SEED-HEAD FLY INTERACTIONS ACROSS DIVERSE KNAPWEED PATCHES

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ABSTRACT - Short-fringed or tyrol knapweed, *Centaurea dubia* (Asteraceae) is an invasive plant of fields and roadsides in the eastern United States. Insects from the plant's native Eurasian range have been introduced into North America in an attempt to control the spread of related *Centaurea* species. One of these biological control agents, *Urophora quadrifasciata* (Diptera: Tephritidae), a picture-winged seed-head fly, has dispersed throughout northeastern North America. This study examined the response of this seed-head fly to a nontarget host's (*C. dubia*) patch characteristics and seed production in an old field. Ninety percent of all stems contained at least one seed-head attacked by *U. quadrifasciata* and 59% of *C. dubia* seed-heads were infested. Neither location in the field, plant height, nor number of stems per patch influenced *U. quadrifasciata* numbers within seed-heads. Number of seeds per seed-head was influenced by location and patch size but not stem height.

INTRODUCTION

Host plant patch characteristics can affect the activity of herbivorous and granivorous insects. Host plants frequently influence phytophagous insect demography and life history (e.g., McCauley 1991). For example, patchy distributions of plants may lead to patchy distributions of beetles, and beetles may stay longer in large host-plant patches (McCauley 1991). Root (1973) concluded that large host patches should contain more host-specific herbivores. Small, isolated plant patches frequently have small insect populations because of emigration (McCauley 1991, Root 1973, Solbreck and Sillén-Tullberg 1986). For example, populations of the fly *Euphranta connexa* Fabricius (Tephritidae) increased when the host plants, white swallow-wort, *Vincetoxicum hirundinaria* Medikus (Asclepiadaceae), was abundant, but flies became locally extinct when plant populations dwindled below a threshold (Solbreck and Sillén-Tullberg 1986).

Knapweeds or star-thistles (*Centaurea* spp., Asteraceae), are Eurasian weeds that have spread rapidly in North America. Since their introduction, these plants now thrive on rangeland in the west and farmland, disturbed fields, and roadsides in the east. In their native range, knapweed seeds are vulnerable to many insects, mites, and

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pathogens (Maddox et al. 1991, Rosenthal et al. 1994, Wheeler 1989). In North America, knapweed success may be due, in part, to the paucity of specialist herbivores and seed predators (Müller-Schärer and Schroeder 1993, Rosenthal et al. 1994). Control of weedy *Centaurea* spp. in North America is being attempted with predators and pathogens from the plants' original range (Maddox et al. 1991, Rosenthal et al. 1994, Wheeler 1989).

Tyrol knapweed, *Centaurea dubia* (= *C. nigrescens* and *C. vochinensis*) (Asteraceae) (Gleason and Cronquist 1991), is a common inhabitant of field edges, roadsides, and recently disturbed areas in central New Jersey. Like its congener spotted knapweed, *Centaurea maculosa* Lam. (Wheeler 1989), *C. dubia* is an invasive perennial that probably arrived in the United States in shipments of alfalfa seeds in the early 1900s (Müller-Schärer and Schroeder 1993). *C. dubia* is widely established in southeastern Canada and the northeastern United States, south to West Virginia (Gleason and Cronquist 1991). All knapweeds in New Jersey have been introduced (Hough 1983). There have been no releases of knapweed biological control agents in New Jersey (Hoebeke 1993), and *C. dubia* has not been the target of biological control projects elsewhere.

Urophora quadrifasciata Meigen (Tephritidae) belongs to a group of *Centaurea*-attacking, picture-winged seed-head flies from Eurasia. Females oviposit in developing flower buds. The developing larvae consume bud tissue and form galls within the capitulum (seed-head) where the pupae develop. The galls cause a reduction in seed production. Larvae overwinter in the seed-head galls and adults emerge in the spring. Unlike *U. affinis* Frauenfeld, a related biological control agent, *U. quadrifasciata* is bivoltine, oviposits later, chooses larger buds, and forms thinner-walled galls (Myers and Harris 1980). *U. quadrifasciata* is an active disperser and seems likely to colonize remote knapweed patches (Müller-Schärer and Schroeder 1993; Story et al. 1992). Males of *Urophora* sp. generally emerge several days before females and the fly life cycle is closely synchronized with *Centaurea* life histories (Story et al. 1992).

HYPOTHESES

At a study site in an old field in New Jersey, I discovered larvae of *Urophora quadrifasciata* in the mature seed-heads of *Centaurea dubia* Suter. This plant has not been reported as a host of *U. quadrifasciata* in the United States. Hoebeke (1993) reported the first distribution of *U. quadrifasciata* in the eastern United States, noting that this quick-dispersing fly appears to have naturally spread east into New Jersey. The goal of this study was to determine the pattern of *U. quadrifasciata*

infestation in patches of *C. dubia*. This study tested three hypotheses: 1) seed-head infestation is influenced by knapweed patch size; 2) fly larvae density varies with *C. dubia* patch location; and 3) the number of seed-head flies per plant is influenced by plant height.

METHODS

Field-site description

Field work was conducted at The Hutcheson Memorial Forest Center (HMF) in East Millstone (Somerset County), NJ, approximately 15 km west of New Brunswick. HMF is a mosaic of old-growth and young mixed hardwood forest and abandoned agricultural fields. These fields were dominated by perennial forbs such as goldenrods, *Solidago* spp., and nodding foxtail-grass, *Setaria faberi* R. Herrm. *C. dubia* occurred in the old fields at HMF, especially along edges of fields.

Field sampling

In October 1994, 12 patches of *C. dubia* were examined for seed-head infestation and quantities of seed within old fields at HMF (Fig. 1). Six patches were sampled in the fields at HMF and six patches were sampled along a path bordering the fields. Patches also were selected to represent a variety of sizes (number of stems per patch, range = 1-150 stems). A patch was defined as a contiguous group of stems with a

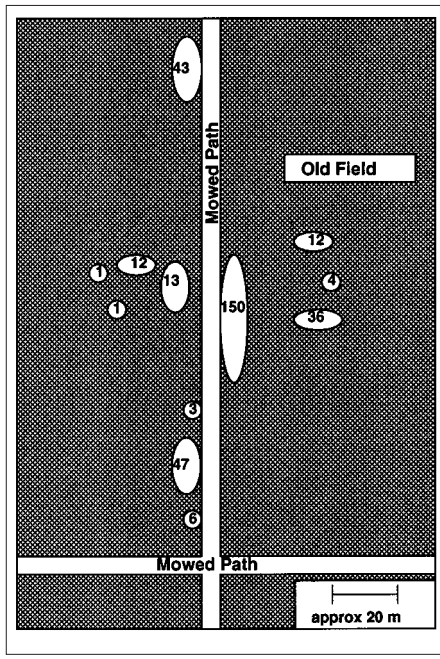

Figure 1. Relative location of twelve *Centaurea dubia* patches sampled for seed-head flies in old fields at Hutcheson Memorial Forest, New Jersey, October 1994. Numbers indicate plant patch sizes (number of stems). Patches are not drawn to scale and distances shown between patches are approximate.

distinct boundary. It was not determined if plants were connected underground; therefore, the term "stems" is used rather than "plants." Within each patch, a subset of stems was chosen arbitrarily, measured (height in cm), and surveyed for seeds and fly pupae. Sixty-nine stems were examined. After counting seeds, all seed-heads on a stem were inspected to count overwintering fly larvae. Seed-heads were left intact to allow for rearing of flies in the spring.

Laboratory rearing

After counting larvae and seeds, 200 randomly sampled *C. dubia* seed-heads were saved to rear *U. quadrifasciata* for positive identification. These seed-heads were chilled at 5˚C for 1 month, and then placed in 500 ml covered beakers with moist sand and kept at room temperature. Beakers were checked each day for emerging flies. The Systematic Entomology Laboratory, USDA, verified fly identification.

Analyses

Total fly counts per stem (n = 69) and seed-head (n = 424) were compared for location (field edge or field interior), knapweed patch size class [small (1-6 stems), medium (12-47 stems), and large (150 stems)], and stem height effects, using an analysis of covariance (ANCOVA) with location and patch size class as fixed effects and height as a covariate. Student-Neuman-Keuls (SNK) post-hoc means comparisons were utilized to compare mean *U. quadrifasciata* numbers and simple regression analyses were conducted to determine linear relationships of significant effects.

Seed counts per stem and seed-head were compared for location (field edge or field interior), knapweed patch size, and stem height effects using an ANCOVA with location and patch size class as fixed effects and height as a covariate. SNK means comparisons were utilized to compare mean seed numbers, and simple regression analyses were conducted to determine linear relationships of significant effects. Stem heights were compared for location effects using an analysis of variance (ANOVA) with location (field edge or field interior) as a fixed effect.

RESULTS

Urophora quadrifasciata

Ninety percent (SD = 12.84) of the stems contained at least one fly-infested seed-head and 59% (SD = 22.81) of seed-heads were attacked by *U. quadrifasciata* (range = 66-100% and 36-100% respectively). Patch location (P = 0.08), patch size (P = 0.06), and height (P = 0.05) had no significant effect on the number of *U. quadrifasciata* per seed head (n = 424) although the results were nearly significant. There was a

highly significant patch size class by height interaction (df 2,414, F = 5.11, P = 0.006). However, when analyzed within patch size classes, there were no significant linear relationships between the height of stems and flies per stem and percentage of seed-heads attacked for small (R = 0.11, P = 0.72; R = 0.22, P = 0.45), medium (R = 0.07, P = 0.63; R = 0.16, P = 0.29), or large (R = 0.45, P = 0.26; R = 0.45, P = 0.26) patch classes. The mean number of larvae within seed-heads was 1.89 (SD = 2.5, n = 424). The same three parameters also had no effect on number of *U. quadrifasciata* per knapweed stem (P >0.05).

The sex ratio of flies that emerged in the laboratory was nearly equal (48:52 male:female). Male flies emerged before females as reported by Story et al. (1992).

Centaurea dubia

The overall mean height of *C. dubia* stems was 86.5 cm (SD = 30.1, n = 69). The mean height of *C. dubia* stems was significantly greater in the field interior [92.3 + 28.1 cm (SD), n = 27] than field edge [69.0 ± 23.1 cm (SD), n = 42] patches (ANOVA df 1, F = 14.10, P = 0.0004).

The number of seeds per knapweed seed-head was significantly affected by patch location (df 1,414, F = 4.55, P = 0.034) and patch size (df 2,414, F = 3.62, P = 0.028). Stem height (P = 0.99) did not significantly affect the number of seeds. The same three parameters also had no effect on number of seeds per knapweed stem (P >0.05). The mean number of seeds per stem was 23.4 (SD = 27.9, n = 28) in the field and 33.8 (SD = 36.7, n = 40) in the edge. Many of the seeds had probably fallen by the time the seed-heads were examined; consequently, this number underestimates seed production.

DISCUSSION

This is the first report of the association between *U. quadrifasciata* and *C. dubia* in the United States. In addition to the reported distribution of *U. quadrifasciata* in the eastern United States (Hoebeke 1993), this study shows that *U. quadrifasciata* is capable of establishing on other nontarget *Centaurea* sp. in New Jersey.

Contrary to some theoretical expectations (McCauley 1991, Root 1973, Solbreck and Sillén-Tullberg 1986), *U. quadrifasciata* infestation patterns did not respond to *C. dubia* patch characteristics across the scales measured. Although insect numbers are frequently correlated with host plant patch size (e.g., McCauley 1991, Root 1973, Solbreck and Sillén-Tullberg 1986), the relationship was not supported in this study. This may be a result of *U. quadrifasciata* behavior, insufficient sample size, or a combination of these factors.

Overall, stem infestation was high within *C. dubia* patches. The combination of a very mobile fly (Story et al. 1992) and the proximity of *C. dubia* patches at HMF may explain why *U. quadrifasciata* larvae were no more abundant in larger patches than smaller patches. These patches may function as part of one metapopulation. Furthermore, although many studies indicate that increased host plant density may attract more insects (e.g., Evans 1983, Moore 1978), this may not be true with interactions between *C. dubia* and *U. quadrifasciata*. In fact, patch size may have variable effects on insect populations. Brody (1992) discovered that both clumped and highly dispersed scarlet gilia [*Ipomopsis aggregata* (Pursh) V.E. Grant (Polemoniaceae)] were attacked more frequently by pre-dispersal seed predators, anthomyiid flies, *Hylemya* sp. (Diptera: Anthomyiidae) than were patches of intermediate sizes. Finally, Myers and Harris (1980) concluded that although *U. quadrifasciata* may have a clumped distribution within a site, flies were not attracted to high knapweed flower density.

Physical features such as knapweed stem height may be a more important influence on seed-head fly distribution in an old field. Slightly higher (but not significant) fly numbers in edge plots of *C. dubia* at HMF may be a result of easier access for ovipositing females and the contagious spread of flies within infested patches. Field edge patches of *C. dubia* may be more visible and accessible to searching flies. Searching female *U. quadrifasciata* may then move from edge patches into the interior of fields. Because of the limited size of this system and the proximity of knapweed patches, what appears to be separate patches of *C. dubia* may be perceived by the flies as one large knapweed population.

Since *U. quadrifasciata* is now known to establish on other introduced *Centaurea* spp., and *U. quadrifasciata* effectively locates remote knapweed populations (Story et al. 1992), the quick-dispersing *U. quadrifasciata* should continue to spread east across New Jersey. Although New Jersey was not listed as a target state for a knapweed biological control program (Hoebeke 1993), *U. quadrifasciata* could eventually colonize *C. dubia* and other knapweed species' populations in the state.

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