18 Musk Thistle (Nodding Thistle)

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PEST STATUS OF WEED

Musk thistle, *Carduus nutans* L., is an invasive weed that has become widespread in the contiguous states of the United States. It is a highly competitive weed of Eurasian origin that has replaced much of the native vegetation in pastures and disturbed areas (Surles et al., 1974; Kok, 1978a,b).

Nature of Damage

Economic damage. Musk thistle invades pastures, rangeland, and forest lands, and areas along roadsides, railroad right-of-ways, waste areas, and stream banks. In agricultural systems, the invasive nature and prolific seed production of musk thistle result in large populations of the weed, which compete with crops for space, nutrients, and light. Thus, infestations may reduce productivity of pasture and rangeland by suppressing growth of desirable forage plants, as well as preventing livestock from eating plants growing in the vicinity of thistles due to the sharp spines on their stems, leaf margins and blooms (Trumble and Kok, 1982; Desrochers *et al*., 1988a). In the northeastern United States, the highest economic losses due to musk thistle infestations occur on fertile soils formed over limestone.

Ecological damage. Musk thistle generally does not pose a great threat to high-quality natural areas, although it has been known to invade native and restored grasslands despite the presence of dense, native prairie vegetation. Musk thistle may retard natural secondary succession processes. Because musk thistle is unpalatable to wildlife and livestock, selective grazing leads to severe degradation of native meadows and grasslands as grazing animals focus their foraging on other plants, giving musk thistle a competitive advantage. Successful biological control of musk thistle (Kok and Surles, 1975) is often accompanied by increased growth and coverage of pasture grasses such as fescue (*Festuca arundinaria* Schreb.) and orchard grass (*Dactylis glomerata* L.), or less desirable plants such as spotted knapweed (Kok and Mays, 1991).

Extent of losses. The rate of expansion of musk thistle populations in North America has been very rapid since the mid-1950s, when it was first recognized as a weed (Dunn, 1976). A single musk thistle per 1.49 m^2 can reduce pasture yields by 23%. In Canada, stands of 150,000/ha have been observed (Desrochers *et al*., 1988a). Direct losses are difficult to quantify due to lack of long-term monitoring programs and data.

Geographical Distribution

Musk thistle was first reported in the United States in 1953 at Harrisburg, Pennsylvania (Stuckey and Forsyth, 1971). In the 1970s, the musk thistle complex (see Taxonomy for definition) has been found in at least 3,068 counties in 42 of the mainland states, with 12% of those counties rating their infestations as economically severe (Dunn, 1976). Musk thistle is declared a noxious weed in some 20 states, including Illinois, Iowa, Kansas, Kentucky, Maryland, Minnesota, Missouri, Nebraska, North Carolina, Ohio, Oklahoma, and Pennsylvania (USDA, NRCS, 1999). Thus, musk thistle extends from the east to west coast in both the deciduous forest and prairie biomes. It grows from sea level to about 2,500 m elevation. It prefers moist alluvial soils but will grow in eroded uplands without difficulty.

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The *C. nutans* complex in North America has been treated either as one species with four subspecies (subsp. *nutans*, subsp. *leiophyllus* [Petrovic] Stoj. and Stef., subsp. *macrolepis* [Peterm.] Kazmi, and subsp. *macrocephalus* [Desf.] Nyman), or as three species: *Carduus nutans* with two subspecies (subsp. *nutans* and subsp. *macrolepis*), *C. thoermeri* Weinm., and *C. macrocephalus* Desf. (McCarty, 1978; Desrocher *et al.*, 1988b). Recent work by Desrochers *et al.* (1988b) has supported the existence, in Canada, of only two closely related groups of taxa referred to as subsp. *nutans* and subsp. *leiophyllus*. *Carduus thoermeri* Weinm. and *C. nutans* subsp. *leiophyllus* refer to the same taxon. In North America, *C. nutans* ssp. *macrocephalus* has only been collected from the United States. *Carduus nutans* ssp. *nutans* is distinguished from ssp. *leiophyllus* by its moderate to dense pubescence on leaves and phyllaries, by its generally smaller head diameter (1.5 to 3.5 cm in subsp. *nutans* and 1.8 to 4.5 cm in subsp. *leiophyllus*) and by the shape of its phyllary. In subsp. *nutans*, the lower portion of the phyllary is more or less equal to the upper portion, while in subsp. *Leiophyllus,* the lower portion is distinctly narrower than the upper portion. The two subspecies also can be separated by their flavonoid compounds. *Carduus nutans* subsp. *macrocephalus* differs from subsp. *nutans* by a wider head diameter and phyllaries. It also differs from subsp. *leiophyllus* by being pubescent on leaves and phyllaries, and by having phyllaries that have the lower portion more or less equal to the upper portion. Hybridization between *C. nutans* and *Carduus acanthoides* L. also has been reported (Warwick *et al.*, 1990). Presumably, the distribution of subsp. *nutans* in the United States is similar to its distribution in Canada, where it is mainly distributed in the eastern part of the country, while only subsp. *leiophyllus* and subsp. *macrocephalus* are present in the Great Plains (McGregor, 1986).

Figure 1. Musk thistle rosette. (Photograph by L.-T. Kok.)

Figure 2. Musk thistle in bloom. (Photograph by L.-T. Kok.)

Biology

The biology of musk thistle has been reviewed by Desrochers *et al*. (1988a). *Carduus nutans* L. is a herbaceous biennial though occasionally it becomes a winter annual. It is 20 to 200 cm tall, with a long, fleshy taproot. The taproot is large, corky, and hollow near the surface of the ground. One or more highly branched stems grow from a common rootcrown. Musk thistle grows in all soil textures, although the soils must be well drained. Leaves are dark green with light green midribs with a white margin (Fig. 1). The plant blooms in May and June. The showy flowers (Fig. 2) are terminal, large, solitary, and nodding (slightly bent). They are deep rose to violet or purple in color. The seeds are straw colored and do not have a light requirement for germination, but are affected by temperature. Higher germination rates occur at temperatures between 20 and

28 °C. Musk thistle does not appear to have any specific climatic requirements other than a cool period of vernalization, a minimum of 40 days below 10 °C for flowering. It does not reproduce vegetatively and is propagated by seeds dispersed primarily by wind. Most seeds are deposited within 50 m of the release point and less than 1% are blown farther than 100 m (Smith and Kok, 1984). Up to 11,000 achenes may be produced per individual with as many as 1,500 seeds per flower head. Seed viability remains high for more than ten years.

Analysis of Related Native Plants in the Eastern United States

There are no native North American species in the genus *Carduus*. *Carduus nutans* belongs to the tribe Cardueae (family Asteraceae) which is largely an Old World group. The tribe is further divided into four subtribes (Echinopsidinae, Carlininae, Carduinae, and Centaureinae) including some 13 genera in North America (Bremer, 1994; USDA, NRCS, 1999). From these, only three contain native species – *Centaurea* (two species, subtribe Centaureinae), *Saussurea* (seven species, subtribe Carduinae, but the position of the genus in the tribe remains uncertain), and *Cirsium* (subtribe Carduinae). The genus *Cirsium* includes about 100 native species, of which 21 species occur in the eastern United States. One of these, *Cirsium pitcheri* (Torr. ex Eat.) Torr. and Gray, is listed as threatened under the Endangered Species Act. This species occurs in sand dunes along the shores of the Great Lakes in Illinois, Indiana, Michigan, Wisconsin, and Ontario.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Musk thistle was among the first 19 weeds selected for biological control when the USDA overseas laboratory was established at Rome, Italy in 1959. In the early 1960s, staff of the USDA intensively surveyed *Carduus* spp. in Italy, whereas the Commonwealth Institute of Biological Control (now CABI Bioscience), funded by Canada Department of Agriculture, extended the survey area across Europe from western France to eastern Austria on more than 30 species in the subtribe Carduinae. The history of biological control of thistles was reviewed by Dunn (1978) and by Schroeder (1980).

Area of Origin of Weed

The genus *Carduus* is native to the Eastern Hemisphere, where its distribution extends over Europe, central Asia, and East Africa. Franco (1976) recognized 48 species in *Flora Europaea.* Several taxa have been reported in North America and separated into three groups: the slender-flowered thistles (*Carduus tenuiflorus* Curt. and *Carduus pycnocephalus* L.), the small-flowered thistles (*Carduus acanthoides* L. and *Carduus crispus* L.), and the large-flowered thistle (*Carduus nutans s.l.*). Southern Europe is considered to be the center of origin for *Carduus* because of the many endemic *Carduus* species found there.

Areas Surveyed for Natural Enemies

Areas surveyed included southern England, France, Austria, Germany, Italy and the northern part of the former Yugoslavia (Zwölfer, 1965; Boldt and Campobasso, 1978). Other surveys have been carried out in Pakistan, Iran, and Japan (Schroeder, 1980).

Natural Enemies Found

Some 130 insect species have been recorded on *C. nutans s.l.* in Europe (Zwölfer, 1965; Boldt and Campobasso, 1978). In Italy alone, 109 species from six orders and 33 families fed or reproduced on musk thistle. Some 25 species were reported to be broadly oligophagous on plants in the subtribe Carduinae (Table 1), and only very few were considered to have a host range restricted to plants in the genera *Carduus*, *Cirsium*, and *Silybum*, or to be monophagous. Since there was no concern about non-target impact on native thistles in the earliest phase of the program, oligophagy on several thistle species in the genera *Carduus*, *Cirsium*, and *Silybum* was considered as an advantage and only those species recorded as economic pests were eliminated from further consideration. After a few other candidate biological control agents had been discarded on the grounds that they did little damage to the target weeds, fewer than 10 species were considered as potential biological control agents of *Carduus* species and bull thistle, *Cirsium vulgare* (Savi) Tenore. Preference was given to seed-

Table 1. Oligophagous Arthropods (Restricted to Carduinae) Recorded on Selected European Thistles (With Contributions from A. McClay)

Insect Species	*Carduus nutans s.l.*	*Carduus acanthoides*	*Carduus tenuiflorus/ pycnocephal-us*	*Cirsium vulgare*	*Cirsium arvense*	Food Niche
DIPTERA						
Agromyzidae						
Agromyza n.sp.nr. reptans	b					Leaf miner
Liriomyza soror Hendel					a	Leaf miner
Melanagromyza aeneoventris (Fallen)	d	d		d	d	Stem
Phytomyza cardui Hering				a		Leaf miner
Anthomyiidae						
Pegomya nigricornis (Strobl)			c			Stem?
Cecidomyiidae						
Clinodiplosis cirsii Kieffer					a	Flower head
Jaapiella cirsiicola Rübsammen				a	a	Flower head
Macrolabis cirsii Rübsammen					a	Flower head
Syrphidae						
Cheilosia albipila (Meigen)	d	d		d	d	Root collar
C. corydon (Harris)	b released		c released			Root collar
C. cynocephala Loew	b					Root collar
Tephritidae						
Orellia winthemi Meigen		a				Flower head
Tephritis hyoscyami L.	a	a				Flower head
T. cometa (Loew)					a	Flower head
Terellia serratulae L.	a b (1)	a	a c	a		Flower head
T. ruficauda Fabricius					a (2)	Flower head
Urophora cardui (L.)					a d released	Stem gall
U. sibynata Rondani	b					Flower head
U. solstitialis (L.)	a b released	a released	c			Flower head
U. stylata Fabricius	b	a		a released	a	Flower head
Xyphosia miliaria Schrank	a b			a	a	Flower head

Table 1. Oligophagous Arthropods (continued)

Insect Species	*Carduus nutans s.l.*	*Carduus acanthoides*	*Carduus tenuiflorus /pycnocephal-us*	*Cirsium vulgare*	*Cirsium arvense*	Food Niche
COLEOPTERA						
Apionidae						
Apion carduorum Kirby	a b	a	a	a	a	Root collar/stem
A. gibbirostre Gyllenhal	d	d			d	Root collar/stem
A. onopordi Kirby	d			d	d	Root collar/stem
Curculionidae						
Ceuthorhynchidius horridus (Panzer)	a released	a released	c		a	Root collar/stem?
C. urens Gyllenhal					a	Root collar/stem?
Ceutorhynchus litura Fabricius					a d released	Root collar/stem
C. trimaculatus Fabricius	a b (1)		a c	d		Root collar/leaf buds
Cleonus piger Scopoli	a	a		a	a (2)	Root collar/ stem
Larinus cynarae Fabricius	b					Flower head
L. jaceae Fabricius	a	a	c			Flower head
L. planus (Fabricius)	a	a	a	a	a (2)	Flower head
L. turbinatus Gyllenhal				a	a	Flower head
Lixus cardui Olivier	a b	a	a c		a	Stem
L. elongatus Goeze	a b d	a d	a c	a d	a	Stem
Rhinocyllus conicus Frölich	a b released	a released	a c released	a	a	Flower head
Cerambycidae						
Agapanthia dahli Richter		d				Stem
Chrysomelidae						
Altica carduorum Guérin-Méneville					a released	Leaf
A. cirsii Israelsen					a	Leaf
Cassida deflorata Suffrian			a c		a	Leaf
C. rubiginosa Müller	a b		a	a	a (2)	Leaf
Lema cyanella (L.).					a (1)	Leaf
Psylliodes chalcomera (Illiger)	b released		c			Leaf buds/leaf
Sphaeroderma testaceum Fabricius	a b			a	a	Leaf

Table 1. Oligophagous Arthropods (continued)

Insect Species	***Carduus nutans s.l.***	***Carduus acanthoides***	***Carduus tenuiflorus /pycnocephal-us***	***Cirsium vulgare***	***Cirsium arvense***	**Food Niche**
LEPIDOPTERA						
Cochylidae						
Aethes badiana Hübner				a		Root/stem?
A. cnicana Westwood				a		Root/stem?
Lobesia fuligana Haworth					a	Stem
Noctuidae						
Gortyna flavago Den. & Schiff.		d				Root
Porphyrinia purpurina Den. & Schiff.	b			a	a	Root crown/stem
Olethreutidae						
Epiblema pflugiana (Haworth)	b					Root crown/leaf
Pyralidae						
Myelois cribrumella (Hübner)	d	a		d		Stem/flower head
Sesiidae						
Euhagena palariformis (Lederer)					f	Root
HETEROPTERA						
Lygaeidae						
Tingis ampliata Herrich-Schäffer				a	a	Leaf
T. cardui L.	a b	a	a	a	a	Leaf

Table 1. Oligophagous Arthropods (continued)

Insect Species	*Carduus nutans s.l.*	*Carduus acanthoides*	*Carduus tenuiflorus /pycnocephal-us*	*Cirsium vulgare*	*Cirsium arvense*	Food Niche
HOMOPTERA						
Aphididae						
Aphis acanthi Schrank					a	?
Brachycaudus cardui (L.)	b g			g	g (2)	Leaf/stem/ root
Capitophorus braggi Gyllenhal					a (2)	Leaf/stem
C. carduinus Walker	a g (2)	a		a g	g (2)	Leaf/stem
C. flaveolus Walker		a			a	?
Chomaphis cirsii Börner					a	?
Dactynotus aeneus HRL.	a g	a			g	Leaf/stem
*D. cirsi*i HRL					a g (2)	Leaf/stem
Psyllidae						
Trioza agrophila Loew					a	?
ACARINA						
Eriophyidae						
Aceria anthocoptes (Nalepa)					e (2)	Flower/leaf

a = from Zwölfer (1965) and Zwölfer and Harris (1984). Survey area: s-England, France, s-Germany, Austria, northern former Yugoslavia, n-Italy
b = from Boldt and Campobasso (1978). Survey area: Italy
c = from Goeden (1974) and Dunn (1978). Survey area: Italy and Greece
d = from Freese (1993). Survey area: Germany
e = from Petanovic *et al*. 1997. Survey area: Yugoslavia
f = from Tosevski (pers. com). Survey area: Turquey
g = from Redfern (1983). Survey area: western Europe
(1) studied but not released in the United States
(2) accidental introduction in the United States (from Maw, 1976; Story et al., 1985; Julien and Griffiths, 1999 ; http://www.sel.barc.usda.gov/acari/content/eriophyoidea.html)

feeding insects for biological control of *Carduus* spp. and bull thistle because these weeds are short-lived species and reproduce by seeds. In contrast, defoliating beetles were selected for the perennial thistle *Cirsium arvense* (L.) Scop. (see Chapter on Canada thistle).

In 1964, the seed-feeding weevil *Rhinocyllus conicus* (Frölich) was the first insect selected for biological control of *Carduus* species. Zwölfer (1971) believed that because of *R. conicus*' high egg potential and a tendency to disperse its eggs, this weevil should exert strong pressure on its host plant, especially after the weevil was released from limitation by its coevolved competitors and parasitoids. Shortly after biological studies had started with *R. conicus*, the rosette weevil *Trichosirocalus horridus* (Panzer) and the two rosette beetles *Ceutorhynchus trimaculatus* (F.) and *Psylliodes chalcomera* (Illiger) also were considered because they occupy different food niches and have different phenologies. Concern about non-target impact was increasing and, in the early 1980s, permission for field release of *C. trimaculatus* and *P. chalcomera* was denied. Consequently, more specific species were selected to complement the impact of *R. conicus* and *T. horridus.* The syrphid root-crown fly *Cheilosia corydon* (Harris) has the same feeding niche as *T. horridus* but it has a different phenology. The seed-feeding tephritid fly *Urophora solstitialis* (L.) was selected for biological control of *C. acanthoides* because *R. conicus* was not well synchronized with this thistle in many parts of North America (Surles and Kok, 1977). Later, Dunn and Campobasso (1993) showed that native North American *Cirsium* species were not exploited by *P. chalcomera* under field test conditions, and this flea beetle was finally released in the United States in 1997. Thistle insects discovered in Asia have not been exploited yet. The host specificity of *Terrelia serratulae* L., a trypetid fly from Pakistan, has been examined (Baloch and Khan, 1973), but it has not been considered further.

Host Range Tests and Results

***Rhinocyllus conicus* (Frölich).** Field host records for the seed-feeding weevil *R. conicus* in Europe include thistles in several genera in the subtribe Carduinae (*Carduus, Cirsium, Sylibum*, and *Onopordum*)(Zwölfer and Harris, 1984). The plant species tested in the screening trials in the 1960s included primarily agricultural crops and horticultural species in the Asteraceae family, plus a few European thistles. Since the cultivated plants tested (*Cynara scolymus* L., *Carthamus tinctorius* L., *Helianthus annuus* L., *Lactuca sativa* L.) were not used by the weevil, and the potential use of native North American *Cirsium* species was not a concern at that time, *R. conicus* was approved and released in Canada (in 1968) and in the United States (in 1969). Feeding by *R. conicus* on native Cirsium species in North America was first reported by Laing and Heels (1978) and Rees (1978). *Rhinocyllus conicus* has been reported in flowerheads of nearly 20 native *Cirsium* spp. in the west and in the central plains and mountains (Louda, 2000). Genetic variation among populations of *R. conicus* does exist, but its role in host plant use is not well understood. The concept of host races associated with the main thistle species in Europe (Zwölfer and Preiss, 1983) has been challenged recently (Klein and Seitz, 1994; Briese, 1996).

***Trichosirocalus horridus* (Panzer).** Field records of the rosette weevil *T. horridus* in Europe include a few genera in the subtribe Carduinae (*Carduus*, *Cirsium*, *Onopordum,* and *Galactites*). Host range studies were carried out in the late 1960s and early 1970s (Ward *et al.*, 1974; Kok, 1975). As for *R. conicus*, the plant species tested included cultivated plants and a few European thistles. Some larval feeding occurred on lettuce (*L. sativa*), cauliflower (*Brassica oleracea* L.) and artichoke (*C. scolymus*), but none of these species supported normal larval development. Preferred hosts were species of *Carduus*, *Cirsium,* and *Onopordum*. *Trichosirocalus horridus* has only occasionally been reported to feed and develop on native North American thistles (McAvoy *et al*., 1987).

***Cheilosia corydon* (Harris).** In Europe, the root-crown fly *C. corydon* has been reared from *Carduus nutans s.l.*, *Carduus crispus* L., and *Carduus pycnocephalus* L., and rarely from *Cirsium vulgare*, *Cirsium eriophorum* (L.) Scop., and *Cirsium palustre* (L.) Scop. In laboratory tests, larvae survived on all six *Carduus* species tested as well as on the native North American species, *Cirsium crassicaule* (Greene) Jeps. None of the other nine *Cirsium* species (including six native North American species) were suitable for *C. corydon* development. In field trials in Italy, oviposition was recorded on *Carduus nutans* but not on the seven native *Cirsium* species tested (Rizza *et al*., 1988).

***Ceutorhynchus trimaculatus* (Fab.).** Field records of this thistle-rosette weevil in Europe include

Carduus spp., *Cirsium* spp., *Onopordum* spp., *Silybum marianum* (L.) Gaertn., and *Galactites tomentosa* Moench (Boldt *et al*., 1980). *Ceutorhynchus trimaculatus* was found to complete development on artichoke (*C. scolymus*) and several *Cirsium* species in quarantine screening tests (Kok *et al*., 1979, 1982; Kok and McAvoy, 1983). In field tests carried out in Italy in 1984 and 1985, larvae of *C. trimaculatus* were found on all three North American native *Cirsium* spp. exposed, but not on artichoke (Dunn and Campobasso, 1993).

Psylliodes chalcomera **(Illiger).** Under experimental conditions, adult feeding, oviposition, and larval development by this thistle-rosette weevil occurred on European *Carduus* and *Cirsium* species (Dunn and Rizza, 1977). Adult feeding and oviposition, but no larval development, were recorded on artichoke under no-choice conditions. In field tests carried out in Italy between 1987 and 1989, this flea beetle did not use any of the three North American *Cirsium* species offered (Dunn and Campobasso, 1993).

Puccinia carduorum **Jacky.** This rust has been accidentally introduced to North America and also was the first plant pathogen tested and released in the United States for biological control of musk thistle. In greenhouse tests, limited infection occurred on some species of *Cirsium*, *Cynara*, *Saussurea*, and *Sylibum*, but older plants were resistant. Attempts to maintain *P. carduorum* on 22 native North American species of *Cirsium* and *C. scolymus* failed. Musk thistle was the only host that became severely diseased (Politis *et al*., 1984; Bruckart *et al*., 1996). No rust development was observed on any of the nontarget plants (10 North American *Cirsium* spp. and artichoke) in a field trial carried out in 1988 in Virginia (Baudoin *et al*., 1993). *Puccinia carduorum* has not been reported from native North American *Cirsium* species. It has spread rapidly in the eastern United States and was found in Missouri in 1994 (Baudoin and Bruckart, 1996). It can be transmitted by the thistle insects *R. conicus, T. horridus,* and *Cassida rubiginosa* Müller (Kok and Abad, 1994).

Releases Made

Information in this section is from Rees *et al*., 1996; Julien and Griffiths, 1999; and shipment records of L. T. Kok.

Rhinocyllus conicus. Introductions of *R. conicus* from eastern France via Canada began in 1969 in the United States with releases in Virginia, California, Montana, and Nebraska. Following excellent results in Virginia, weevils were collected in Virginia and released in most of the thistle-infested 48 contiguous states. These included Alabama, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Minnesota, Missouri, New Jersey, New York, Ohio, Oklahoma, Pennsylvania, Tennessee, Texas, West Virginia, and more recently in the southern states of Alabama, Georgia, and North Carolina.

Trichosirocalus horridus. This species was first released in Virginia in 1974 (Kok and Trumble, 1979). Weevils collected from Virginia were subsequently released in many other states, including Alabama, Colorado, Georgia, Illinois, Indiana, Kansas, Kentucky, Maryland, Montana, North Carolina, Oklahoma, Tennessee, Texas, Washington, Wyoming, several western states, and also in Argentina and Canada.

Cheilosia corydon. This fly has been released in low numbers in Maryland, New Jersey, Montana, Nevada, Oregon, and Texas.

Urophora solstitialis. This species was released in 1996, only in Montana.

Ceutorhynchus trimaculatus: This species was not released because it feeds and develops on native *Cirsium* species (Kok *et al*., 1979, 1982; Kok and McAvoy, 1983).

Psylliodes chalcomera. This species was released in 1997, in Kansas and Texas (DeQuattro, 1997).

Puccinia carduorum. This pathogen was deliberately introduced in Virginia in 1987 (Baudoin *et al*., 1993), but had been accidentally introduced to North America before 1987 (Julien and Griffiths, 1999).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

Rhinocyllus conicus (Coleoptera: Curculionidae).

The biology of this seed-feeding weevil has been described by Zwölfer and Harris (1984). Following adult emergence from overwintering sites in litter and sheltered areas, mating and oviposition occur in spring and early summer. In Virginia, overwintered adult weevils (Fig. 3) were observed to become active in mid-to-late April (Surles and Kok, 1977). Eggs are laid externally on bud bracts (Fig. 4), either individually or in small clusters of two to five eggs. Caps

Figure 3. *Rhinocyllus conicus* adult. (Photograph by L.-T. Kok.)

Figure 4. *Rhinocyllus conicus* eggs on thistle head. (Photograph by L.-T. Kok.)

Figure 5. *Rhinocyllus conicus* larva feeding on receptacle of thistle head. (Photograph by L.-T. Kok.)

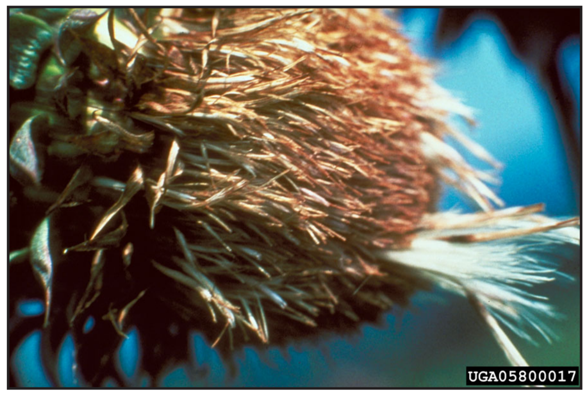

Figure 6. Tufts of hair arising from *R. conicus* infested thistle head. (Photograph by L.-T. Kok.)

Figure 7. *Rhinocyllus conicus* pupa. (Photograph by L.-T. Kok.)

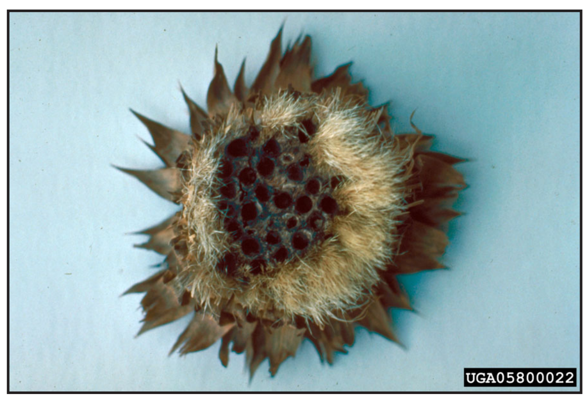

Figure 8. Thistle head showing pupation chambers of *R. conicus.* (Photograph by L.-T. Kok.)

of masticated host plant material, which appear as "warts," cover and protect the eggs from predation. Larvae hatch after six to nine days and bore through the bracts into the receptacle. Larvae feed on both the developing receptacles (Fig. 5) and the florets, pushing out characteristic tufts of hair from an infested head (Fig. 6), and sometimes the supporting peduncle under the head. Four larval instars complete development in about four to six weeks (Rowe and Kok, 1985). Larval feeding induces the formation of a gall-like callus of modified parenchyma tissue that provides the larvae with additional food and shelter (Shorthouse and Lalonde, 1984). Larval survivorship is strongly density-dependent, suggesting intraspecific competition causes much of the observed larval mortality (> 80%) within heavily infested inflorescences (Zwölfer, 1979). In North America, *R. conicus* has acquired a large number of parasitoids, but levels of parasitism are low (Rees, 1977; Goeden and Ricker, 1977, 1978; Puttler *et al*., 1978; Dowd and Kok, 1981, 1982, 1983; Smith and Kok, 1983). The pupal period is seven to 10 days, and pupae (Fig. 7) usually are found from mid-June through July. A partial second generation may be found in late August and September. Adults usually remain within pupation cells (Fig. 8) for several more weeks, before emerging to disperse to overwintering sites in litter. Phenology and life-cycle details vary geographically according to local climate. Zwölfer and Harris (1984) indicated that a partial second generation could occur for individuals that complete development early, if the photoperiod exceeds 16 hours.

Trichosirocalus horridus (Coleoptera: Curculionidae).

This rosette weevil has a single generation per year. Eggs are laid on the lower side of leaves along the midrib and the primary veins and hatch in about 13 days. Larvae migrate down the petiole to rosette crowns to feed soon after hatching. Mature larvae abandon the plant and enter the soil near the roots where they create pupation cells, made from silk and soil particles (Kok *et al*., 1975). In Virginia, oviposition occurs from mid-December until early April, and larvae are found in rosettes from late December (first instars) through late May (third instars) (Trumble and Kok, 1979). *Trichosirocalus horridus* may overwinter as an adult, egg, or larva (Kok and Mays, 1989). Teneral adults appear from mid-May through June and aestivate in July through September. This life cycle is similar to that of *T. horridus* in southern Europe, although the climatic conditions in southwestern Virginia resemble conditions of central Europe, where the life history of *T. horridus* is substantially different. In central Europe, oviposition of *T. horridus* occurs from the middle of May through June. Pupation occurs in July and August, and adults emerge in September and overwinter.

Cheilosia corydon (Diptera: Syrphidae)

In southern Europe, adults of this root-crown fly emerge at the end of February or March, and eggs are laid from mid-March to mid-April. Larvae feed in thistle crowns and large flower-bearing stems. Eggs are laid on young leaves in the center of the thistle rosette and young shoots. Newly hatched larvae mine directly into tender, young shoots. As shoots grow, the second and third instars mine up and down the stems. There are three larval instars. In May, larvae tunnel into the shoot base and the root. Pupation occurs in November (Rizza *et al*., 1988). *Cheilosia corydon* has one generation per year.

Ceutorhynchus trimaculatus (Coleoptera: Curculionidae)

This rosette weevil has one generation per year. Adults emerge at the end of April and feed on the leaves of new rosettes or mature plants for three to four weeks. At the end of May, weevils enter the soil to aestivate. Adults gradually become active again in autumn and feed on the leaves of young rosettes. Oviposition starts in November and continues through March or April. Larvae feed gregariously, boring into leaf buds or growing tips, and moving down into the crown. Pupation occurs in the soil (Boldt and Campobasso, 1981; Kok and McAvoy, 1983).

Psylliodes chalcomera (Coleoptera: Chrysomelidae)

In southern Europe, adults of this thistle-rosette flea beetle emerge in early June, feed heavily on maturing *Carduus* plants, and begin aestivation during late June. Aestivation ends in early November. Oviposition takes place between January and June. Eggs are laid at the base of plants or into soil adjacent to plants. Larvae feed on leaf buds and on young rosette leaves. Larvae mature in mid-May, and pupate in the soil nearby. In the laboratory, some females are long-lived and go through two aestivation and two oviposition periods (Dunn and Rizza, 1976).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents (from Julien and Griffiths, 1999)

Rhinocyllus conicus. Establishment of this seed-feeding weevil has been confirmed in Iowa, Illinois, Kansas, Kentucky, Maryland, Minnesota, Missouri, North Dakota, South Dakota, Pennsylvania, Tennessee, Texas, New York, and Virginia as well as in several western states. In recent years, it also has become established in the southern states of Georgia (Buntin *et al.*, 1993) and North Carolina (McDonald and Robbins, 1993). In Virginia, dispersal was only 1.6 km three years after release, but after six years, both eggs and adults were detected 32 km from the original release site (Kok and Surles, 1975).

Trichosirocalus horridus. Establishment of the rosette weevil was confirmed within two years of its release in Virginia study sites, and weevil populations had reached high levels by the third year. The weevil was found 27 km from release sites four years after initial introduction. By 1981, *T. horridus* was well established in the immediate release area and covered approximately 609 km^2. By 1985, the weevil had extended its range to 4,345 km^2 despite having had to move across forested areas where no thistles occur as well as areas with low thistle populations. Dispersal by flight probably occurs after aestivation during late summer or early fall (McAvoy *et al.*, 1987). *Trichosirocalus horridus* also is established in North Carolina (McDonald and Robbins, 1993), Kansas, Maryland, Missouri, and several western states.

Cheilosia corydon. Establishment has not been confirmed.

Urophora solstitialis. Establishment has not been confirmed.

Psylliodes chalcomera. Establishment has not been confirmed.

Puccinia carduorum. This species is established in Virginia and Missouri (Baudoin *et al.*, 1993; Baudoin and Bruckart, 1996) and was recorded in Wyoming in 1996.

Suppression of Target Weed

Rhinocyllus conicus. Effects of the weevil on *C. nutans* in Virginia were not apparent until 1973, after a steady increase in weevil densities. By 1974, 16 out of 20 releases resulted in successful establishment, and six showed more than 75% reduction in thistle density (Surles *et al.*, 1974; Kok 1978a, b). Establishment rates were better for spring releases of reproductive adults than summer releases (Kok, 1974). At one location, 90% of the plants were heavily infested, and in 1975 all but one of the 11 plots showed at least 90% reduction in thistle density (Kok and Surles, 1975; Kok and Pienkowski, 1985). Biological control is usually achieved in five to six years (Kok and Surles, 1975; Kok, 1986; Kok and Mays, 1991) [Figs. 9, 10]. Decrease in thistle density was slower at sites

Figure 9. Musk thistle site before *R. conicus* release. (Photograph by L.-T. Kok)

Figure 10. Musk thistle site five years after *R. conicus* release. (Photograph by L.-T. Kok)

with little competing vegetation. Grass competition was found to be important in restricting thistle growth and keeping weed population levels low. Control by *R. conicus* is enhanced when combined with proper land management, especially prevention of overgrazing.

Trichosirocalus horridus. Damage results from larval feeding on meristematic tissues in the rosette, resulting in crown tissue necrosis. Cartwright and Kok (1985) found that *C. nutans* changed its growth pattern in response to feeding by *T. horridus*. Infested plants produced more stems and a larger crown than uninfested plants, which did not produce multiple stems in this study. Large thistles were stimulated by weevil damage to produce larger stems and more capitula, but small and medium thistles were shorter and produced fewer seeds and capitula than uninfested thistles. Response of thistles also is influenced by larval density (Sieburth *et al.*, 1983). In Virginia, a 96% reduction of musk thistle density occurred at two of three study sites within six years of initial releases (Kok, 1986). The collapse of thistle populations after three years of heavy weevil attack was not unusual, as pasture plants re-established and reduced thistle recruitment. The extent of thistle reduction caused by *T. horridus* varies. If weevil populations are large and grass competition is strong, thistle densities can be reduced dramatically. Suppression of musk thistle growth is greatest when the two weevils (*R. conicus* and *T. horridus*) act in conjunction with plant competition. Tall fescue grass (*Festuca arundinacea* Schreb.) together with thistle weevils suppressed musk thistle growth more quickly than the use of thistle weevils alone (Kok *et al*.,1986).

RECOMMENDATIONS FOR FUTURE WORK

The musk thistle program has been reassessed recently (Nechols, 2000). For a long time, the debate has focused on the effect of the biological control agents on the population level of the target thistle and the degree of their non-target feeding. Of the five insects approved for release, two have established with certainty – the seed head weevil, *R. conicus*, and the rosette weevil, *T. horridus*. Long-term impact studies conducted in Virginia (Kok, 1986; Kok and Mays, 1991) suggest that the two weevils are capable of exerting some control of *C. nutans,* although experimental data are generally lacking from most of the other states. Thus, long-term experiments are needed in which post-dispersal seed mortality, various levels of plant competition, and the impact of both weevils (alone and combined) are considered.

Both the seed head and the rosette weevils have relatively broad host ranges. In addition to various exotic thistles, *R. conicus* feeds and develops in nearly 20 native North American *Cirsium* species, and in some cases, heavy infestations cause significant reduction in seed (Louda, 2000). There is considerable controversy over whether or not biotypes *R. conicus* (or other thistle head insects like *U. solstitialis*, reviewed by Gassmann and Louda, 2000) might exist, each with a somewhat narrower host range. The existence or absence of such biotypes has important implications in the biological control program against *C. nutans* and other exotic thistles in North America. This controversy might be due in part to the lack of an accepted definition of the term itself, but the existence of weevil biotypes with inherited differences in their ability to use different hosts still needs to be demonstrated. Genetic variation occurs in *R. conicus* reared from different thistle species (Unruh and Goeden, 1987), but the extent to which this genetic variation drives host selection and acceptance is unknown. Rather, the evidence available to date suggests that the phenology of thistle species in the subtribe Carduinae plays a major role in their exploitation by *R. conicus*. Therefore, the redistribution of *R. conicus* in areas where the weevil has not spread naturally should not be considered without an ecological assessment of the targeted area.

In contrast to *R. conicus*, *Trichosirocalus horridus* has been reported only occasionally from native North American *Cirsium* species (McAvoy *et al*., 1987). In light of available evidence to date, two questions need to be considered. (1) Is intensive exploitation of native thistles by *T. horridus* just a matter of time even though it has not been commonly found on non-target weeds after 25 years of release? (2) Is the exploitation of native *Cirsium* by *R. conicus* the result of the broad diet of the weevil, or the combination of phenology, host plant affinities, and other biological characteristics? The availability of reproduction sites (synchronization with flowering periods of "any" thistles) rather than preference, weevil aggregation, or altered competitive ability of *R. conicus* in the flower heads of thistles may play an important role in the exploitation of native *Cirsium* species by *R. conicus* (Gassmann and Louda, 2000). If this is the case, it follows that insects with biological characteristics different from those of *R. conicus*, such as *T. horridus*, will not necessarily exploit native North American *Cirsium* species in the same way as *R. conicus*.

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