., 2004; Fisher et al., 2006), but it does not appear to be causing significant damage to the plant. The combined effect of these natural enemies has not significantly reduced yellow starthistle over most of its range (Balciunas and Villegas, 1999; Pitcairn et al., 2002; Smith, 2002), although there are some local reductions, especially in the presence of competing vegetation (Pitcairn et al., 2005; E.M. Coombs, personal communication). Comparative life history studies of the plant in California (Pitcairn et al., 2002) and Turkey (Uygur et al., 2004) suggest that natural enemies that damage the rosettes may be most

effective for controlling it. Additional agents are needed, especially ones that attack the foliage, stem, and roots of rosettes and young bolting plants (Smith, 2004).

1.3. Life history and behavior of *Ceratapion basicorne*

Ceratapion basicorne (Illiger) (Coleoptera: Apionidae) is a weevil native to Europe and the Near East that develops in rosettes of yellow starthistle (Clement et al., 1989; Alonso-Zarazaga, 1990a; Wanat, 1994). In the wild this insect has been reared from *Ce. solstitialis*, *Ce. cyanus* L., and *Cnicus benedictus* L., which suggests that it is highly host-specific (Alonso-Zarazaga, 1990a; Wanat, 1994; Campobasso et al., 1999). The insect is common on yellow starthistle in Turkey, Greece, and Georgia (Rosenthal et al., 1994; Balciunas, 1998; Uygur et al., 2005) and is widely distributed in Europe and western Asia (Alonso-Zarazaga, 1990a; Wanat, 1994). Overwintering adults become active in the early spring and feed on rosette leaves (Clement et al., 1989). Eggs are deposited inside leaves, and larvae tunnel down the leaf petiole and develop inside the upper root and basal stem (root crown), where they pupate (Smith and Drew, 2006). Females oviposit about 1.5 eggs per day during an oviposition period of about 20 days. Development time of eggs until eclosion of larvae is 8.5 days at room temperature (19°C), and development time from oviposition until adult emergence is about 77 days. Adults emerge from the plant in early summer, when it bolts. Adults feed briefly on yellow starthistle foliage then aestivate and hibernate until the following spring. Mating occurs soon after new adults emerge in early summer and after hibernation ends in the following spring (Smith and Drew, 2006). There is one generation per year.

Some data on host specificity were reported by Clement et al. (1989), indicating that *Carthamus tinctorius* L. (safflower), *Galactites tomentosus* Moench, and *Carduus pycnocephalus* L. can support larval development. However, absence of reports of the development of this insect from these hosts in the field (Alonso-Zarazaga, 1990a; Wanat, 1994; Campobasso et al., 1999; Uygur et al., 2005) prompted me to further evaluate its host specificity. The purpose of the present study was to determine what non-target plants are susceptible to damage by *C. basicorne* and to measure the relative amount of damage the insect can cause under no-choice laboratory conditions. Such data provide part of the basis for assessing the risk that the insect would pose to non-target plants if it were to be introduced as a biological control agent (USDA-APHIS, 1998; Withers et al., 1999; Jacob and Briese, 2003; Coombs et al., 2004; Smith, 2006).

2. Materials and methods

2.1. Insect population

The parental generation and descendants of a colony of *C. basicorne* held in the USDA-ARS quarantine laboratory in Albany, CA were used for these experiments. The colony was established from adults reared from naturally infested,

wild yellow starthistle plants that were collected at 15 sites near Kayseri, Sivas, Erzincan, Erzurum, and Malatya, Turkey between 28 May and 2 June 2001 (Smith and Drew, 2006). Emerged adults were identified by the author before using them in experiments. Identification of representative specimens was confirmed by B.A. Korotyaev, and vouchers were deposited at the USDA-ARS Systematic Entomology Laboratory in Beltsville, MD. Reproductive diapause was terminated by holding adults in the dark at 5 °C for at least three months (Smith and Drew, 2006). Experiments were conducted between March 2002 and April 2005.

2.2. Test plants

Test plant species were selected following Technical Advisory Group (TAG) guidelines, which emphasize evaluation of native and economically important species (USDA-APHIS, 1998; see discussion below). We generally used plants grown from seed that were two to four months old and in the rosette stage (except for species that do not form a rosette). However, because of scarcity of seed, many of the *Saussurea americana* Eaton plants were transplanted from the field. Cuttings of *Hemizonia minthornii* Jepson were used instead of potted plants. Seeds for test plants were obtained from commercial sources or from the wild with the assistance of cooperators (see Acknowledgements). A representative specimen of each species was grown to maturity to provide herbarium vouchers that are kept at the USDA-ARS Western Regional Research Center, Albany, CA. Identifications were confirmed by G.F. Hrusa (California Department of Food and Agriculture).

2.3. No-choice tests

Individual mated females that had completed reproductive diapause were held in a sealed container with a cut leaf of yellow starthistle, inserted in a water vial, until she oviposited (Fig. 1A). Each female was then placed in a clear plastic

tube (3.5 cm diameter × 11 cm long) mounted on an intact rosette leaf of a nontarget plant species for four to 5 days (Fig. 1B). Afterwards, we put each female back with a cut yellow starthistle leaf for two to three days to determine if she could still oviposit. If the female failed to oviposit on the post-trial yellow starthistle or died during the experiment, then the trial was considered invalid and the experiment was repeated. After removing the insect from the test plant, the exposed leaf was labeled, and we counted the number of adult feeding holes and eggs oviposited. After 10–21 days, which allowed time for eggs to hatch and larvae to tunnel down the petiole and into the root crown, the leaf was removed and examined under a microscope for signs of egg hatch and larval tunneling (see Smith and Drew, 2006). Six weeks after exposure to oviposition, each plant was enclosed in a fine mesh bag and held in a quarantine greenhouse until the insects could complete development (three months), then the plants were dissected to observe signs of insect damage and development. Any plants that deteriorated prematurely were dissected immediately. In general, we tested eight replicates per plant species in the tribe Cardueae and four in the more distantly related taxa. We doubled the number of replicates if there were any signs of larval development.

In general, no statistical tests were conducted on the results, because the purpose was to describe the risk and amount of damage or oviposition rather than to test hypotheses. However, χ^2 tests of independence were conducted to compare adult feeding damage and oviposition rates among the varieties of safflower tested to determine if any were more susceptible than the others.

3. Results and discussion

3.1. Test plants

Test plant species were selected following Technical Advisory Group (TAG) guidelines, which emphasize protection of native and economically important species

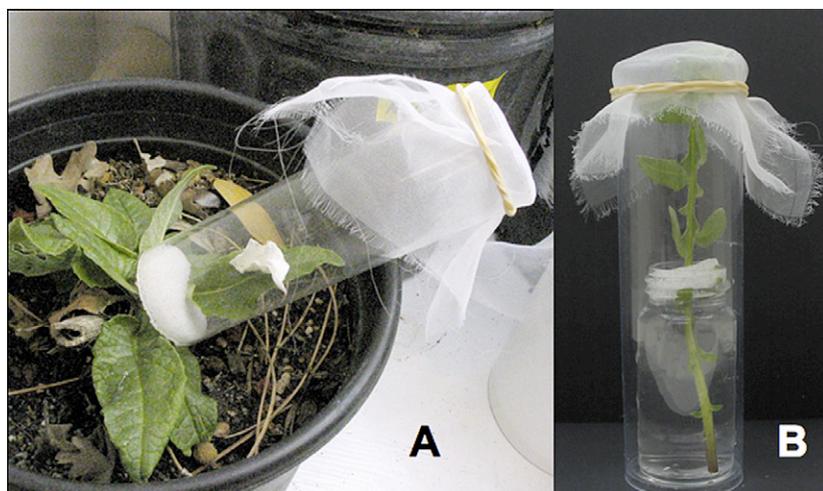


Fig. 1. Individual females were held in a sealed plastic cylinder on an intact leaf of a nontarget test plant for 5 days (A), then placed in a tube with a cut yellow starthistle leaf (B) to feed and oviposit before use in a subsequent test.

(USDA-APHIS, 1998; TAG, 2006). The guidelines generally follow the “centrifugal phylogenetic” approach outlined by Wapshere (1974), in which more species are tested in taxonomic ranks closely related to the target weed, and the number of test species decreases as relatedness to the target decreases. The validity of this approach is supported by the historical data that indicates that close relatives are most likely to suffer damage (Pemberton, 2000; Sheppard et al., 2005). Other factors that contributed to the choice of test species included: nativity in North America; ornamental or other economic value; whether the species is sympatric with the target’s present or potential range in North America; similarity of growth form, life history and secondary chemistry, if known; the presence of rare or protected species in the same genus; and availability of the species for testing. For rare or protected species that were proposed for testing, we often tested a close relative to avoid negatively impacting an already stressed species and/or because of unavailability of specimens. Species names are based on the PLANTS Database (USDA-NRCS, 2006) with the support of other regional flora, primarily Barkley (1986), Keil (1993) and Hitchcock and Cronquist (1998). Test plant species were selected following the higher taxonomy of Bremer (1994). A recent phylogenetic revision (Funk et al., 2005) has changed some taxonomic relationships; however the level of significance of the cladogram branches was not reported, so the relationships should be interpreted as the current, though possibly imperfect, state of knowledge. In particular, the subfamily Cichorioideae was reduced and Carduoideae was erected. The tribe Cardueae was previously placed in the subfamily Cichorioideae s.l.; however, the latter was determined to be a paraphyletic grade (Garcia-Jacas et al., 2002) and has since been redefined as a monophyletic group that does not include Cardueae (Funk et al., 2005). The tribe Mutisieae was removed from Cichorioideae s.s. and is now a basal, probably still paraphyletic, clade of the Asteraceae (Funk et al., 2005).

Yellow starthistle is in the family Asteraceae, subfamily Carduoideae, tribe Cardueae, and subtribe Centaureinae (Bremer, 1994; Funk et al., 2005). Both the subfamily Carduoideae and the tribe Cardueae appear to be monophyletic groups. The exact taxonomic relationships within the tribe Cardueae are not completely understood, but the subtribe Centaureinae segregates as a monophyletic group from the rest of the tribe, whereas the subtribe Carduinae is a paraphyletic grade (Bremer, 1994; Susanna et al., 1995; Garcia-Jacas et al., 2002). However, of the Carduinae genera of interest in this study, *Carduus*, *Cirsium*, *Cynara*, and *Silybum* appear to be in a monophyletic group, whereas *Onopordum* is positioned more basally (Funk et al., 2005). So, all these genera are more distantly related to *Centaurea* than are those in the Centaureinae. The monophyletic *Arctium*–*Cousinia*–*Saussurea*–*Jurinea* group within the Centaureinae is considered to be the closest related monophyletic group that includes *Centaurea*, *Acroptilon*, *Carthamus*, *Cnicus*, and probably *Crupina* (Garcia-Jacas et al., 2002; Funk et al., 2005, J.F. Gaskin, unpublished data).

The two subtribes Centaureinae and Carduinae have distinctly different secondary chemical compounds (Susanna et al., 1995), which are probably important in determining host plant specificity of specialist herbivores. Centaureinae produce acetylene aldehydes, chlorhydrins, and acetates, germacrolide-type sesquiterpenoids, highly methoxylated flavonoids (including flavanones), and fully methoxylated lignans (Wagner, 1997). In contrast, the Carduinae produce distinctive classes of acetylenes, including C₁₇ acetylenes and acetylene glycosides, gainolide-type sesquiterpenoids, monomethoxylated flavonoids, and simple cinnamic acids and their derivatives.

The genus *Centaurea* is very large, comprising 200–600 species, and its definition and extent is still being resolved (Klokov et al., 1963; Dostál, 1976; Susanna et al., 1995; Garcia-Jacas et al., 2000; Hellwig, 2004). Some groups within the genus *Centaurea* (e.g., *Centaurea sensu stricto*, *Cyanus*, *Jacea*, and *Psephellus* groups) appear to be as phylogenetically distinct as other well recognized genera (e.g., *Amberboa*, *Carduncellus*, *Carthamus*, *Cnicus*, *Crupina*, and *Seratula*) (Garcia-Jacas et al., 2001; J.F. Gaskin, unpublished data). Two North American species, *Centaurea americana* Nutt. and *Centaurea rothrockii* Greenm. have been assigned to the genus *Plectocephalus*, which has distinct pollen morphology and is thought to have diverged from the *Centaurea* clade during late Oligocene and Miocene (Wagenitz, 1955; Hellwig, 2004). This is much earlier than the divergence of *Cyanus* and the *Carthamus*/*Carduncellus* groups, which probably arose during the Pliocene–Pleistocene transition. The *Flora of North America* (Keil and Ochsmann, 2006) uses the treatments: *Centaurea benedicta* (= *Cn. benedictus*), *Plectocephalus americana* and *Plectocephalus rothrockii*, although the PLANTS website has not adopted these changes (USDA-NRCS, 2006). Although many of the phylogenetic relationships among the remaining species within the genus *Centaurea* are not precisely known, some groups have clearly emerged. The strongest grouping reflects differences in pollen structure (Wagenitz, 1955) and DNA nucleotide base sequences (Susanna et al., 1995; J.F. Gaskin, unpublished data). Yellow starthistle is in the *Jacea* group, which is monophyletic and includes many of the other weedy *Centaurea* species adventive to North America.

Plants of economic interest in the family Asteraceae distributed within the geographic range of yellow starthistle in North America include artichoke (*Cynara scolymus* L.), safflower (*Ca. tinctorius* L.) and sunflower (*Helianthus annuus* L.). Because a population of *C. basicorne* from Italy has been reported to damage and develop in safflower (Clement et al., 1989), and this is an important crop in California and other western states, we evaluated nine varieties. Bachelor’s button (*Ce. cyanus*) is an introduced ornamental in North America, but is also considered an invasive weed in some areas of the western US (Lorenzi and Jeffery, 1987; Taylor, 1990), and is a common weed in wheat fields in eastern Europe (Voronov, 1977; Kapeluszy and Pawlowski, 1978; Snarska, 2004). The native North American plants

most closely related to yellow starthistle include: *Ce. americana* and *Ce. rothrockii* (discussed above), *S. americana*, and the many species of *Cirsium*. Several *Cirsium* species are becoming rare, and six species or varieties are federally listed as endangered (E) or threatened (T): *Cirsium fontinale* (Greene) Jepson var. *fontinale* (E), *Ci. fontinale* (Greene) Jepson var. *obispoense* J.T. Howell (E), *Ci. hydrophilum* (Greene) Jepson var. *hydrophilum* (E), *Cirsium loncholepis* Petrak (E), *Cirsium pitcheri* (Torr. ex Eat.) Torr. and Gray (T), and *Cirsium vinaceum* Woot. and Standl. (T) (USFWS, 2005). A total of 20 native species, including *Ci. fontinale* var. *fontinale* and *Ci. fontinale* var. *obispoense*, occur in California. Eleven California species are considered rare (Tibor, 2001), and *Cirsium ciliolatum* (Henderson) J.T. Howell and *Cirsium rhotophilum* Blake are listed by the state of California as endangered and threatened, respectively.

3.2. No-choice tests

We tested a total of 51 species of nontarget host plants from the Asteraceae family, including 25 native species and 4 economic species (Table 1). This includes species from all five genera in the subfamily Carduoideae, all three tribes in the subfamily Cichorioideae s.s., and all eight tribes in the subfamily Asteroideae that contain native North American species or economic species. In no-choice oviposition tests, *C. basicorne* females oviposited at least once on 94% of the plant species in the subtribe Centaureinae, including *Ca. tinctorius* (safflower) and the native species *Ce. americana* and *Ce. rothrockii*. At least one egg was deposited on 62% of the plant species in other subtribes of the Cardueae, and most frequently on *S. americana* and *Ci. loncholepis*. Eggs were observed on only three plants outside the tribe Cardueae: one egg on one plant of *Liatris punctata* Hook., two eggs on one plant of *Gazania rigens* (L.) Gaertn., and six eggs on one plant of *Pluchea odorata* (L.) Cass. None of the eggs on the first two plants hatched. Two eggs on *P. odorata* hatched, but larvae died when they reached the end of the petiole. These results indicate no risk of significant larval damage to plants outside the tribe Cardueae.

The highest rates of larval survival and development were observed on *Ce. solstitialis* (yellow starthistle) and *Ce. cyanus* (bachelor's button), and there was development on *Centaureinae melitensis* L. (Napa starthistle, tocalote), *Centaureinae montana* L., *Centaureinae nigrescens* Willd. (= *Centaureinae x pratensis*, meadow knapweed), *Centaureinae sulphurea* Willd., *Cn. benedictus* L. (blessed thistle), *Ca. tinctorius* (safflower), and *Crupina vulgaris* Cass. (common crupina). There was no larval development on any *Cirsium* species tested, which is consistent with Clement et al.'s (1989) results for *Cirsium douglasii* DC. and *Cirsium campylon* H. Sharsm. There was no larval development in any threatened or endangered species, nor their surrogates that we tested. Regarding the two North American native *Centaurea* species, no development was observed in 18 trials of *Ce. rothrockii* or 21 trials of *Ce. americana*. The roots

of two *S. americana* plants were damaged, but the damage was not consistent with that usually caused by *C. basicorne*. These plants had been collected from the field shortly before being tested, so it is likely that the damage was caused by other species of insect that had attacked the plant in the field. Other *S. americana* plants that were not infested by *C. basicorne* had similar damage. These results indicate that there is zero to very low risk that *C. basicorne* will damage any North American native plant species.

Our results generally corroborated those of Clement et al. (1989), indicating no larval development on any *Cirsium* species tested, *Cy. scolymus* (artichoke) or *Ce. calcitrapa* L. However, there were some discrepancies. Clement et al. (1989) reported larval development on *Car. pycnocephalus* L. in 11% of trials, in which four neonate larvae were transferred to each replicate plant, whereas we observed no development on *Car. pycnocephalus*, despite oviposition of ten eggs on one out of ten plants tested. The seven eggs oviposited in the leaf blade either did not hatch or the larvae failed to reach the midrib. Of the three eggs oviposited in the midrib, two larvae tunneled down the petiole, but no damage to the stem was observed. Apparently placing neonate larvae in a hole in the central rosette meristem is more conducive to larval development. On the other hand, we observed development of some larvae on *Cn. benedictus*, whereas Clement et al. (1989) observed no development on the three plants tested. Although we did not test *G. tomentosus* Moench, absence of development in any Cardueae outside the subtribe Centaureinae, suggests that we would not have observed development in this plant; however, Clement et al. (1989) reported development in 20% of their larval transfer trials. The differences between our results and those of Clement et al. (1989) indicate that estimates of host plant suitability that are based on transfer of neonate larvae to a potentially susceptible part of the plant (into a hole in the central meristem) can differ from those based on naturally oviposited eggs. The reason is probably because eggs and emerging larvae oviposited in the leaf blade and midrib face different plant defenses than larvae artificially placed in the central meristematic tissue. Thus, when designing larval transfer experiments, it is important to place larvae in as natural a location as possible to improve the validity of extrapolating the results to predict what would occur under natural conditions. Larval transfer is less preferable for insects that oviposit into plant tissue than for those that oviposit externally (Sheppard, 1999).

Development of larvae in safflower and bachelor's button may not be normal for *C. basicorne* because these plants do not form a rosette. Thus, when young larvae tunnel down a leaf on either of these plants, they cannot reach the root crown. The stem of these plants has a pithy center, and larvae only feed in the woody outer portion of the stem. The relatively thin cortex provides a limited space for the insect, and as the plant continues to grow, it sometimes crushes the pupae. Nevertheless, there was high infestation and survivorship to the pupal stage on bachelor's button and safflower in no-choice experiments, so both these

Table 1
Oviposition and immature development of *C. basiscorne* on test plants in no-choice conditions (one female per plant, held in tube on a leaf for 5 days on nontarget species or for 2–3 days on yellow starthistle)

Plant species	No. of trials oviposition	Adult feeding holes/day (±SE)	Eggs/day (±SE)	No. of trials development ^a	Percentage of trials				
					Adult feeding holes present	Eggs present	Internal plant damage present	Adults or pupae present	
Subfamily Cardioideae									
Tribe Cardueae									
Subtribe Centaureinae									
<i>Acroptilon repens</i> (L.) DC., Russian knapweed ^d	10	4.09 ± 0.82	0.16 ± 0.06	9	90	40	0	0	0
<i>Carduus trictorius</i> L., safflower	100	10.66 ± 0.82	0.47 ± 0.05	76	57	61	42	38	0
<i>Centaurea americana</i> Nutt., American basketflower ^b	23	6.04 ± 1.42	0.22 ± 0.08	21	91	39	0	0	0
<i>Centaurea calcitrapa</i> L., purple starthistle ^d	8	9.59 ± 2.20	0.25 ± 0.08	8	100	75	0	0	0
<i>Centaurea cherraria</i> L., dusty miller ^e	10	0.51 ± 0.13	0.00 ± 0.00	10	80	0	0	0	0
<i>Centaurea cyanus</i> L., cornflower, bachelor's button ^{c,d}	8	22.66 ± 3.30	1.73 ± 0.29	8	100	100	100	100	0
<i>Centaurea dealbata</i> Willd., whitewash cornflower ^d	11	10.71 ± 2.54	0.85 ± 0.30	13	100	82	9	0	0
<i>Centaurea diffusa</i> Lam., diffuse knapweed ^d	8	24.28 ± 5.22	1.50 ± 0.43	7	100	88	0	0	0
<i>Centaurea stoebe</i> L. (= <i>maculosa</i>), spotted knapweed ^d	8	8.84 ± 1.78	0.56 ± 0.13	6	100	75	0	0	0
<i>Centaurea meliensis</i> L., Napa starthistle, tocalote ^d	20	11.25 ± 2.01	0.60 ± 0.12	17	95	75	44	44	0
<i>Centaurea montana</i> L., perennial cornflower ^e	17	4.31 ± 2.04	0.25 ± 0.15	15	53	35	13	7	0
<i>Centaurea nigrescens</i> Willd. (= <i>C. x pratensis</i>), meadow knapweed ^d	14	10.24 ± 2.25	0.74 ± 0.21	15	93	64	42	10	0
<i>Centaurea rothrockii</i> Greenm., Rothrock's basketflower ^b	18	12.83 ± 1.91	0.30 ± 0.09	15	100	56	0	0	0
<i>Centaurea solstitialis</i> L., yellow starthistle ^d	349	16.58 ± 0.46	1.54 ± 0.05	32	100	99	89	88	0
<i>Centaurea sulphurea</i> Willd., Sicilian starthistle ^d	13	5.18 ± 1.13	0.34 ± 0.13	12	77	54	10	10	0
<i>Centaurea virgata</i> Lam. ssp. <i>squarrosa</i> (Willd.) Gugler, squarrose knapweed ^d	16	7.91 ± 1.11	0.51 ± 0.12	10	100	81	0	0	0
<i>Chicus benedictus</i> L., blessed thistle ^d	8	5.58 ± 1.14	0.50 ± 0.17	9	100	88	50	38	0
<i>Crupina vulgaris</i> Cass., common crupina ^d	9	3.51 ± 1.12	0.24 ± 0.13	11	89	44	22	22	0
Subtribe Carduinae									
<i>Carduus pycnocephalus</i> L., Italian thistle ^d	10	1.74 ± 1.63	0.20 ± 0.20	9	40	10	0	0	0
<i>Crusium brevisyllum</i> Cronq., Indian thistle ^b	7	0.00 ± 0.00	0.11 ± 0.07	7	0	29	0	0	0
<i>Crusium ciladatum</i> (Henderson) Howell, Ashland thistle ^b	9	0.13 ± 0.09	0.00 ± 0.00	9	22	0	0	0	0
<i>Crusium cymosum</i> (Greene) Jepson, peregrine thistle ^b	11	0.10 ± 0.06	0.00 ± 0.00	8	18	0	0	0	0
<i>Crusium fontinale</i> Greene var. <i>fontinale</i> , fountain thistle ^b	15	0.06 ± 0.03	0.00 ± 0.00	15	27	0	0	0	0
<i>Crusium hydrophilum</i> (Greene) Jepson var. <i>vaseyi</i> (Gray) Howell, Mount Tamalpais thistle ^b	16	0.70 ± 0.39	0.07 ± 0.05	16	56	13	0	0	0
<i>Crusium loncholepis</i> Petrak., la graciaosa thistle ^b	9	4.04 ± 1.92	0.36 ± 0.24	9	78	56	0	0	0
<i>Crusium occidentale</i> (Nutt.) Jepson var. <i>venustum</i> (Greene) Jepson, venus thistle ^b	16	1.40 ± 1.09	0.03 ± 0.03	15	44	6	0	0	0
<i>Crusium vinaceum</i> Woot. and Standl., Sacramento Mountain thistle ^b	7	0.00 ± 0.00	0.00 ± 0.00	7	0	0	0	0	0
<i>Crusium vulgare</i> (Savt.) Ten., bull thistle ^d	8	0.44 ± 0.44	0.06 ± 0.06	8	13	13	0	0	0
<i>Cynara scolymus</i> L., artichoke	11	1.18 ± 0.64	0.00 ± 0.00	11	55	0	0	0	0
<i>Onopordum acanthium</i> L., Scotch thistle ^d	8	0.75 ± 0.30	0.06 ± 0.04	8	88	25	0	0	0
<i>Saussurea americana</i> Eaton, American sawwort ^b	41	4.04 ± 0.91	0.35 ± 0.07	23	73	51	0 ^e	0 ^e	0
<i>Silybum marianum</i> (L.) Gaertn., milk thistle ^d	8	0.19 ± 0.10	0.00 ± 0.00	8	38	0	0	0	0
Subtribe Carlininae									
<i>Xeranthemum cylindraceum</i> Sibth. and Sm., flacc stars ^e	4	3.35 ± 2.89	0.25 ± 0.25	4	75	25	0	0	0
Subtribe Echinopsidinae									
<i>Echinops exaltatus</i> Schrad., tall globehustle ^e	4	1.85 ± 0.88	0.05 ± 0.05	4	100	25	0	0	0

(continued on next page)

Table 1 (continued)

Plant species	No. of trials oviposition	Adult feeding holes/day (\pm SE)	Eggs/day (\pm SE)	No. of trials development ^a	Percentage of trials					
					Adult feeding holes present	Eggs present	Internal plant damage present	Adults or pupae present	Adults or pupae present	
Subfamily Cichorioideae s.s.										
Tribe Arctoteae										
<i>Gazania rigens</i> (L.) Gaertn., treasure-flower ^e	10	2.20 \pm 1.12	0.04 \pm 0.04	10	40	10	0	0	0	0
Tribe Lactuceae										
<i>Agoseris grandiflora</i> (Nutt.) Greene, bigflower agoseris ^b	8	0.00 \pm 0.00	0.00 \pm 0.00	8	0	0	0	0	0	0
<i>Stephanomeria cichoriacea</i> Gray, chicoryleaf wirelettuce ^b	4	0.00 \pm 0.00	0.00 \pm 0.00	2	0	0	0	0	0	0
<i>Lactuca sativa</i> L., garden lettuce	8	0.00 \pm 0.00	0.00 \pm 0.00	8	0	0	0	0	0	0
Tribe Vernoniae										
<i>Stokesia laevis</i> (Hill) Greene, Stokes' aster ^b	4	0.00 \pm 0.00	0.00 \pm 0.00	4	0	0	0	0	0	0
Subfamily Asteroideae										
Tribe Anthemideae										
<i>Artemisia californica</i> Less., coastal sagebrush ^b	6	0.33 \pm 0.33	0.00 \pm 0.00	6	17	0	0	0	0	0
Tribe Astereae										
<i>Symphoricarum</i> (= <i>Aster</i>) <i>chilense</i> (Nees) Nesom var. <i>chilense</i> , Pacific aster ^b	5	0.00 \pm 0.00	0.00 \pm 0.00	5	0	0	0	0	0	0
Tribe Eupatorieae										
<i>Brickellia californica</i> (Torr. and Gray) Gray, California brickellbush ^b	4	0.35 \pm 0.17	0.00 \pm 0.00	4	75	0	0	0	0	0
<i>Liatis punctata</i> Hook., dotted blazing star ^b	5	0.72 \pm 0.40	0.04 \pm 0.04	4	60	20	0	0	0	0
Tribe Gnaphalaceae										
<i>Pseudognaphalium</i> (= <i>Gnaphalium</i>) <i>californicum</i> (DC.) A. Anderb., ladies' tobacco ^b	6	0.00 \pm 0.00	0.00 \pm 0.00	5	0	0	0	0	0	0
Tribe Helentiaeae										
<i>Eriophyllum staechadifolium</i> Lag., seaside woolly sunflower ^b	7	0.37 \pm 0.20	0.00 \pm 0.00	7	43	0	0	0	0	0
<i>Hemizonia minihornii</i> Jepson, Santa Susana tarweed ^b	4	0.00 \pm 0.00	0.00 \pm 0.00	4	0	0	0	0	0	0
Tribe Heliantheae										
<i>Echinacea purpurea</i> (L.) Moench, eastern purple coneflower ^b	6	0.17 \pm 0.17	0.00 \pm 0.00	6	17	0	0	0	0	0
<i>Helianthus annuus</i> L., common sunflower ^b	4	0.00 \pm 0.00	0.00 \pm 0.00	4	0	0	0	0	0	0
Tribe Inuleae (formerly in Plucheeae)										
<i>Pluchea odorata</i> (L.) Cass., salt marsh fleabane ^b	6	0.13 \pm 0.10	0.20 \pm 0.20	6	33	17	0	0	0	0
Tribe Senecioneae										
<i>Senecio cineraria</i> DC., silver ragwort ^c	8	0.00 \pm 0.00	0.00 \pm 0.00	6	0	0	0	0	0	0
<i>Senecio vulgaris</i> L., old-man-in-the-Spring ^d	4	0.35 \pm 0.35	0.00 \pm 0.00	4	25	0	0	0	0	0
Grade 1 (formerly in Cichorioideae)										
Tribe Mutisieae s.s.										
<i>Trixis californica</i> Kellogg, American threefold ^b	5	0.12 \pm 0.08	0.00 \pm 0.00	5	40	0	0	0	0	0

All plants are in the family Asteraceae. Higher taxonomy is based on Bremer (1994) and Funk et al. (2005).

^a Number of trials for insect development was less than the number of oviposition trials when plants were discarded because of deterioration caused by other factors.

^b Native to North America.

^c Alien ornamental

^d Alien weed

^e Two *S. americana* plants were damaged, but the damage was not consistent with *C. basicorne*. Other plants not infested by *C. basicorne* had similar damage, which was presumably caused by infestation by other insects in the field before entry to quarantine laboratory.

plants require additional choice testing in the laboratory and field to determine risk of infestation under more natural conditions (Smith et al., 2006).

The host plants suitable for *C. basicorne* development correspond to a clearly defined phylogenetic group. Our results indicate that *C. basicorne* is able to develop on a small number of plants within a monophyletic “derived clade” within the subtribe Centaureinae that includes the Jacea, Cyanus and Carthamus groups (Fig. 2). Delineation of this clade is based on nucleotide sequences of ITS nuclear ribosomal DNA and agrees with other morphological characters (Garcia-Jacas et al., 2001); however, the relationships within it are not fully certain because of low bootstrap values (J.F. Gaskin, unpublished data). The clade includes the suitable species: *Ce. solstitialis*, *Ce. melitensis*, *Ce. nigrescens*, *Ce. sulphurea* and *Cn. benedictus* in the Jacea group, *Ce. cyanus* and *Ce. montana* in the Cyanus

group, and *Ca. tinctorius* in the Carthamus group (Garcia-Jacas et al., 2001; J.F. Gaskin, unpublished data). Within this clade, there are no native North American plants, and the only plants of economic interest are *Ca. tinctorius*, a significant crop, and *Ce. cyanus*, an ornamental. The two native North American species, *Ce. americana* and *Ce. rothrockii*, which were not suitable hosts, are in a different clade and have recently been assigned to the genus *Plectocephalus* (Susanna et al., 1995; Hellwig, 2004). *Cr. vulgaris* may be an outlier because it appears to be more distantly related to *Ce. solstitialis* than other groups containing unsuitable plants: *Acroptilon*, *Plectocephalus* and *Psephellus*. Some species within the “derived clade” were not suitable for *C. basicorne* development: *Ce. calcitrapa*, *Ce. cineraria*, *Centaurea diffusa*, and *Centaurea stoebe* (often called *Centaurea maculosa* in North America (Ochsmann, 2001)). So, although the “derived clade” includes almost all

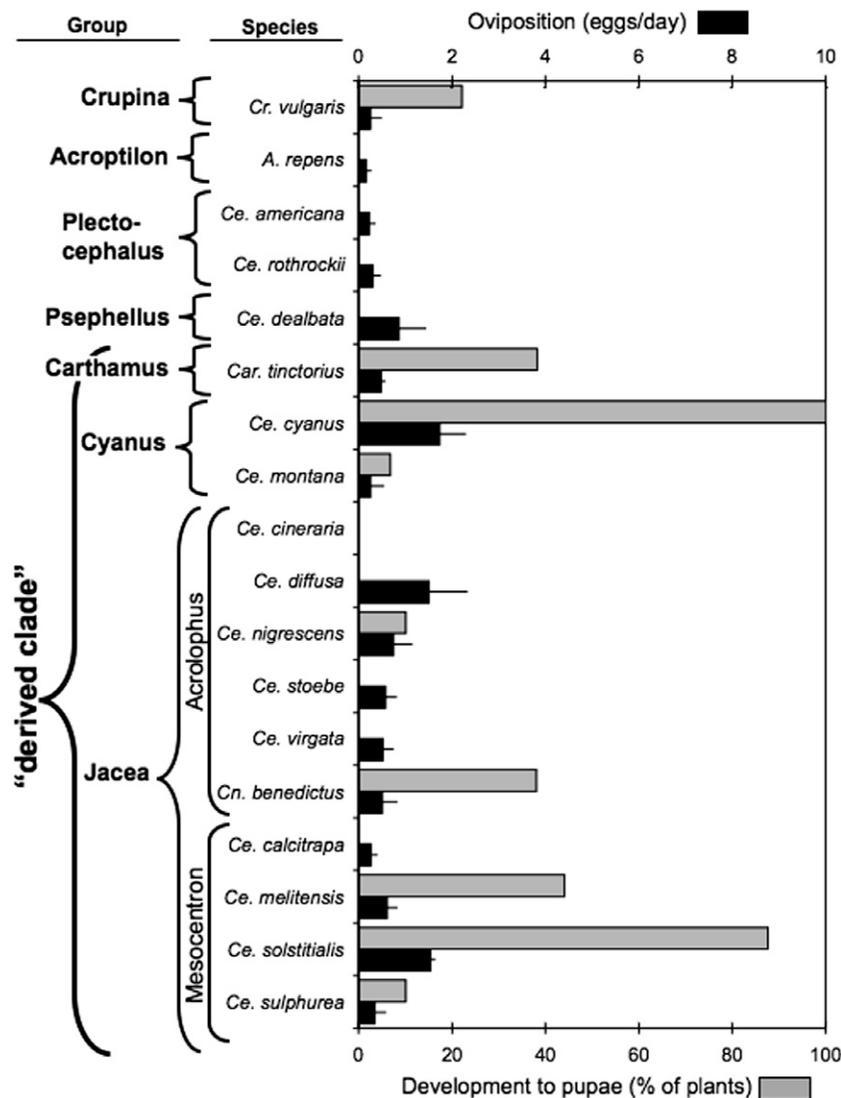


Fig. 2. Suitability of plants within the subtribe Centaureinae to oviposition and larval development by *C. basicorne*. Classification of the species into “groups” is based on plant morphology, pollen type and DNA sequences of introns (Garcia-Jacas et al., 2001; J.F. Gaskin, unpublished data). Oviposition is mean eggs per female per day of exposure to the plant ($\pm 95\%$ CI), and development is percentage of oviposition trials in which at least one insect developed to at least the pupal stage.

species that are suitable, not all species within the clade are suitable. These results confirm that although phylogenetic relationships explain a high degree of host plant specificity, they do not explain all of it. The exceptions presumably are caused by evolutionary divergence of critical characters (e.g., allelochemicals and plant morphology) in close relatives that cause them to be less suitable, and evolutionary convergence in more distant relatives that make them more suitable. Thus, selection of plant species to test should not rely only on phylogeny, as some have proposed (Briese, 2005, 2006), lest we overlook a more distant relative that may be suitable because of similarity of critical characters (e.g., Wheeler, 2005; Haines et al., 2004).

All the reported larval host plants from field collections: *Ce. solstitialis*, *Ce. cyanus*, and *Cn. benedictus* (Alonso-Zarazaga, 1990a; Wanat, 1994; Campobasso et al., 1999; J. Balciunas, unpublished data) were suitable in the laboratory experiments. However, other species that were suitable in the laboratory, such as *Ca. tinctorius*, *Ce. melitensis*, *Ce. sulphurea*, *Ce. nigrescens* and *Ce. montana*, have not been reported as a host in the field. This agrees with current theory that the physiological range, delineated in no-choice laboratory experiments, is broader than the ecological range realized in the field (Briese, 2005; Sheppard et al., 2005). Field experiments conducted in Turkey indicated that *Ca. tinctorius* was not attacked by *C. basicorne*, despite natural infestation of 48–98% of adjacent *Ce. solstitialis* plants (Smith et al., 2006). Thus, *Ca. tinctorius* is not likely to be attacked in the field. Similar experiments have not been done for *Ce. cyanus*, so risk to this species in the field is not well known.

Intensity of adult feeding on leaves was highly correlated to the number of eggs oviposited in test plants ($R^2 = 0.88$, $P < 0.0001$; Fig. 3), probably because adult feeding is necessary for egg development. Adult feeding damage was highest on *Ce. solstitialis* (yellow starthistle), *Ce. cyanus* (bachelor's button) and *Ce. diffusa* Lam. (diffuse knapweed) (Fig. 3 and Table 1). Feeding rate on *Ce. solstitialis* may have been underestimated because (1) exposure was usually for 3 days on cut leaves versus for 5 days on intact plants

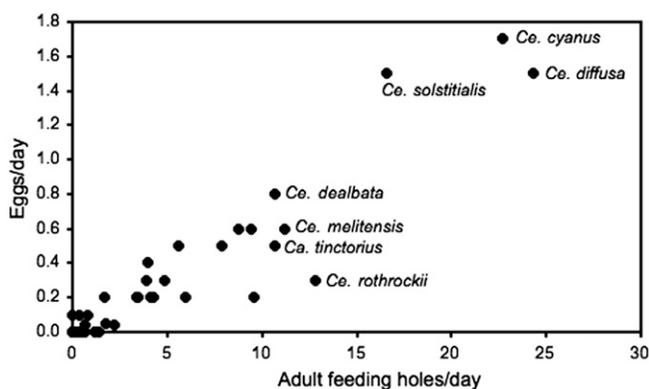


Fig. 3. Relationship of mean number of adult feeding holes (ca. 1-mm²) to mean number of eggs on the different test plant species under no-choice conditions. Each point represents a different test plant species (YST = *Centaurea solstitialis*, safflower = *Ca. tinctorius*).

for nontarget species, and (2) it included the “positive control” trials that followed exposure to nontarget plants, many of which may have negatively affected the insects. There was moderate acceptance of nine other species of *Centaurea*, *Ca. tinctorius* (safflower) and *Cn. benedictus*. Low adult feeding occurred on the other Centaureinae, about half the other Cardueae, and one other species of Cichorioideae (*G. rigens*). There was, at most, only trace feeding on test plants in the subfamily Asteroideae. These results suggest that under extreme conditions *C. basicorne* adults may feed on other species of plants, particularly in the subtribe Centaureinae. Risk of adult feeding damage is generally limited to plants within the tribe Cardueae. Each adult feeding hole is about 1-mm², and they were smaller on most nontarget species. Therefore, adult feeding is not expected to cause any noticeable damage to nontarget species except possibly to *Ce. cyanus* and *Ce. diffusa*.

3.3. Safflower varieties

All nine safflower varieties were susceptible to adult feeding and oviposition under no-choice conditions (Table 2). Adult feeding (7.4–16.2 holes/days) and oviposition (0.3–0.8 eggs/days) rates tended to be lower than on yellow starthistle (16.6 and 1.5, respectively) but are clearly a concern regarding susceptibility of this plant. Larval damage and development to at least the pupal stage occurred in 30–50% of plants tested, depending on variety. There were no significant differences among varieties (χ^2 , $df = 9$, $P > 0.5$), even when varieties with less than ten replicates were excluded from analysis. These results confirm those of Clement et al. (1989) indicating that *C. basicorne* is physiologically able to feed, oviposit and develop on safflower under no-choice laboratory conditions.

3.4. Relationship of host range to *Ceratapion* phylogeny

The genus *Ceratapion* contains 55 species and subspecies, divided among five subgenera: *Acanephodous*, *Ceratapion*, *Clementiellus*, *Echinostroma*, and *Angustapion* (Wanat, 1994). Most speciation occurred in Pliocene–Miocene, with the last events in the Pleistocene Glacial Period (including vicariance of sibling species). Species are distributed almost throughout the entire Palearctic. In general, larvae and adults of species in the genus *Ceratapion* feed only on Asteraceae in the tribe Cardueae (=“Cynareae”) (Alonso-Zarazaga, 1990b). Genera recorded as food plants are: *Arctium*, *Carduus*, *Centaurea*, *Cirsium*, *Cynara*, *Echinops*, *Galactites*, *Onopordum*, *Silybum*, and *Xeranthemum*. Hypotheses of the phylogenetic relationships among species of *Ceratapion* have been proposed by Alonso-Zarazaga (1990a) and Wanat (1994), based on morphological characters (Fig. 4). Species in the subgenus *Echinostroma*, which includes *C. basicorne*, are associated with plants in the genera *Arctium*, *Carlina*, *Carthamus*, *Centaurea* and *Silybum* (Alonso-Zarazaga, 1990a; Wanat, 1994). Larval host plants of *Ceratapion curtii* (Wagner), the closest relative of

Table 2
Physiological suitability of different varieties of safflower to oviposition and development of *Ceratapion basicorne* in a no-choice oviposition experiment

Safflower variety ^a	No. of trials oviposition	Adult feeding holes/day	Eggs/day	No. of trials development	Percentage of trials			
					Adult feeding holes present	Eggs present	Internal plant damage present	Adults or pupae present
CW-88-OL ^b	23	10.7	0.6	10	91	61	50	50
CW-1221	16	16.2	0.4	16	44	63	31	31
CW-4440	16	9.1	0.5	15	38	63	40	40
Gila ^c	10	7.4	0.4	—	80	80	—	—
Hartman ^d	7	—	0.3	7	—	43	43	43
S-345-OL	6	14.8	0.8	6	100	67	50	33
S-400 ^d	2	—	0.3	2	—	100	50	0
S-518-OL	10	8.4	0.4	10	90	50	40	30
S-541 ^d	10	—	0.4	10	—	50	50	50

^a Seed producers: CW, CalWest; S, SeedTec; OL, high oleic oil content.

^b Cut leaves in vials were used in 12 trials of CW-88, for which no development data are available.

^c No development data are available because plants died during malfunction of cooling system.

^d Adult feeding holes were not counted.

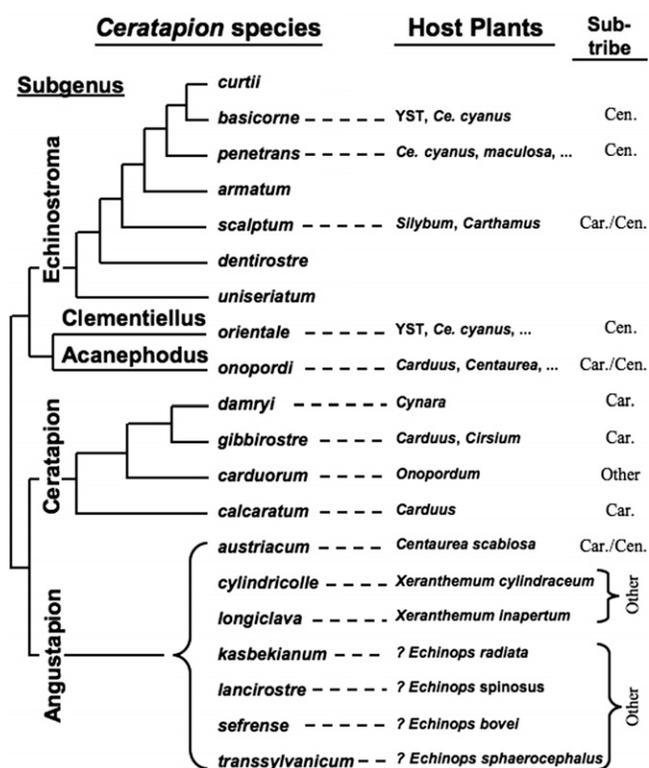


Fig. 4. Phylogenetic relationships among species and subgenera in the genus *Ceratapion* are after Alonso-Zarazaga (1990a) and Wanat (1994). Larval host records are from both authors and Balciunas (unpublished data). Hosts of *C. curtil*, *C. armatum*, *C. dentirostre* and *C. uniseriatum* are unknown. All host plants are in the tribe Cardueae, and subtribe assignments are from Funk et al. (2005). (YST, *Ce. solstitialis*; "...", other Cardueae species; "?", uncertain host plant).

C. basicorne, are unknown. Reported hosts of the next closest relative, *Ceratapion penetrans* (Germar), which has three subspecies, are: *Centaurea rhenana* [= *stoebe*, = *maculosa*, = *paniculata*], *Centaurea jacea*, *Ce. cyanus*, *Ce. diffusa*, *Centaurea nigra*, *Centaurea scabiosa*, and *Ce. solstitialis* (Alonso-Zarazaga, 1990a; Wanat, 1994; Balciunas unpublished data). Older reports of *Arctium lappa* and *Carlina*

vulgaris (Ehret, 1983) as hosts for this species may be mistaken. *Ceratapion scalptum* (Mulsant and Rey), which is also in the same subgenus, has one subspecies that develops on *Carthamus* and another on *Silybum*. Thus, each of the species or subspecies in the subgenus *Echinostroma* appear to develop only on plants within a genus. The historical restriction of evolutionary radiation of species within the genus *Ceratapion* to host plants within the Cardueae, and of species within the subgenus *Echinostroma* to a few genera within the Cardueae, suggests that *C. basicorne* is not likely to ever adapt to host plants outside this tribe. Interestingly, the two species that attack crops, *Cer. scalptum* (Mulsant and Rey) on safflower and *Ceratapion damryi* (Desbrochers) on artichoke (*Cy. scolymus*), are very specific and have never been reported to develop on *Ce. solstitialis* or *Ce. cyanus*. So, conversely, it is not surprising that *C. basicorne*, which is specific to the latter species, does not develop on either of the former species, at least under field conditions (Smith et al., 2006).

The current theories on the phylogeny of species within the tribe Cardueae (Bremer, 1994; Susanna et al., 1995; Garcia-Jacas et al., 2002; Funk et al., 2005) and the genus *Ceratapion* (Alonso-Zarazaga, 1990a; Wanat, 1994) suggest that there is not an overall one-to-one pattern of *Ceratapion* species coevolving with Cardueae species (Fig. 4). For example, *Ceratapion onopordi* appears to be relatively polyphagous, being reported from hosts in six genera from both the Centaureinae and Carduinae (Alonso-Zarazaga, 1990a; Wanat, 1994). The two *Cer. scalptum* subspecies attack different genera in different subtribes (*Carthamus* spp. [Centaureinae] and *Silybum marianum* [Carduinae]), suggesting taxonomically how far a species in this group can jump when adopting a new host. However, most of the species in the subgenera *Echinostroma*, *Clementiellus* and *Acanephodus*, for which host plants are known, use hosts in the Centaureinae (especially *Centaurea* and *Carthamus* species); however, *Silybum* is in the Carduinae. Species in the subgenus *Ceratapion* are associated with Carduinae (*Carduus*, *Cirsium*, *Cynara*, and *Onopordum*), and those in

the subgenus *Angustapion* are generally associated with more basal taxa of the Cardueae (*Echinops*, *Xeranthemum*), but one species is associated with *Ce. scabiosa*.

Although all *Ceratapion* species are restricted to plants in the tribe Cardueae, they vary in their degree of host plant specificity. Because all species within the subgenus *Echinostroma* are only known to develop on plants in the Centaureinae and Carduinae, it appears that *C. basicorne* and its recent ancestors have been specializing on these host plants for a long time. This suggests that host plant specificity is deeply ingrained and that the insect is not likely to drastically change its host range. Thus, it appears that if *C. basicorne* were to adopt a new host after being released in North America, it would most likely be a close relative of *Ce. solstitialis* and *Ce. cyanus*. The closest native species are *Ce. americana* and *Ce. rothrockii*, but they are so distantly related as to be considered in a different genus (*Plectocephalus*), and they were not able to sustain larval development in our no-choice experiments. Therefore, it seems improbable that the insect could adapt to developing on any native North American species in the foreseeable future.

4. Conclusions

The no-choice results indicate that no plant species outside the subtribe Centaureinae are at risk of significant larval damage. Although adult feeding on foliage and oviposition occurred on many nontarget plants under no-choice conditions, they were at much lower rates than on *Ce. solstitialis*, *Ce. cyanus* and *Ce. diffusa*. Under choice conditions, the nontarget attack rates would be expected to be lower. Because *C. basicorne* is synovigenic, and must feed to continue producing eggs, absence of its preferred host plant would probably reduce egg production and consequently the risk of oviposition on nontarget plants. The oviposition rates that we observed on nontarget plants are probably elevated because of feeding on *Ce. solstitialis* prior to exposure to each nontarget test plant. Nontarget plants that supported oviposition and larval development warrant further evaluation under choice conditions to further assess the degree to which they are at risk. These include the two cultivated species: *Ca. tinctorius* (safflower) and *Ce. cyanus* (bachelor's button), and the native North American species: *Ce. americana*, *Ce. rothrockii*, *Ci. loncholepis* and *S. americana*. Larval damage to *Acroptilon repens*, *Cn. benedictus*, *Cr. vulgaris* and the other *Centaurea* species is acceptable because are all alien noxious weeds in North America.

Successful development of an insect on a crop in laboratory experiments is usually sufficient to discourage further evaluation of it as a biological control agent. However, the absence of field records of *C. basicorne* developing on safflower, despite records of its close relative, *Cer. scalptum*, on this plant, suggest that risk to safflower under field conditions may be insignificant. Only by conducting further choice experiments under laboratory or field conditions can we improve our estimation of this risk. Field trials that were

conducted at sites with natural populations of *C. basicorne* in Turkey showed no larval development on safflower by *C. basicorne* (Smith et al., 2006). However, three other insects did develop on safflower: *Cer. scalptum*, *Ceratapion orientale*, and *Ceratapion onopordi*. Therefore, if *C. basicorne* is approved for release, it will be important to correctly identify all specimens to prevent accidental introduction of any of these species. Taxonomic keys with detailed illustrations have been developed to assist proper identification of *C. basicorne* (J.K. Balciunas and B.A. Korotyaev, unpublished manuscript).

Centaurea cyanus (bachelor's button) is at risk of adult feeding, oviposition and larval damage. This plant has previously been reported as a host of *C. basicorne* in its native range in Eurasia, but the frequency of such attack has not been studied. The plant is both an ornamental and an invasive weed in parts of North America. The developing larva causes a small swelling of the stem at the base of the petiole down which it tunneled. Although this may cause cosmetic damage to the ornamental, it is not known how frequently this may occur, especially when the plant is grown as an intensively managed monoculture. Because this plant is an invasive weed in some regions of the western US, damage to it in rangeland habitats would be beneficial.

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