

Understanding invasions: the rise and fall of diffuse knapweed (*Centaurea diffusa*) in North America

Timothy R. Seastedt¹, Katharine N. Suding² and Katherine D. LeJeune³

¹*Institute of Arctic and Alpine Research, Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO 80309-0450, USA*

²*Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697-2525, USA*

³*Stratus Consulting, Boulder, Colorado 80303, USA*

Introduction

Diffuse knapweed (*Centaurea diffusa* Lam.) is an aster of Eurasian origin that has colonized 1.4 million hectares of semiarid grasslands in western North America over the last century [1, 2]. The species can be found from Washington to Michigan and from British Columbia to New Mexico. This species is a short-lived perennial that often produces a rosette in the first year and in the second year will flower, set seed, and die. The senesced adult plant can function as a tumbleweed to disperse seeds. The weed reduces grassland forage and has the potential to exhibit negative effects on other ecosystem services of these rangelands [3–5].

Midway through the last century *C. diffusa* was sufficiently widespread to implement biological control efforts. The first species of biological control insects (gall flies, *Urophora* spp) were released in North America in 1970, followed by the release of about 10 additional species of insects over the next two decades [6]. By 2000, 13 insects had been released [7]. In spite of these efforts, diffuse knapweed continued to spread, and through the 1990s, biological control efforts appeared unsuccessful. As summarized by Carpenter and Murray [8] “At least nine biological control agents that attack *Centaurea diffusa* are established in parts of the United States. Unfortunately, it appears that none of these agents, alone or in combination, effectively controls diffuse knapweed populations.”

While evidence was accumulating indicating that top-down controls were not affecting dominance for this and related species of *Centaurea*, the importance of bottom-up controls (competitive and resource acquisition mechanisms) were being documented. Gerlach and Rice [9] indicated that a relative of diffuse knapweed, *C. solstitialis*, was successful as an invader due to its abilities to persist within a community and exploit resource opportunities. Research on diffuse knapweed at our site [5] indicated that the characteristics

of persistence and opportunism also described the invasiveness and dominance of *C. diffusa* as well. Suding et al. [10] demonstrated that rosettes of diffuse knapweed were strong competitors under ambient nutrient conditions, but were less competitive under lower nutrient conditions that may have characterized North American grasslands until recently. Elsewhere, the role of soil biota – collectively the benefits provided by mycorrhizae and the absence of soil pathogens – has also been indicated in the success of invasive species of *Centaurea*. Mycorrhizae fungi provide a competitive advantage to invasive spotted knapweed *C. maculosa* [11, 12]. Callaway et al. [13] demonstrated that mycorrhizal interactions allowed *C. melitensis* to exhibit compensation to grazing damage. Those findings added to the work showing that overcompensation to root herbivory occurred in *C. maculosa* [14].

Allelopathy was also identified as a competitive mechanism used by *Centaurea* species. Spotted knapweed was found to possess an allelopathic agent, (–)-catechin [15]. Another allelopathic chemical, 8-hydroxyquinoline, was subsequently identified for diffuse knapweed [16], supporting the contention of Hierro and Callaway [17] that *C. diffusa* used allelopathy to achieve a competitive advantage. This particular chemical contains nitrogen, an element that is generally more available in many areas of North America due to increased atmospheric nitrogen deposition and chronic fire suppression [18]. Callaway and Ridenour [19] suggested that the relatively high production of allelopathic compounds could explain the dominance of invasive *Centaurea* species.

While specific findings were being reported for *Centaurea* spp, Klironomos [20] demonstrated that invasive plant species with strong dominance (high abundance in their respective communities) often exhibit positive feedbacks with soil biota. Mitchell and Power [21] found that those invasive species that exhibited dominance and were identified as noxious and invasive tended to be those that had escaped their native fungal pathogens and viruses. These same species had yet to accumulate an equivalent number of pathogens in their introduced environments. Not surprisingly, Callaway et al. [22] subsequently showed that *C. diffusa* growth exhibited positive feedbacks in soils of invaded communities. Collectively, these results argue that the combination of traits – persistence and opportunism, allelopathy, and potential positive feedbacks from soil biota – allow for *Centaurea* species, including diffuse knapweed, to function as something we might call “super-invaders” [23]. Such plants appear to be superior competitors and capable of dominance across a broad range of ecological conditions.

By 2003, however, evidence suggested that certain insects were having a strong influence on diffuse knapweed densities in Colorado [24]. Subsequent reports from Montana [25] and British Columbia [26] indicated that this response was widespread. The common factor in this reduction was the addition, to the existing suite of herbivores, of a weevil that consumed both seeds and maturing plants. Differences in nutrient availability and plant competition have the potential to mediate weed responses to herbivory (e.g., [27, 28]).

Accordingly, tests at multiple sites and under multiple climatic regimes are warranted to establish the generality of top-down controls on diffuse knapweed.

Here, we use results from studies of insect herbivory on diffuse knapweed populations in the Colorado Front Range to make inferences about factors controlling invasiveness of diffuse knapweed and its relatives in North America. We show that top-down controls negate the characteristics that made knapweed successful as an invader in Colorado. We also hypothesize that these controls, as represented by the current list of biological control insect species released in North America, may not be uniformly effective for all of the invasive *Centaurea* species.

Monitoring effects of herbivores on knapweed populations and seed production

A monitoring site dominated by diffuse knapweed (25–30% of plant cover) was established in Boulder County, Colorado, USA in 1997. In that year small numbers of *Sphenoptera jugoslavica* Obenb., (Coleoptera: Buprestidae), *Cyphocleonus achates* Fahraeus (Coleoptera: Curculionidae), both root feeders of rosettes, and *Larinus minutus* Gyllenhal (Coleoptera: Curculionidae), the lesser knapweed flower weevil, were released at the site. In addition, there were existing populations of *Urophora quadrifasciata* Meigen, (the knapweed seed head fly, Diptera: Tephritidae). A second species of fly, *Urophora affinis* Frauenfeld, the banded gall fly, invaded the site from unknown sources by 1999.

Knapweed abundance and reproduction was obtained by counting rosettes, flowering stems, seed heads per plant, and seeds per seed head. The abundance of *Larinus minutus*, which reproduces by placing eggs in flowers of the knapweed, was also obtained by during the inventory of seed heads. Details on data collection procedures at the Boulder site are reported in Seastedt et al. [24].

In addition to quantifying seed production and weevil abundance at the above site, additional areas containing large densities of knapweed were sampled for seeds and weevils. Sites included three mountain meadow sites and eight additional grasslands at distances up to 100 km from the original study site. Insects were released at these sites in the late 1990s or insects from other sites eventually colonized the areas. Data on seed and weevil densities in seed heads reported here were collected during the 2001–2004 interval. With one exception, counts were based on inspection of 180 seed heads from 30 different plants at each site collected in the mid August to mid September interval. At one site this analysis was limited to 108 seed heads from 18 plants.

The patterns observed for knapweed stem densities at our 1997 release site show that about four years were required for insect populations to build up to levels where knapweed densities were significantly reduced (Fig. 1). In contrast to the sharp decline in densities observed at this site, other sites not experiencing these levels of insect herbivory continued to maintain high densities

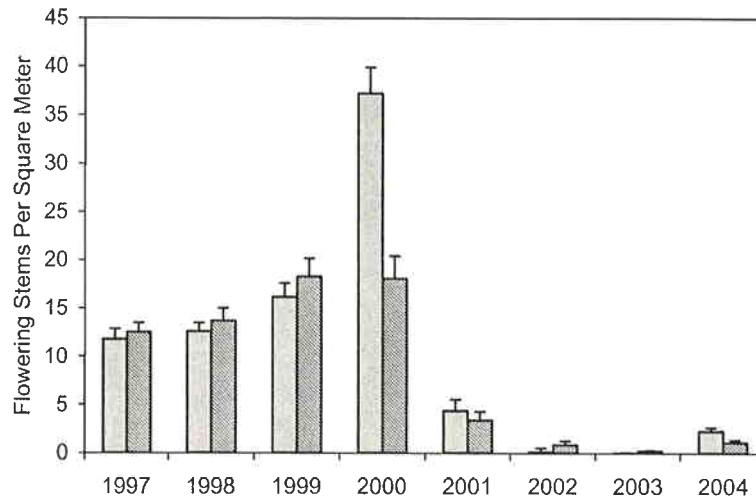


Figure 1. Flowering stem densities of diffuse knapweed at two monitoring sites where insects were released in 1997. Seed head weevils were relatively uncommon until 2000. Each bar represents the mean and one standard error of 30 samples taken from 1 m² quadrats at two sites over the eight year period. Data for the 1997–2001 interval were reported in [24]

and cover of knapweed [24]. By 2004, the seed head weevils had expanded to almost all remnant grasslands in the area, and two plots that had substantial knapweed when first censused in 2001 had no flowering stems or rosettes of this species in 2004.

Summer precipitation during the study interval was variable and typical of semiarid grassland found in a continental climate. During the last five years rainfall was average or above average in 2001, 2003, and 2004. The year 2000 was moderately dry and the autumn and winter of 2001 and all of 2002 were extremely dry. Knapweed rosettes may have refrained from flowering in 2002 but persisted through the drought. Seeds germinated by substantial rains in 2003 produced a modest increase in knapweed in 2004, but at levels well below those observed prior to 2001. Rosette densities of knapweed were about 50 plants m⁻² in 1997 [24], but ranged from 1–3 plants m⁻² at the release site in 2004 (data not shown). Given the potential persistence of a seed bank for this species [29] the decline in rosettes likely reflected both the reduction in seed production as well as substantial mortality of seedlings.

A single *Larinus* weevil larva will consume all of the seeds found in a diffuse knapweed seed head. Thus, the average seed production of knapweed impacted by this insect is determined by the number of seed heads with weevils (all contributing zero seeds) as well as the seeds produced in those seed heads not containing weevils. The relationship is 'triangular', i.e., when weevil abundance is high, seed production is uniformly low, but when weevil

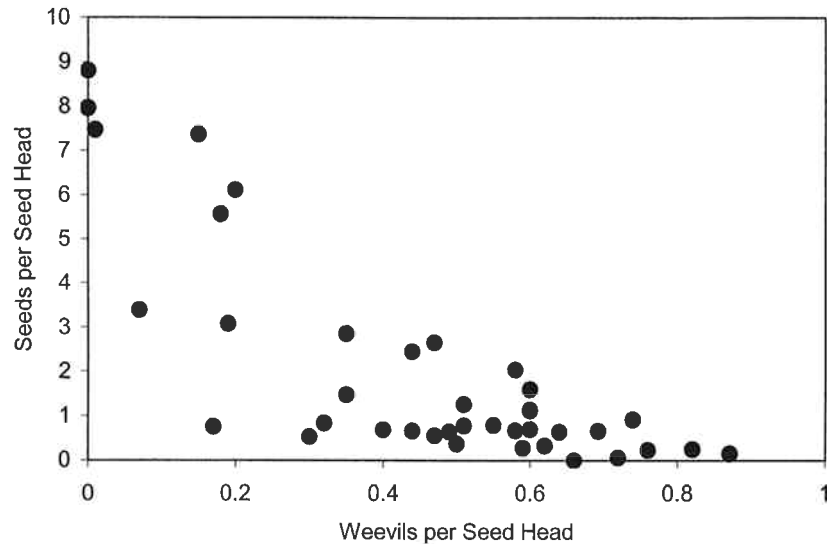


Figure 2. Relationship between seed and weevil production in seed heads of diffuse knapweed. Each point represents the mean value of seeds per seed head and weevils per seed head for 12 sites in the Colorado Front Range area collected during the 2001–2004 interval. ($n = 38$; not all sites were sampled in all years.)

abundance is moderate-to-low, seed production can be low, moderate or high (Fig. 2). The difference in seed production likely relates to the amount of defoliation experienced by the flowering plants. *Larinus minutus* over-winters as adults beneath the knapweed, and they tend to defoliate plants in the spring following their emergence from the soil. If sufficient defoliation occurs, the vigor of flowering is suppressed, and weevils apparently lay few eggs on stressed plants. Such plants produce few seeds and contain few weevils, providing the low seed–low weevil results seen in Figure 2. The weevils that defoliate flowering plants disperse to healthy plants that do produce seeds in those seed heads not fed upon by the weevil larvae. Those plants produce the moderate seed–low weevil points seen in Figure 2.

Knapweed not subjected to significant weevil herbivory generally produced 4–8 seeds per seed head (Fig. 3). Once weevil populations become established, seed production is greatly reduced, both by the direct consumption of seeds and the reduction in plant vigor caused by the feeding activities of the adults. While the summer of 2004 was spectacular in terms of rainfall and plant growth, weevil damage on a seed head basis was about the same as that seen in previous years (Fig. 3). Seed rain, the amount of seed produced per m^2 , was initially above 4,000 seeds per m^2 in 1997, declined to about 700 seeds per m^2 in 2000 (the year before the large population decline shown in Fig. 1), and was estimated below 200 seeds per m^2 in 2004 (Fig. 3). The failure for knapweed to maintain its flowering stem densities, given these seed inputs, argues

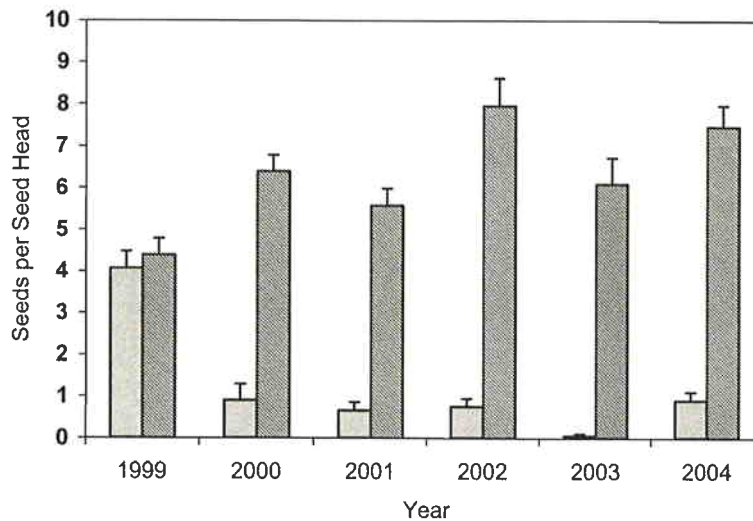


Figure 3. Seed production from the insect release site (shaded bars) compared with sites experiencing little or no herbivory by the seed head weevil, *Larinus minutus* (hatched bars). Weevil densities at the release site were estimated to be below 0.1 weevil per seed head in 1999, but were above 0.5 per seed head in subsequent years. Values are means and standard errors of a minimum of 180 seed heads sampled from 30 plants at each site for each of the six years

for substantial mortality of seeds, seedlings, and rosettes. We do not know the extent to which that mortality results from plant competition *versus* direct mortality from herbivory and pathogens, but we believe this mortality is likely important in the sustained low densities of the knapweed. Interestingly, 'weevil rain' (number of adult weevils emerging from seed heads) has been as high as 2,000 weevils per m². Unless an effective predator or parasite for this species appears, knapweed experiencing these densities of herbivores is doomed to either an early death or very low reproduction.

Harris [30] suggested that the objective of knapweed control should be to achieve less than 5% cover by the weed on rangelands. This has been accomplished in Colorado, and similar results are underway in other regions (e.g., [25, 26] and unpublished results). Myers and Bazely [31] make the strong case that this decline is likely due to the combination of effects that the insects have on multiple stages of the knapweed lifecycle.

The reduction in knapweed densities in Colorado is attributed largely to activities of the lesser knapweed flower weevil, *Larinus minutus*. The other insects present in this study have not been able to control the weed [31], or, as in the case of *Cyphocleonus achates*, were not particularly abundant during intervals of knapweed decline (Seastedt, unpublished results). However, these observations do not exclude the possibility that the addition of the other species collectively have more impact on the rate and extent of knapweed decline than *L. minutus* operating alone. Seedling mortality appears to be a significant