AN ABSTRACT OF THE THESIS OF

Stacy Schumacher for the degree of Master of Science in Rangeland Resources presented on June 12, 2001. Title: The Effects of Defoliation on Yellow Starthistle (*Centaurea solstitialis* L.) Reproductive Capacity.

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Yellow starthistle (*Centaurea solstitialis* L.) is an introduced Asteraceae that has become established on 10 million acres in the Pacific Northwest and California. This weed functions as an annual or short-lived perennial and depends on seeds for reproduction. Strategies of control that reduce plant fitness or lower seed production or viability may help limit the rate of spread of yellow starthistle. Previous work has shown that grazing and mowing can influence seed production. This study tested the hypothesis that proper timing and frequency of defoliation can reduce the number and viability of seeds produced. The study was conducted in Umatilla County, Oregon using a randomized block design with 4 replications of each of 4 defoliation treatments: (1) single defoliation at the bolting stage; (2) single defoliation at the bud stage; (3) two defoliations, once at the bolting stage and again at the bud stage; (4) non-defoliated control. Each of 4 blocks consisted of a 12 x 12m area, with 16 plots measuring 3 x 3m. Plants were defoliated at ground level using a gas-powered string-type mower. Response measurements were collected at the end of the growing season (September) following potential regrowth and included: (1) number of seedheads per plant; (2) number of seeds per

seedhead; (3) number of seeds per plant; (4) number of seeds m^{-2}, (5) seed viability (% germination rates). Supporting measurements included: seedhead diameter; plant height, number of branches per plant; pre-dawn xylem pressure; soil moisture; and documentation of 5 biological control insect species. A single defoliation at bolting resulted in fewer seeds per seedhead, and fewer seeds per plant than non-defoliated controls. A single defoliation at the floral bud stage or repeated defoliation (bolting and again at the bud stage) resulted in equally fewer seeds per plant and fewer seeds m^{-2} compared to non-defoliated controls. There was no statistical difference in percent germination of seeds among treatments. Defoliation had no effect on the infestation rates of seedheads by biological control insects. A second study examined nutrient content of yellow starthistle during 6 phenological stages from sites in Union, Baker and Umatilla Counties, Oregon during each of 2 years. Acid detergent fiber, lignin, cellulose and neutral detergent fiber contents increased through phenological development. Crude protein ranged from 16.7 to 5.0%. *In Vitro* dry matter digestibility ranged from 84.8% to 57.0%. Mineral nutrients P, K, CA, Mg, Mn, Fe, Cu, Zn, and Na were analyzed and determined to be adequate for maintenance needs of ewes.

The Effects of Defoliation on Yellow Starthistle (*Centaurea solstitialis* L.) Reproductive Capacity

By

Stacy Schumacher

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Introduction

Yellow starthistle (*Centaurea solstitialis* L.) is an herbaceous member of the Asteraceae introduced into the United States from Eurasia in the mid-1800's. The earliest herbarium specimen collected in North America was from California in 1869 (Maddox and Mayfield 1985). Since then, it has become a widespread and troublesome weed of 23 western states, primarily California, Oregon, Idaho and Washington (Maddox et al. 1985). It is established on more than ten million acres in the Pacific Northwest and California (Thomsen et al. 1997), and has the potential to invade nearly all the arid and subhumid rangelands of the western United States (Callihan et al. 1982). Callihan et al. (1989) estimated yellow starthistle is increasing at a rate of about 10,000 ha per year in Washington and Idaho alone. It is a pernicious weed of rangelands, croplands, orchards, vineyards, pastures and wastelands. Seeds of yellow starthistle are important contaminants of commercial seeds (Maddox and Mayfield 1985). The weed can displace desirable vegetation and is associated with reductions in forage production as high as 95% on native rangelands (Roche and Roche 1988). Increases in yellow starthistle diminish recreational values, lessen wildlife habitat, reduce biodiversity, increase soil erosion and help carry wild fires. It is poor forage for all classes of livestock and is toxic to horses, causing nigropallidal encephalomalacia ("chewing disease"), a

neurological disorder characterized by brain lesions and an inability to eat or drink (Cordy 1978, Roy et al. 1995).

Yellow starthistle is an annual, but occasionally functions as a biennial. As with other such plants, it relies on seeds for reproduction. It produces dimorphic seeds that disseminate for months following flowering. An individual plant can produce as many as 10,000 seeds (Maddox 1981). Sheley and Larson (1994) observed a seed output of 21,600 seeds m^{-2} and adult populations of 200 plants m^{-2}.

Management that seeks to reduce seed production or viability has provided useful control strategies. Six insect species that feed directly on seeds or damage seed heads have been approved and released in the United States for biological control of yellow starthistle (Jette et al. 1999, Balciunas and Villegas 1999). Mowing can reduce seed production but results vary with plant phenology and frequency of defoliation (Thomsen et al. 1997, Benefield et al. 1999). Similarly, effects of grazing by cattle and sheep have produced mixed results on California annual grasslands (Thomsen et al. 1989, Thomsen et al. 1993).

If grazing is to be used as a control measure of yellow starthistle, it is desirable to know the effects of timing and frequency of defoliation on reproductive effort and fitness of plants. Knowledge of the nutrient composition of the plant at various phenological stages would also be beneficial in designing grazing strategies to control the weed. Objectives of this study are to (1) determine whether removal of above ground biomass can be used as a tool to decrease reproductive potential

and plant fitness of yellow starthistle, and (2) determine the chemical composition of yellow starthistle relative to animal nutrition

Literature Review

Biology and Life History

Yellow starthistle (Asteraceae: Cynareae) is an herbaceous weed of Eurasian decent introduced into the United States in the mid-1800's. The earliest herbarium specimen was collected in California in 1869 (Maddox and Mayfield 1985). It was introduced accidentally, likely as a contaminant in crop seeds such as alfalfa (*Medicago sativa* L.) (Roche 1965). Twenty-three of the 48 contiguous states report infestations of yellow starthistle (Maddox et al. 1985). The largest infestation occurs in California, with 3, 085,000 ha reported in 1985. Maddox (1985) stated that the western United States has the greatest potential for supporting yellow starthistle populations. Callihan et al. (1989) estimated yellow starthistle is increasing at a rate of about 10,000 ha per year in Washington and Idaho alone. It is adapted to many environments and is capable of establishing in deep, well-drained or shallow, rocky soils where annual precipitation varies between 25 to 100 cm, and elevation ranges from sea level to 2500 m (Maddox et al. 1985). It is a pernicious weed of rangelands, croplands, orchards, vineyards, pastures and wastelands. Yellow starthistle can displace desirable vegetation and is associated with reductions in forage production as high as 95% on native rangelands (Roche and Roche 1988). It is poor forage for all classes of livestock and is toxic to horses, causing nigropallidal encephalomalacia ("chewing disease"), a neurological

disorder characterized by brain lesions and an inability to eat or drink (Cordy 1978, Roy et al. 1995). Increases in yellow starthistle diminish recreational values, lessen wildlife habitat, reduce biodiversity, increase soil erosion and help carry wildfires. Its seeds are economically important contaminants of commercial seeds (Maddox and Mayfield 1985).

Yellow starthistle is an annual but may function as a biennial. As with other such plants, it relies on seeds for reproduction. It produces dimorphic seeds (plumed and non-plumed) which aids in establishment of successive waves of population cohorts from fall through spring. Yellow starthistle plants produce a composite flower head. Seed type is an achene. Non-plumed seeds develop along the outer florets of the composite flower head, called ray flowers. They are dark colored and lack bristles. Seeds that develop in the central part of the receptacle, disk flowers, are light colored and topped with two rows of white, divergent bristles (Joley et al. 1997). The majority of non-plumed seeds develop before most plumed seeds (Maddox et al. 1996). Plumed seeds are adapted for greater dispersal from the parent plant and have faster germination rates than non-plumed seeds, which remain on the parent plant until winter (Joley et al. 1997, Sheley and Larson 1994, Larson and Kiemnec 1997). In one study, seed rain was observed from late June through February in a population near Walla Walla Washington (Sheley and Larson 1994). Total achene dispersal is correlated with daily maximum air saturation deficit and maximum wind gust per day. Non-plumed seeds fall off the parent plant to repopulate immediate area, while plumed seeds are transported short

distances to promote the advancing invasion front. Ninety-two percent of plumed seeds were found within 0.6 m from the parent plant following dispersal (Roche 1991). Viable seeds are formed as early as the mid-flowering stage, when most florets are fully opened except for those in the center of the flower head (Maddox et al. 1996). Pitcairn et al. (1998) described the relationship between the number of fertile flowers (Y) and flower head diameter (X) for a California population:

$$Y = 6.22X - 6.21 \quad (r^2 = 0.82) \qquad \text{(Equation 1)}$$

The ratio of production of plumed vs. non-plumed seeds varies, possibly due to environmental conditions and phenotypic variations. Maddox (1981) described 4.7:1, 8.7:1 and 3.4:1 ratios of plumed and non-plumed seeds for populations found at different elevations that received different precipitation amounts.

Many environmental factors have been found to affect seed production. Increased precipitation resulted in increased seed production. Reduced spring precipitation affected seed production in one population in Washington (Sheley and Larson 1994) where production varied from 21,600 seeds m^{-2} to 5,200 seeds m^{-2}. In deep soils yellow starthistle shows increased seed production due to taproot development aiding the ability to utilize soil moisture at greater depths (Sheley and Larson 1995). Available sunlight influences total seed production. Shaded plants are tall and slender compared to the open, spreading form which grow in full sunlight (Roche et al. 1997). However, growth form did not affect timing of reproductive development (Roche et al. 1997). Seed predation from pheasants, quail and finches may increase the range of dispersion of seeds (Roche 1991).

Seeds are small enough that they can be transported on shoes or clothing and plumed seeds can be transported in animal fur and wool. Whole plants can be transported in the undercarriage of vehicles. Plumed seeds have been found to be viable for ten years and non-plumed seeds survive 6 years in soil (Callihan et al. 1993). In Washington 13% of the estimated total annual seed production was represented in the soil seed bank and all were non-plumed seeds (Sheley and Larson 1994).

Environmental factors have been found to affect germination. Plumed seeds have greater germination rates than non-plumed seeds at varying osmotic potentials simulating water stress (Larson and Kiemnec 1997). Germination was reduced by 50% for both seed types as osmotic potential dropped from 0 to -1.5 MPa. Varying salt concentrations did not affect germination. Field germination of plumed seeds was greater than non-plumed seeds and viability was not influenced by timing of burial or burial depth of 1 or 2 cm (Larson and Kiemnec 1997). Plumed seeds weigh more than non-plumed seeds (Callihan et al. 1993). Yellow starthistle has a high rate of germination over a range of temperatures. Germination of plumed seeds reached 100% at constant temperatures of 10C, 15C and 20C when exposed to light while germination of non-plumed seeds in intact capitula was never greater than 21% (Joley et al. 1997). Seeds stored for three months had a 29% increase in germination over fresh seeds at varying temperatures

Germination occurs in the fall with seedling recruitment continuing through spring (Sheley and Larson 1994). Dry spring conditions increased seedling

mortality and decreased overall population seed production. Radicle elongation is not different between the two types of seeds (Sheley et al. 1993, Larson and Kiemnec 1997). Yellow starthistle has a fast growing, deep taproot, which increases the depth from which soil water can be obtained (Borman et al. 1992), thus extending the period of resource extraction and increasing seed production (Sheley et al. 1993). Yellow starthistle seedlings averaged 17 mm of root growth per day and 638 mm^{-2} of area growth per day (Sheley et al. 1993). After 14 days yellow starthistle roots were longer than cheatgrass and continued that trend for the remainder of the study. Roots excavated on deep soil sites developed one primary taproot with short secondary branches (Roche et al. 1994). In August, taproots branched where they reached broken rock 91 cm below the soil surface. DiTomaso (2000) speculated that soil moisture is depleted faster on rangelands dominated by yellow starthistle than annual grasses or perennial wheatgrass and has a negative impact on soil moisture recharge at greater depths.

Major phenological stages of yellow starthistle were described by Maddox (1981). Emergence is in the fall with oblong, tongue-shaped cotyledons. Frost heaving can cause seedling mortality throughout winter and spring (Sheley and Larson 1994). Plants that survive seedling establishment develop 8-15 basal leaves and form a rosette. At this time resources are allocated to root extension (Roche et al. 1994). The rosette growth form of yellow starthistle enables the plant to ameliorate temperature and wind effects of harsh winter environments (Regehr and Bazzaz 1976). The plant begins to bolt in late spring, sending up a central stalk

with no bud formation present. Reproductive development is late in the season often after native bunchgrasses and exotic annual grasses are dormant (Roche et al. 1994). The time between bolting and reproduction is a critical period of development for yellow starthistle. Sheley and Larson (1994) observed a mortality rate of 75% under drought condition. Plant density did not influence timing of development of reproductive stages of yellow starthistle (Roche et al. 1997). Bud formation stage begins with the formation of terminal buds on branches and development of spines around buds. Flowering stage is signaled by the development of yellow florets extending out of the bud continuing through full flowering. Seed formation stage occurs after the florets have lost their bright yellow appearance and become straw colored. Seed dissemination stage occurs when seeds are detached from the receptacle and actively disperse. Sheley and Larson (1994) suggested that by looking at sensitivity values calculated for life history transitions, the number of plants surviving to produce seed was more important to total seed production than a reduction in the number of seeds produced per plant. Percent cover of yellow starthistle is correlated to available soil moisture for summer reproduction and light for winter growth (Roche et al. 1994). Management strategies that reduce carbohydrate production or storage before flowering may affect subsequent seed production. Lacey et al. (1994) observed reduced carbohydrate pools in spotted knapweed (*Centaurea maculosa* Lam.) after frequent defoliations.

Chemical Composition

Nutrient and mineral composition of yellow starthistle is only partially known. In one study crude protein was found to exceed 9% and acid detergent fiber concentration was less than 32% during the rosette and bolting stages of growth (Thomsen et al. 1989). It has been reported in some weed species that as plants mature there is a decrease in crude protein, soluble carbohydrates, ether extract, and *in vitro* dry matter digestibility with an increase in fiber content (Kelsey and Mihalovich 1987). Ewes require a minimum of 8.9% protein concentration in diet dry matter for maintenance needs (NRC 1985). Levels of crude protein and nonstructural carbohydrates in spotted knapweed were highest during spring growth when stems were developing. Spotted knapweed is nutritionally adequate to support livestock grazing prior to flowering (Kelsey and Mihalovich 1987). Neutral detergent fiber concentrations were 24.2 to 53.0% (dry wt.), ether extract was 3.1 to 9.0%, crude protein was 6.2 to 18.2%, total nonstructural carbohydrates were 11.0 to 27.5%, ash 4.9 to 9.3%, *in vitro* dry matter digestibility was 53.2 to 61.8%, and gross energy 4,088 to 4,539 cal/g. Palatability is reduced by concentrations of the bitter tasting sesquiterpene lactone, cnicin in the leaves. Concentrations were lowest in the spring at 0.5% dry wt. and reached a maximum of 1.0% before flowering. The use of spotted knapweed as hay or silage is recommended for forage and as a control practice (Kelsey and Mihalovich 1987).

Yellow starthistle is known to cause the fatal condition nigropallidal encephalomalacia (or chewing disease) in horses (Stevens and Merrill 1985). It

results from consuming an amount equal to the animal's body weight (450kg) (Cordy 1978). Cattle and sheep are not affected. Lesions develop in the brain causing an inability to eat or drink. The sesquiterpene, lactone repin, has been implicated in the toxicity of starthistle in horses (Stevens and Merrill 1985). Other neurotoxic compounds present in yellow starthistle include aspartic acid and glutamic acid (Roy et al. 1995).

Allelopathic potential has been attributed to yellow starthistle. There are 62 volatile components of yellow starthistle (Binder et al. 1990). Of the total volatiles, 58% were found in buds, 56% in flowers, and more than 89% in leaves and stems. Chromenes were found to retard germination and reduce radicle and hypocotyl growth of weed and crop plant seedlings (Merrill 1989). Allelopathic properties are difficult to identify in the field and no known incidence has been reported.

Management

Studies have been undertaken to determine whether livestock grazing can be used as an economical form of starthistle control. A preliminary report showed no reductions in plant densities were detected when comparing an early (February) and late (May) grazing treatment, but plant height, canopy size and seed production showed differences (Thomsen et al. 1989). Grazing trials suggest that yellow starthistle seed production can be reduced but may also be increased depending on timing and frequency of defoliation (Thomsen et al. 1993). These authors found heavy cattle grazing at the bolting stage resulted in few plants dying and most

resprouting from basal and axillary buds. The authors suggested plants should be regrazed before spines develop. Higher flower densities occurred if plants were not regrazed (Thomsen et al. 1993). However, repeated grazing of starthistle before flowering with sheep increased flowerhead densities (Thomsen et al. 1993). It was proposed that the regrowth developed increased numbers of branches with an increased number of seedheads, however that was not measured. Thomsen et al. (1993) reported that early grazing did not suppress reproductive ability of yellow starthistle, due to its ability to regrow from basal buds and its ability to utilize water from a deeper soil profile. They reported that cattle regrazed yellow starthistle more readily than sheep and goats. Cattle tended to avoid plants with developing spines but goats continued to graze plants through the flowering stage (Thomsen et al. 1993).

Mowing represents a similar approach to starthistle control. In one California study, mowing at early flowering reduced seedhead number, plant height and dry weight (Benefield et al. 1999) In this study regrowth resulted in the formation of low-growing multiple branched individuals that yielded sufficient seed production to render the treatment unsuccessful. By contrast, a combination of two mowing treatments during early flower and regrowth with a follow-up treatment of seeding with subclover (*Trifolium subterranean* L.) greatly reduced seedhead production (Thomsen et al. 1997). This later approach reduced starthistle seedhead production to zero in three years.

Chemical control of yellow starthistle can provide fast, short-term control. Picloram (0.14 or 0.28kg ae/ha) has proven effective in controlling yellow starthistle (northeastern Oregon) when used as a seedbed preparation for grass seeding (Larson and McInnis 1989). Yellow starthistle resistance to picloram applied over a ten-year period has been documented in a field in Dayton, Washington but the exact mechanism is not known (Fuerst et al. 1996). Applying 2,4-D (3/4 ae/ac in 30gallons) at the rosette stage (California) after intensive grazing can reduce plant densities to 1 per square foot. However, this treatment also limited growth of other broadleaf plants and reduced total production (Thomsen et al. 1989). Clopyralid provided greater than 90% control of yellow starthistle seedlings and rosettes in California when applied in a window extending from December through April at 1-6oz ae/ac (DiTomaso et al. 1999).

Five species of insects have been approved and released for control of yellow starthistle in the United States (Rees et al. 1996). Collecting and transplanting biological control agents may be an economical long-term control method. Two of these biological control species are flies and three are weevils. Larvae of the peacock fly *(Chaetorellia australis)* feed on developing seeds inside the seedhead. Mature larvae overwinter in the old flower heads and adults emerge in the spring. Accidentally introduced with this species was the false peacock fly *(Chaetorellia succinea).* It has multiple generations each year and can infest later developing flowers in the yellow starthistle population. The yellow starthistle gall fly *(Urophora sirunaseva)* has two generations each year. More than one gall may

develop in a flower head. Damage caused by feeding larvae and the formation of galls reduce seed production.

The weevils produce one generation each year. Adult weevils lay eggs on flower heads and larvae feed on developing seeds. Adult *Bangasternus orientalis* weevils can be identified by the lack of a long snout and egg deposition on the flag leaf of yellow starthistle flower heads. A single larvae can completely consume all seeds in a seedhead (Campobasso et al. 1998). This weevil has successfully established and shown that it can disperse and utilize yellow starthistle in California (Maddox et al. 1986). Adult *Eustenopus villosus* weevils have a long snout and stripped white markings. Eggs are laid through an opening the adult weevil makes on the bract of the flower head. Developing weevils produce a noticeable pupal chamber within the flower head. Adult *Larinus curtus* weevils have a long snout and brown appearance. Eggs are laid at the base of the flowers in open flower heads.

Materials and Methods

Studies were conducted in Baker, Union and Umatilla Counties, Oregon during 1998 and 1999. Defoliation studies were conducted in Umatilla County, and population samples for nutrient analysis were collected from sites in Baker, Union and Umatilla Counties.

Defoliation Study

A study was conducted in 1999 to evaluate the influence of timing (phenology) and frequency of defoliation on the fitness and reproductive effort of yellow starthistle. Four treatments were studied: (1) a single defoliation during bolting; (2) a single defoliation during floral bud; (3) two defoliations, once during bolting and again during floral bud; and (4) a control group with no defoliation. Response measurements were collected at the end of the growing season and included metrics associated with (1) seed production; (2) seed viability; and (3) plant morphology. The study was conducted on four south-facing sites near Pendleton, Oregon ($45^0$40'20"N, $118^0$47'15"W). Site 1, located at the Eastern Oregon Regional Airport, has an elevation of 500 m and is on Anderly silt loam (coarse-silty mixed mesic typic haploxeroll). The plant community is dominated by bulbous bluegrass (*Poa bulbosa* L.), cheatgrass brome (*Bromus tectorum* L.) and yellow starthistle. Site 2 was located on the campus of Blue Mountain Community College at an elevation of 500 m on Lickskillet very stony loam (loamy-skeletal,

mixed mesic lithic haploxerall). Dominant vegetation was cheatgrass brome, soft chess (*Bromus mollis* L.), common wheat (*Triticum aestivum* L.), and yellow starthistle. Site 3 was located off Mission Highway on the Umatilla Indian Reservation. The soil is an Entic Durochrept and has an elevation of 350 meters, contains a hardpan overlain with a variety of materials that range from loams to clay with varying amounts of amounts of gravel and cobble. The plant community is composed of cheatgrass and yellow starthistle. Site 4 was located on Kirkpatrick Road on the Umatilla Indian Reservation. Soil type is Pilot Rock silt loam (coarse-silty, mixed mesic haplic durixeroll), with an elevation of 350 meters, and is a moderately deep, well-drained soil on terrace scarps. This soil formed in loess overlying a hardpan of cemented alluvium. The plant community at site 4 consists of cheatgrass, bulbous bluegrass, and yellow starthistle.

Climatological records were obtained from the Columbia Basin Agricultural Experiment Station near Pendleton, Oregon. Total precipitation for the 1998-1999 water year was 40.4 cm, while the 30-year average is 37.9 cm. Precipitation is characteristically received from October through May in northeastern Oregon. Summers are typically dry, receiving less than 3.8 cm precipitation during each month from July through September. The 30-year mean maximum temperature is 17 C, and the mean minimum temperature is 6 C.

Phenological stages were defined using the criteria of Maddox (1981) (Table 1). The phenological stage of individual plants was determined by examining all the buds and flowers on the plant and determining which

Table 1. Descriptions of yellow starthistle phenological stages (adapted from Maddox 1981).

Phenophase	Description
Rosette	8-26 basal leaves radiating from the center, of which at least 5 are lobed.
Bolting	Full complement of radiating, deeply lobed, basal leaves. Erect stem with no bud formation is present.
Bud	Branched stems with buds enclosed in bracts. Buds have spines beginning to rotate away from the bud.
Flowering	Yellow florets extend from the opening of the buds and continue through full flowering.
Seed Formation	Loss of yellow pigment in the florets. Involucral bracts still retain chlorophyll.
Mature Seed	Plumed achenes ready for dissemination; florets are absent and involucral bracts are dry and tan.
Seed Dissemination	Seedheads appear dry. Apex of seedhead has opened; plumed achenes are detached and freely suspended in the open bowl of the seedhead.
Senescence	All plumed achenes have dispersed, seedhead an empty bowl. Non-plumed achenes are still attached to the perimeter of the seedhead.

phenological stage the majority of buds and flowers were in. When the majority of the plants at a location were determined to be in the correct phenological stage then the defoliation treatment was applied. Plants were defoliated using a gas-powered string-type lawn mower or hand clippers.

The experiment consisted of a randomized complete block design with 4 blocks and 4 replications of each treatment per block. The experiment was blocked by site. Each of 4 blocks consisted of a 12 x 12 m area with 16 plots, each measuring 3 x 3 m (Figure 1). Data were tested for normality using Hartley's Test for homogeneity of variances (Dowdy and Wearden 1983). Data not normally distributed due to unequal variances were transformed using the natural log before analysis. Analysis of variance was used to determine significance of block and treatment means:

Source of Variation	Degrees of Freedom
Total (n-1)	63
Block (B-1)	3
Treatment (T-1)	3
Block*Treatment (B-1)(T-1)	9
Error (n-1)-(B-1)-(T-1)-(B-1)(T-1)	48

If block and treatment interaction was not significant the analysis was redone without using the block and treatment interaction increasing the error degrees of freedom to 57. Treatment means were separated using least significant difference ($p \leq 0.05$). All data are presented in their original scale.

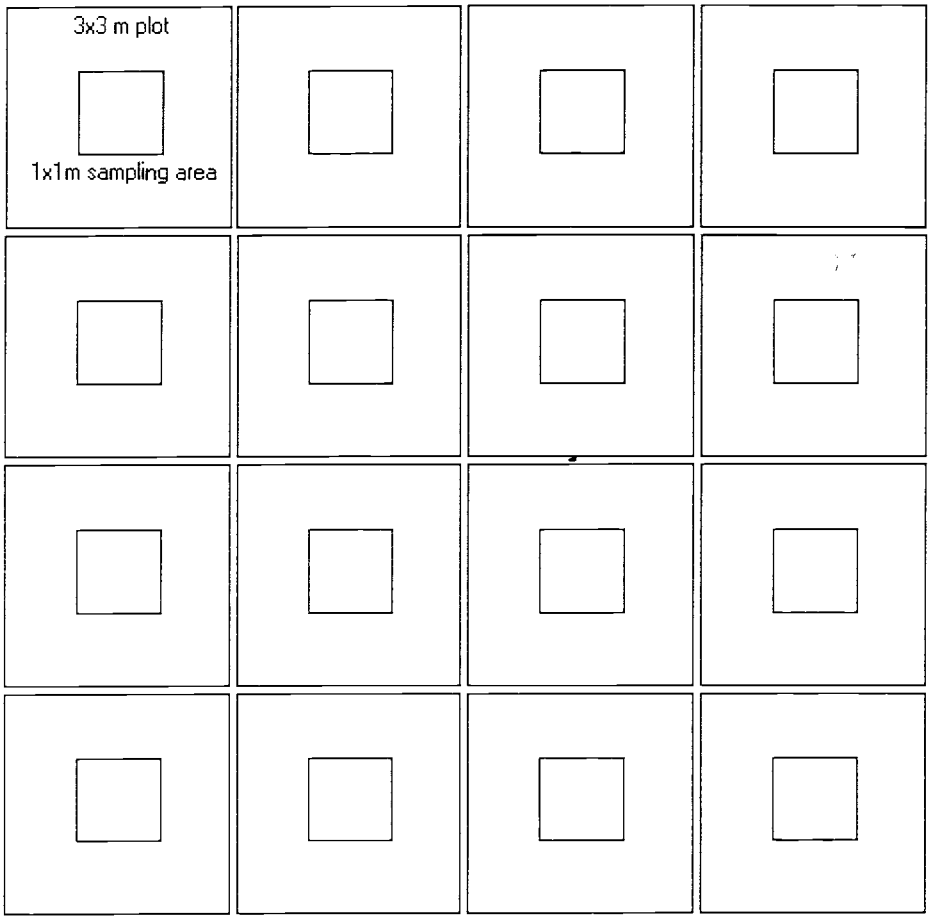

Figure 1. Experimental design of one block consisting of a 12x12m area with 16 plots each measuring 3x3m. Within each plot was a 1x1m sampling area in which treatment response was measured.

Block preparation included removal of all standing vegetation in September 1998 by clipping to ground level. All treatment response measurements were taken within 1 m square area near the center of each plot. This allowed a buffer strip of 2 m between sampling areas, limiting the effects of neighboring treatments on sampling areas.

Response measurements included number of seedheads per plant, seedhead diameter, number of seeds per seedhead, number of seeds per plant, number of plants m^{-2}, number of seeds m^{-2}, percent germination, number of branches per plant and plant height. Additionally, pre-dawn xylem pressure and gravimetric soil moisture was also measured. Measurements of response to defoliation treatments were collected at the end of the growing season during the seed dissemination phenological stage.

Treatments were also evaluated using actual measurements of numbers of seeds ("actual seed yield") and an estimate of seed production ("estimated seed yield") based on the predictive regression equation of Pitcairn et al. (1998):

$$Y = 6.22X - 6.21 \qquad \text{(Equation 1)}$$

where Y = the number of fertile flowers and X = widest outside flower head diameter measured to the nearest millimeter. The authors found good correlation ($r^2 = 0.82$) using this equation. Use of the model here assumes that the population of yellow starthistle plants in northeastern Oregon had the same correlation between seedhead diameter and number of seeds per seedhead as populations in California and that the control agents did not influence seedhead diameter. Estimated seed

yield was determined for all seedheads, whether infested with insects or not. Actual seed yield data were not combined with estimated seed yield data for analysis. Analysis of the numbers of actual seed yield and estimated seed yield included numbers of seeds per seedhead, seeds per plant and seeds m^2. Density of yellow starthistle (plants m^{-2}) was measured to determine number of seeds m^{-2}. Analysis of seeds was conducted on the combined numbers of plumed and non-plumed seeds; separate analyses based on seed types were not conducted to compare actual yield with estimated yield because the predictive equation is for total combined number of plumed and non-plumed seeds per seedhead.

Collections of seedheads were made when seedheads were in the mature seed stage. A total of 471 seedheads were collected. Collection dates varied based on the regrowth of the treatments. Seedheads were collected on July 29, 1999 for treatments not defoliated; August 9, 1999 for treatments defoliated at the bolting stage; August 16, 1999 for treatments defoliated at the bud stage; and August 19, 1999 for treatments defoliated both at the bolting stage and again at the bud stage. Upon collection, each seedhead was placed in a separate paper bag in case the seed began to disseminate during storage. For each plot five to 10 seedheads were collected. Seedheads were collected from separate plants unless enough plants were not available. The actual number of seedheads collected per replication depended on the available number of plants. Measurements taken at the lab included seedhead diameter and a count of the total number of seeds per seedhead, or actual yield. The widest outside diameter of each seedhead was measured to the

nearest millimeter using calipers (Pitcairn et al. 1998). Seedhead diameter is used in estimating the number of seeds per seedhead. Seedheads were carefully opened after seedhead diameter was recorded and the number of plumed and non-plumed seeds counted. Average number of seeds per seedhead for each plot was used in analysis of variance as actual yield data providing 64 total degrees of freedom for the analysis of variance. Treatment means are the average of all 16 plots for each treatment across the 4 blocks, while block means are the average of all 16 plots at each block.

The number of seedheads per plant and the density of yellow starthistle plants were determined for each treatment at the time of seedhead collections. The number of seedheads per plant was determined by randomly identifying 20 plants per plot and counting total number of seedheads per plant. In many cases there were less than 20 plants available and all plants per plot were identified. Density of yellow starthistle was measured in a 1m x 1m area using a square plot placed inside each 3m x 3m treatment plot.

Estimated number of seeds per plant for each plot was derived by multiplying the number of seedheads per plant by the estimated number of seeds per seedhead. This calculation used the estimated number of seeds per seedhead derived from the regression equation (Pitcairn et al. 1998). Number of seeds m^{-2} was derived by multiplying the number of seeds per plant with the number of plants m^{-2}. Both the number of seeds per plant and the number of seeds m^{-2} were

analyzed in the same way that the number of seeds per seedhead were analyzed using analysis of variance:

Source of Variation	Degrees of Freedom
Total (n-1)	63
Block (B-1)	3
Treatment (T-1)	3
Block*Treatment (B-1)(T-1)	9
Error (n-1)-(B-1)-(T-1)-(B-1)(T-1)	48

Pre-dawn xylem pressure measurements were taken 7-10 days following defoliation using a pressure chamber (PMS Inc., Corvallis, Ore.) to evaluate plant water status (Waring and Cleary 1967, Turner 1988). Three plants within each plot were measured on the specified date. There were 5 treatments measured for pre-dawn xylem pressure potential. Treatment three of the defoliation study, defoliation at bolting stage and again at bud stage, was divided into two treatments corresponding to treatment 3 and 4 for measurements of pre-dawn xylem pressure potential:

Treatment 1	Bolting
Treatment 2	Bud
Treatment 3	First cutting of bolting
Treatment 4	Second cutting of bud
Treatment 5	No defoliation

Pre-dawn xylem pressure measurements of defoliated treatments were compared to the control using analysis of variance:

Source of Variation	Degrees of Freedom
Total (n-1)	98
Block (B-1)	3
Treatment (T-1)	4
Block*Treatment (B-1)(T-1)	12
Error (n-1)-(B-1)-(T-1)-(B-1)(T-1)	79

Soil moisture was determined using the gravimetric method of Reynolds (1970). Soil moisture was calculated as the mass of water per oven dry weight of soil sample (θm). Soil was collected from 3 replications/block at each of 3 depths (0-15 cm, 15-30 cm, and 30-46 cm) and was placed in separate soil tins. Due to shallow soils, site numbers 3 and 4 were measured only at the 0-15 cm and 15-30 cm depths. Soil moisture samples were collected to correspond to phenological stages; and when forage analysis samples were collected, approximately once a month from April through September 1999.

Germination trials were conducted to determine differences in viability of plumed seeds among the defoliation treatments. Non-plumed seeds were not used because there were too few collected. Two replications of 50 plumed seeds collected from each treatment were used in a controlled environmental chamber (model SG 30, Hoffman Mfg. Co., Albany, Ore.). Seeds were maintained in the dark at a constant 20 C (Joley et al. 1997). Fifty seeds were arranged in a 100 mm x

15 mm disposable petri dish on 2 sheets of filter paper (VWR, grade 417). Five-ml distilled water was added to each dish. Moisture in petri dishes was maintained as described by AOSA (1994). Petri dishes were sealed in plastic bags with moistened paper towels to help maintain humidity. The criterion for seed germination was emergence of a radicle. Seeds were examined daily at 0730 and 1630 hrs for 10 days to determine rates of germination. Germinated seeds were discarded after counting. Total germination was compared using analysis of variance:

Source of Variation	Degrees of Freedom
Total (n-1)	31
Block (B-1)	3
Treatment (T-1)	3
Block*Treatment (B-1)(T-1)	9
Error (n-1)-(B-1)-(T-1)-(B-1)(T-1)	17

Treatment means were compared using least significant difference ($p \leq 0.05$).

Two measures of plant morphology (number of branches and plant height) were used as indicators of plant fitness in response to defoliation. Measurements were taken when plants had reached the seed dissemination stage. Five plants were randomly selected from each plot for measurement. Plant height (cm) was measured from the ground to the tip of the terminal bud. If the top of the plant branched, plant height was measured to the tip of the longest terminal branch. Number of branches per plant were also counted at this time. Analysis of variance was used to determine significance of block and treatment means:

Source of Variation	Degrees of Freedom
Total (n-1)	63
Block (B-1)	3
Treatment (T-1)	3
Block*Treatment (B-1)(T-1)	9
Error (n-1)-(B-1)-(T-1)-(B-1)(T-1)	48

Means were compared using least significant difference ($p \leq 0.05$).

Because of the presence on the study area of the introduced biological control insects, *Bangasternus orientalis, Larinus curtus, Eustenopus villosus, Urophora sirunaseva* and *Chaetorellia ssp.*, attempts were made to separate the effects of the defoliation treatments from damage caused by these insects on seed production. In an effort to exclude biological control insects from the seedheads, hand-sewn bags of 1/4mm netting were placed over seedheads during the flowering stage. For each plot two bags were used and placed over two separate seedheads on different plants. The mean number of seeds from those seedheads was used in analysis to determine the effectiveness of this procedure on excluding insects.

Defoliation may delay floral induction and seed production development of yellow starthistle (Benefield et al. 1999). If so, the synchronization of timing of the life cycle of biological control insects with the plant's phenology may be altered and the effectiveness of those insects reduced. To determine the compatibility of defoliation with biological control insects, the frequency (% infestation) of insects for each plot was measured using the following equation:

$$Y = A / B * 100 \qquad \text{(Equation 2)}$$

Where Y is the percent of seedheads infested, A is the number of seedheads infested with a biological control agents and B is the total number of seedheads examined. Infestation was determined for each seedhead collected in the defoliation study. In the lab, infestation was counted if a larvae or adult insect was found in the seedhead. Evidence that there had been a biological control agent occupying a seedhead included partially eaten seed, no seed and plant chaff or a pupa chamber (Rees et al. 1996). Average percent infestation for each plot was used in analysis. Differences in percent infestation among treatments and blocks were compared using analysis of variance:

Source of Variation	Degrees of Freedom
Total (n-1)	63
Block (B-1)	3
Treatment (T-1)	3
Block*Treatment (B-1)(T-1)	9
Error (n-1)-(B-1)-(T-1)-(B-1)(T-1)	48

To determine if biological control agents were impacted by defoliation treatments, an analysis was conducted on the number of seeds per seedhead from infested seedheads. There was a total of 278 seedheads infested with biological control agents of the total 471 collected. Treatment

means from non-infested seedheads were analyzed separately. Treatment means were analyzed with analysis of variance:

Source of Variation	Degrees of Freedom
Total (n-1)	276
Treatment (T-1)	3
Error (n-1)-(T-1)	273

Percent reduction in number of seeds from infested seedheads was calculated for each biological control species using the following equation:

$$Y = C - D / C * 100 \qquad \text{(Equation 3)}$$

Where Y is percent reduction in number of seeds per seedhead, C is the average number of seeds from non-infested seedheads and D is the average number of seeds from infested seedheads. Means and standard errors were reported along with the total number of seedheads infested by each biological control species.

Chemical Composition Study

A study was conducted in 1998 and 1999 to determine the forage nutrient composition of yellow starthistle at different stages of phenological development. In 1998 samples were collected at 2 sites each in Union (Sites A and B) and Baker (Sites C and D) Counties, and 3 sites in Umatilla (Sites E, F and G) County, Ore. Site A is located at an elevation of 1100 m on Ramo-Conley complex soils (USDA-SCS 1985a). The plant community is composed of yellow starthistle on rocky outcrops within a field of alfalfa. Site B is located on Palouse silt loam (USDA-

SCS 1985b) and has an elevation of 1020 m. It is dominated by yellow starthistle. Site C is located at 3200 m and is situated on Clovercreek-Keating complex soils (USDA-NRCS 1997). Site D is 230 m from Site C and is also located on this soil series. The plant community at both sites is composed of yellow starthistle and medusahead (*Taeniatherum asperum* Nevski.). Site E, F and G correspond to site 1, 2 and 3, respectively, of the defoliation study. During 1999, 4 sites within Umatilla County were sampled for forage analysis. These (Sites E, F, G and H) corresponded to Sites 1, 2, 3 and 4, respectively, of the defoliation study.

Collections of plant samples for forage nutrient composition were made using Maddox's (1981) definitions of phenological development of yellow starthistle. About 400 g (dry matter) of plant material was collected from each site by clipping at ground level. Five separate samples from each site were collected and weighed. All plant material was rinsed with distilled water to remove detritus before oven-drying at 50 C for 48h. The average percent dry weight of the five samples was recorded. Plant material was ground in a Wiley mill through a 1 mm screen and stored in plastic bags for chemical analysis. Crude protein (CP) was determined using the Buchi 316 distillation unit. *In vitro* dry matter digestibility (IVDMD) was determined using the ANKOM Technology Daisy Incubator. Acid detergent fiber (ADF) and neutral detergent fiber (NDF) were determined on the ANKOM 200 Fiber Analyzer. Acid detergent lignin (ADL) was determined using 72% H_2SO_4 in the ANKOM 200 Fiber Analyzer. Percent cellulose and acid insoluble ash were determined by calculation. Mineral components (percent P, K,

Ca, Mg, and parts per million of Mn, Fe, Cu, Zn, Na) were determined by microwave digestion and inductively coupled plasma (ICP) procedures (Tan 1996) at the Central Analytical Laboratory of Oregon State University. Forage nutrient components were compared among phenological stages using analysis of variance:

Source of Variation	Degrees of Freedom
Total (n-1)	48
Treatment (T-1)	9
Error (n-1)- (T-1)	39

Treatment means were compared using least significant difference ($p \leq 0.05$) for unequal replication.

Results

Plant Population and Structure

Analysis of post-treatment plant density (plants m^{-2}) showed differences among treatment means ($p = 0.0001$) (Appendix). Data were not normally distributed and was log transformed for analysis. Defoliation at the bud stage and defoliation twice (bolting and bud) had fewer plants m^{-2} than defoliation at the bolting stage or non-defoliated controls (Table 2).

Data for average plant height were not normally distributed and the natural log transformation was used in analysis. Differences in plant height were detected among treatment means ($p = 0.0001$) (Appendix). Plots that were not defoliated had taller plants than all defoliation treatments (Table 3). Mean height was 71.6cm for plants not defoliated. Non-defoliated plants were about twice as tall as the mean of plants defoliated once during either the bolting or bud stage. Non-defoliated plants were 3 times taller than plants defoliated twice (bolting and bud).

No treatment differences among the numbers of branches per plant were detected ($p = 0.32$) (Appendix). Average number of branches per plant was 1.7 (Table 4).

Defoliation ($p = 0.0008$) reduced the mean number of seedheads per plant (Appendix). There are a greater number of seedheads on non-defoliated controls than on plants defoliated during the bud stage or defoliated twice (bolting and bud)

Table 2. Post-treatment density (plants m^{-2}) of yellow starthistle plants for four defoliation treatments.

	Plants m^2		
Defoliation Treatment	Mean[a]	SE	LSD[b]
Bolting	37.9	28.9	a
Bud	23.9	36.7	b
Bolt and Bud	12.6	8.2	b
No Defoliation	53.1	44.7	a

a = data were not normally distributed and were transformed using the natural log for analysis and are reported here in their original value.
b = means of transformed data followed by the same letter were not significantly different at the 0.05 level using Least Significant Difference test.

Table 3. Mean height (cm) of yellow starthistle plants following four different timings of defoliation.

	Plant Height (cm)		
Defoliation Treatment	Mean[a]	SE	LSD[b]
Bolting	37.5	13.2	a
Bud	32.9	6.7	a
Bolting and Bud	23.8	9.6	b
No Defoliation	71.6	20.2	c

a = data were not normally distributed and were transformed using the natural log for analysis and are reported here in their original value.
b = means of transformed data followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

Table 4. Mean number of branches on yellow starthistle plants following four different timings of defoliation.

	Number of Branches/Plant		
Defoliation Treatment	Mean	SE	LSD[a]
Bolting	1.8	1.2	a
Bud	1.4	0.8	a
Bolting and Bud	1.6	1.3	a
No Defoliation	2.1	1.7	a

a = means followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

(Table 5). However, there were no differences in number of seedheads between one early defoliation at bolting stage and the non-defoliated controls. There were no differences in mean number of seedheads among defoliated treatments.

Difference ($p = 0.0000$) among seedhead diameters were detected for defoliation treatments (Appendix). Treatments with no defoliation had larger seedhead diameters (Table 6). Seedheads of plants defoliated during bolting averaged 6.8 mm in diameter. This was greater than seedheads of plants defoliated twice, once at bolting and again at bud, but not different from diameter of seedheads defoliated only during the bud stage. There were no differences in seedhead diameter between plants defoliated once during the bud stage and plants defoliated twice (bolting and bud).

Seed Production and Germination

Analysis of variance showed no differences ($p = 0.57$) (Appendix) among treatment means of the numbers of seed per seed head for seedheads not infested with biological control agents. Total number of seedheads used in this analysis was 191 (Table 7). Evidence of a seedhead feeder, *Eustenopus villosus*, may have impacted the number of seedheads available for this analysis. In an attempt to obtain an estimated count of the number of seeds per seedhead a regression analysis on the 191 non-infested seedheads was conducted (Figure 2). The following equation was derived:

$$Y = -0.0452 + 4.1285X \qquad \text{(Equation 4)}$$

Table 5. Mean number of seedheads per yellow starthistle plant following four different defoliation treatments in northeastern Oregon.

	Seedheads per Plant		
Defoliation Treatment	Mean	SE	LSD[a]
Bolting	4.3	0.68	ab
Bud	3.2	0.56	b
Bolting and Bud	3.5	0.41	b
No Defoliation	5.5	0.84	a

a = means followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

Table 6. Seedhead diameter (mm) for yellow starthistle seedheads collected from four defoliation treatments in northeastern Oregon.

Defoliation Treatment	Seedhead Diameter (mm)		
	Mean	SE	LSD[a]
Bolting	6.8	0.2	b
Bud	6.5	0.2	bc
Bolting and Bud	6.0	0.2	c
No Defoliation	8.0	0.2	a

a = means followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

Table 7. Actual yield of plumed and non-plumed yellow starthistle seeds from seedheads collected from four defoliation treatments and four locations in northeastern Oregon.

	Number of Seeds		
Defoliation Treatment	Mean	SE	LSD[a]
Bolting	27.5	2.7	a
Bud	30.1	2.6	a
Bolt and Bud	27.0	2.6	a
No Defoliation	25.1	3.0	a

a = means followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

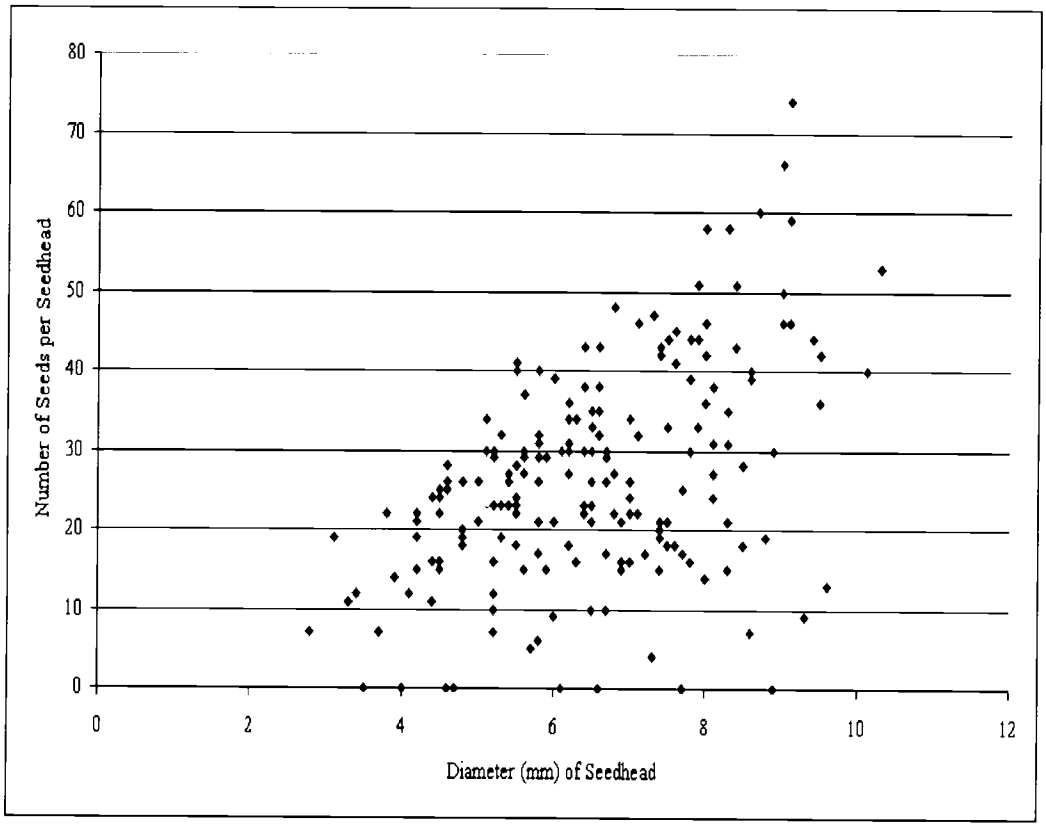

Figure 2. Scatterplot of the 191 seedheads used in developing a regression equation to predict number of seeds per seedhead based on diameter (mm) of the seedhead.

Where Y = the number of plumed and non-plumed seeds per seedhead and X = the diameter of the seedhead. The r^2 value was 0.22 showing that there was a lack of correlation among seedhead diameter and the number of seeds per seedhead (Table 8).

In the absence of developing a good fitting equation, the average equation from a previous study (Equation 1) showing good results for estimating the number of seeds per seedhead based on the average seedhead diameter was used to estimate the number of seeds per seedhead (Pitcairn et al. 1998). In this analysis all the seedheads collected in the study, 471, were used to estimate number of seeds per seedhead based on seedhead diameter. Results of the analysis showed a treatment effect ($p = 0.0000$) (Appendix) in which the non-defoliated control had greater mean number of seeds than all defoliation treatments (Table 9). Plants defoliated during bolting produced an average of 36.2 seeds per seedhead. This was not different from the number of seeds per seedhead produced by plants defoliated during the bud stage, but was greater than plants defoliated twice (bolting and bud).

Data for estimated numbers of seeds per plant were not normally distributed and were transformed using the natural log. Analysis of variance detected differences among treatment means ($p = 0.0049$) (Appendix). The non-defoliated control group produced nearly twice as many seeds per plant as any defoliation treatment. (Table 10). There were no differences in numbers of seeds per plant among the defoliated treatments.

Table 8. Linear regression analysis of 191 seedheads showing a lack of correlation among seedhead diameter and the number of seeds per seedhead.

Coefficients	Value	SE	t-value	P-value
Intercept	-0.0452	3.7300	-0.0121	0.9903
Diameter	4.1285	0.5593	7.3810	0.0000

Residual standard error: 12.02 on 189 degrees of freedom
R-squared: 0.2238

Table 9. Estimated[a] yield of plumed and non-plumed yellow starthistle seeds per seedhead from four defoliation treatments in northeastern Oregon.

Defoliation Treatment	Estimated Seeds per Seedhead		
	Mean	SE	LSD[b]
Bolting	36.2	1.1	b
Bud	33.6	1.3	bc
Bolt and Bud	32.6	1.5	c
No Defoliation	43.1	1.1	a

a = Yield was estimated using the regression equation Y = 6.22(X) - 6.21 where Y is number of seeds and X is seedhead diameter(mm) (Pitcairn et al. 1998).

b = means followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

Table 10. Estimated yield[a] of plumed and non-plumed yellow starthistle seeds per plant from four defoliation treatments in northeastern Oregon.

Defoliation Treatment	Estimated Seeds per Plant		
	Mean[b]	SE	LSD[c]
Bolting	139	28	b
Bud	115	25	b
Bolt & Bud	116	17	b
No Defoliation	246	42	a

a = yield was estimated using the regression equation Y = 6.22(X) - 6.21 where Y is number of seeds and X is seedhead diameter(mm) (Pitcairn et al. 1998).

b = data were not normally distributed and were transformed using the natural log for analysis and are reported here in their original value.

c = means of transformed data followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

Data for the estimated numbers of seeds m^{-2} were not normally distributed and were transformed using the natural log. There were differences among treatment means for the numbers of seeds m^{-2} ($p = 0.0001$) (Appendix). The non-defoliated treatment and the treatment defoliated once at the bolting stage had greater number of seeds m^{-2} than defoliation once at the bud stage or defoliation twice (bolting and bud) (Table 11).

There were no differences among mean percent germination for plumed seeds from different locations ($p = 0.24$) (Appendix). No differences were detected among mean percent germination for plumed seeds of different treatments ($p = 0.19$) (Table 12). The grand mean percent germination of plumed seeds for all locations and treatments was 95%. Almost all germination occurred within the first 72 hours of the trial.

Biological and Environmental Influences

Differences among pre-dawn xylem pressure potentials were detected using analysis of variance ($p = 0.0002$) (Appendix). Defoliation twice, once at bolting and again at bud, had more negative pre-dawn pressure potentials than all other treatments (Table 13). Defoliation once at bud stage and no defoliation treatments had more negative pre-dawn pressure potentials than defoliation once at the bolting stage of growth and first cutting at bolting stage of growth. There were differences among locations ($p=0.0001$) and an interaction between location and treatment effects (p-value = 0.04).

Table 11. Estimated yield[a] of plumed and non-plumed yellow starthistle seeds per square meter from four defoliation treatments and four locations in northeastern Oregon.

	Seeds m^2		
Defoliation Treatment	Mean[b]	SE	LSD[c]
Bolt	5483	1221	a
Bud	1417	373	b
Bolt & Bud	1717	411	b
No Defoliation	10616	2203	a

a = yield was estimated using the regression equation Y = 6.22(X) - 6.21 where Y is number of seed and X is seedhead diameter(mm)

b= data were not normally distributed and were transformed using the natural log for analysis and are reported here in their original value.

c = means of transformed data followed by the same letter are not significantly different at the 0.005 level using Least Significant Difference test.

Table 12. Total percent germination of plumed yellow starthistle seeds from four defoliation treatments and four locations in northeastern Oregon.

	Percent Germination		
Defoliation Treatment	Mean	SE	LSD[a]
Bolting	95.5	3.0	a
Bud	96.1	6.1	a
Bolt and Bud	96.9	3.5	a
No Defoliation	91.1	4.6	a

a = means followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

Table 13. Pre-dawn xylem pressure potential following five defoliation treatments of yellow starthistle plants in northeastern Oregon.

	Xylem Pressure		
Defoliation Treatment	Mean (-MPa)	SE	LSD[a]
Bolting	1.4007	0.8212	a
Bud	1.9320	0.6576	b
First cut of Bolting	1.2329	0.5314	a
Second cut of Bud	2.3421	0.8477	c
No Defoliation	1.9490	0.3460	b

a = means followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

Soil moisture varied from 0.01 to 0.25 θm (Figure 3). Differences among the three depths were not detected ($p = 0.71$) (Appendix).

Bagging seedheads before dissemination in order to exclude the biological control agents was not effective. Of a total of 128 bagged seedheads, 69 were infested with biological control agents. Ten bags were lost or the seed had disseminated before collection. Forty-nine bags excluded biological control agents.

In an effort to understand the impact of biological control agents on seed production an analysis was conducted on all 471 seedheads collected for the defoliation study. Percent infestation was calculated for the 4 defoliation treatments and separately for the 4 locations (Equation 2). Analysis of variance showed no differences in mean infestation among treatments ($p = 0.25$) (Appendix). Mean infestation of all treatments was 62% (Table 14). There were differences among locations ($p = 0.0001$). Sites 1, 3 and 4 had higher infestation rates than site 2.

There was a high percentage of damaged seedheads due to *Eustenopus villosus* at site 2. This damage was not seen at the sites 1, 3 and 4. *Eustenopus villosus* eats into the stem just below the seed head causing the seedhead not to form and to droop sideways on the stem. There were very few seedheads formed in the control plots so seedheads were collected from the immediate surrounding area to represent the control plots which had no defoliation. Seedheads that did form, formed later than at the other sites and they were from buds that developed later and lower on the stems of the plants. These later forming seedheads missed the

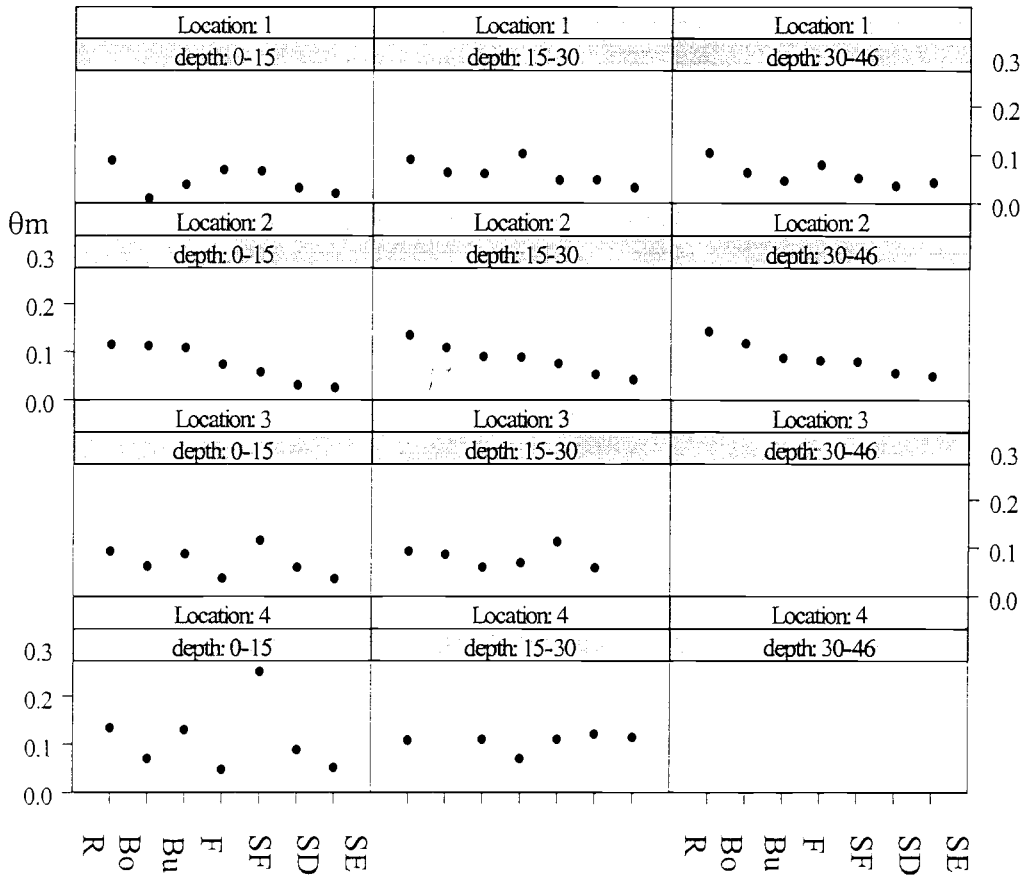

Figure 3. Soil moisture content (θm) at three depths (0-15, 15-30, 30-46cm) from 4 locations. Soil moisture collections corresponded to seven phenological stages: R= Rosette, Bo = Bolting, Bu = Bud, F = Flower, SF = Seed Formation, SD = Seed Dissemination, SE = Senesence.

Table 14. Percent infestation of yellow starthistle seedheads[a] of biological control agents from four defoliation treatments[b] and four locations[c] in northeastern Oregon.

	Percent Infestation		
b) Defoliation Treatment	Mean	SE	LSD[d]
Bolt	66	6	a
Bud	66	8	a
Bolt & Bud	63	7	a
No Defoliation	51	7	a
c) Location	Mean	SE	LSD
1	71	6	a
2	34	8	b
3	72	5	a
4	69	4	a

a = total number of seedheads examined was 471.
d = means followed by the same letter are not significantly different at the 0.05 level using Least Significant Difference test.

window of egg laying by the biological control agents, so due to sampling technique site 2 was represented as having less infestation rates than the other sites.

The number of seeds per infested seedhead were analyzed to see if defoliation treatments influenced the biological control agents and the raw data were summarized (no statistical analysis) for individual control agents. Defoliation treatments did not affect the number of seeds per seedhead from seedheads infested with biological control agents ($p = 0.16$) (Appendix). Total number of seedheads used in this analysis was 278. There was an average of 7 seeds per seedhead from infested seedheads (Table 15).

Species of biological control agent could affect the level of seed reduction. The fly *Chaetorellia ssp.* was the most frequent biological control agent with a 20% infestation of seedheads examined. Its feeding resulted in an average of 6 seeds per seedhead causing a 78% reduction in average number of seeds per seedhead (Equation 3) compared to non-infested seedheads (Table 16).

The weevil *Eustenopus villosus* was the second most frequent biological control agent with an infestation of 16% of the total number of seedheads examined. Feeding by the weevil resulted in an average of 4 total seeds per seedhead, which is an 85% reduction in the average number of seeds per seedhead. The average number of seeds per seedhead for non-infested seedheads was 27. Forty-one percent of the seedheads examined were not infested with biological control agents. Other biological control agents found in the study included 5

Table 15. Average number of seeds per seedhead from seedheads[a] infested with biological control agents for each defoliation treatment.

	Average Number of Seeds per Seedhead		
Defoliation Treatment	Mean	SE	LSD[b]
Bolt	7	6	a
Bud	7	8	a
Bolt & Bud	6	3	a
No Defoliation	6	10	a

a = total number of seedheads examined was 278.
b = means followed by the same letter are not significantly different at the 0.05 level.

Table 16. Percent reduction of yellow starthistle seeds from infested seedheads for each species of biological control agent compared to non-infested seedheads found at four locations in northeastern Oregon.

	Percent Reduction of Seeds per Seedhead		
Species	Mean	SE	n
Chaetorellia spp.	78	23	91
Eustenopus villosus	85	18	74
Urophera sirunaseva	41	29	18
Larinus curtus	94	6	5
Bangasternus orientalis	58	-	1

n=total number of seedheads examined for each species.

Larinus curtus weevils, 1 *Bangasternus orientalis* weevil, and 18 *Urophora sirunaseva* flies.

Chemical Composition Study

There were differences among acid detergent fiber contents at various phenological stages ($p = 0.0001$). Acid detergent fiber was greater than 40% after the flowering stage of growth (Table 17). There were differences in lignin content among phenological stages ($p = 0.0001$). Lignin increased from 1.2 at the rosette stage to 2.9% at seed dissemination. Differences in cellulose content were detected ($p = 0.0001$). Highest cellulose content occurred at the seed formation stage with a mean value of 19.4%. Significant differences in acid insoluble ash content were detected ($p = 0.0001$). Highest concentrations occurred at the rosette stage of growth with a mean value of 1.3%. There were not significant differences among the other stages of growth. Mean acid insoluble ash for the latter stages of growth were 0.5. Significant differences in neutral detergent fiber content were detected ($p = 0.0001$). The lowest neutral detergent fiber content occurred at the rosette stage with a mean of 24.6%. Highest neutral detergent fiber content was at the seed formation stage with a mean of 55.0%. Differences in crude protein content were detected ($p = 0.0001$). Crude protein levels through the bolting stage of growth were adequate for the maintenance of ewes. Ewes require a minimum of 8.9% protein concentration in diet dry matter for maintenance needs (NRC 1985). Crude protein levels at the bolting stage of growth were 10.6%. After the bolting

Table 17. Nutrient composition of six phenological stages of yellow starthistle collected in northeastern Oregon in 1998 and 1999.

Phenological Stage	Acid Detergent Fiber (%)		Lignin (%)		Cellulose (%)		Acid Insoluble Ash (%)	
Rosette	23.8	a[1]	1.2	a	9.6	a	1.3	a
(n=6)[2]	(2.2)[3]		(0.3)		(1.3)		(0.2)	
Bolting	31.6	b	1.1	a	14.0	ab	0.7	ab
(n=7)	(3.9)		(0.2)		(1.9)		(0.1)	
Bud	37.2	b	1.8	ab	16.6	ab	0.6	b
(n=9)	(3.9)		(0.3)		(2.2)		(0.1)	
Flower	37.3	b	2.4	bc	16.2	ab	0.4	b
(n=8)	(4.1)		(0.4)		(1.9)		(0.03)	
Seed Formation	44.1	b	2.8	bc	19.4	b	0.5	b
(n=9)	(5.4)		(0.4)		(3.5)		(0.03)	
Seed Dissemination	43.7	b	2.9	c	18.5	b	0.5	b
(n=4)	(4.5)		(0.2)		(2.1)		(0.1)	

[1]means followed by different letters are significantly different; $p<0.05$

[2]sample size

[3]standard error

Table 17 (continued). Nutrient composition of six phenological stages of yellow starthistle collected in northeastern Oregon in 1998 and 1999.

Phenological Stage	Neutral Detergent Fiber		Crude Protein		*In Vitro* Dry Matter Digestibility	
	(%)		(%)		(%)	
Rosette	24.6	a	16.7	a	84.8	a
(n=6)[2]	(2.7)		(3.4)		(2.7)	
Bolting	35.5	b	10.6	bc	75.1	b
(n=7)	(4.3)		(2.9)		(3.9)	
Bud	46.1	c	8.0	cd	64.0	c
(n=9)	(3.3)		(1.8)		(2.7)	
Flower	46.6	d	5.9	d	63.0	c
(n=8)	(3.9)		(0.63)		(2.7)	
Seed Formation	55.0	e	5.0	d	57.7	c
(n=9)	(6.1)		(1.01)		(5.9)	
Seed Dissemination	54.5	e	5.5	d	57.0	c
(n=4)	(5.9)		(0.42)		(4.9)	

[1]means followed by different letters are significantly different; $p<0.05$

[2]sample size

[3]standard error

stage of growth mean crude protein levels declined. Differences in *in vitro* dry matter digestibility were detected ($p = 0.0001$). Highest digestibility occurred at the rosette stage (84.8%). Mean *in vitro* digestibility dropped to 75.1% at the bolting stage of growth. Differences in *in vitro* digestibility were not detected among the bud stage through the seed dissemination stage of growth with an average *in vitro* digestibility of 60.4%. Mineral composition of yellow starthistle plants was adequate to meet the requirements of sheep (Table 18). Calcium levels were higher than the requirement through all stages of plant growth. No differences ($p = 0.1$) were detected among phenological stages. Maintenance requirements for ewes of 60-80kg range from 0.25 to 0.30% (NRC 1985). Phosphorus levels were also adequate through all stages of plant growth to meet sheep requirements. No differences ($p = 0.1$) were detected among plant phenological stages. Maintenance requirements for ewes of 60-80kg range from 0.24 to 0.28% (NRC 1985). Sodium values showed a wide range among phenological stages but were not different ($p = 0.1$) among phenological stages.

Table 18. Mineral composition of six phenological stages of yellow starthistle collected in northeastern Oregon in 1998 and 1999.

	Phosphorus (%)		Potassium (%)		Calcium (%)		Magnesium (%)	
Rosette	0.4	a[1]	4.5	a	1.7	a	0.5	a
(n=6)[2]	(0.09)[3]		(0.6)		(0.3)		(0.07)	
Bolting	0.3	a	3.7	a	1.5	a	0.3	b
(n=7)	(0.05)		(0.7)		(0.3)		(0.09)	
Bud	0.3	a	2.4	b	1.1	a	0.3	b
(n=9)	(0.05)		(0.5)		(0.2)		(0.02)	
Flower	0.3	a	1.7	b	1.1	a	0.2	b
(n=8)	(0.04)		(0.3)		(0.1)		(0.03)	
Seed Formation	0.3	a	1.7	b	1.3	a	0.3	b
(n=9)	(0.05)		(0.2)		(0.1)		(0.06)	
Seed Dissemination	0.3	a	1.4	b	1.6	a	0.3	b
(n=4)	(0.04)		(0.2)		(0.1)		(0.03)	

[1]means followed by different letters are significantly different; $p<0.05$

[2]sample size

[3]standard error

Table 18 (continued). Mineral composition of six phenological stages of yellow starthistle collected in northeastern Oregon in 1998 and 1999.

	Iron (ppm)		Copper (ppm)		Zinc (ppm)		Sodium (ppm)		Manganese (ppm)	
Rosette	807.5	a	12.7	a	26.8	a	321.3	a	60.8	a
(n=6)[2]	(363.7)		(4.3)		(8.1)		(341.2)		(19.3)	
Bolting	334.3	a	10.6	a	27.6	a	184.0	a	42.6	a
(n=7)	(151.2)		(3.8)		(6.1)		(287.0)		(14.8)	
Bud	294.0	a	10.9	a	28.3	a	57.8	a	28.8	a
(n=9)	(145.8)		(2.9)		(7.6)		(47.3)		(7.9)	
Flower	221.8	a	10.9	a	28.0	a	121.5	a	21.8	b
(n=8)	(58.9)		(2.4)		(9.3)		(136.1)		(2.9)	
Seed Formation	288.0	a	12.6	a	28.3	a	136.1	a	21.9	b
(n=9)	(117.2)		(3.0)		(8.6)		(125.4)		(4.9)	
Seed Dissemination	512.3	a	14.5	a	26.3	a	128.3	a	25.5	a
(n=4)	(189.9)		(4.8)		(6.5)		(33.7)		(1.9)	

[1]means followed by different letters are significantly different; $p<0.05$

[2]sample size

[3]standard error

Discussion

This study showed differences in seedhead diameter among treatments but no differences in number of seeds per seedhead among treatments using counts of actual seed production. Infestation of seedheads by the various biological control agents was widespread and reduced seed production, thereby limiting attempts to build a regression equation predicting number of seeds/seedhead based on average seedhead diameter. By using the regression equation published by Pitcairn et al. (1998) to estimate seed production, significant reductions in number of seeds per seedhead were detected among defoliation treatments. Defoliation twice (once at bolting and again at bud) and defoliation once at bud had the greatest reduction in seeds per seedhead compared to other treatments. Plants that regrew following two defoliations were more water- stressed and produced fewer seeds than plants that were not defoliated. Number of seeds produced by plants defoliated twice was not significantly different from seed production of plants defoliated only once at the bud stage. Potential seed production of plants defoliated once at the bolting stage or bud stage did not differ. However, those treatments produced fewer seeds compared to non- defoliated plants. When using the estimated yield data, any defoliation decreased seed production compared to no defoliation.

A reduction in the number of seedheads per plant combined with a reduction in the number of seeds per seedhead reduced the number of seeds m^{-2}. Seeds that are produced are highly viable and there were no differences in percent germination among treatments.

If grazing is to be effective in reducing seed production of yellow starthistle, defoliation should be timed to coincide with the proper phenological stages. Defoliation twice, once at bolting and again at bud, may not be more effective in reducing potential seed production than only one defoliation timed to coincide with the bud stage. Livestock may not need to be reintroduced to an area for a second grazing to get the same benefit as defoliation once at the bud stage. Prolonged grazing could be detrimental to native species and any grazing strategy should be closely monitored to ensure that grazing impacts met objectives. In areas that receive frequent rains after the bud stage of growth, additional defoliation may be required to suppress the ability of yellow starthistle to regrow (Sheley and Petroff, 1999).

Digestibility levels were high through the bolting stage of growth and met maintenance requirements of domestic sheep throughout the remainder of the growing season. Defoliation twice, once at bolting and again at bud, would result in the greatest reduction of seed per seedhead and seeds m^{-2}. Ewe maintenance needs could be supported by this grazing strategy. Crude protein levels were adequate to the bud stage of development while digestibility levels remained above 60%.

Grazing in combination with biological control agents can reduce seed production. Defoliation did not impact biological control agent's infestation rates. Biological control agents caused an average reduction in numbers of seeds per seedhead of 76%. The added insurance derived from having biological control

agents impacting plants that are not defoliated in a grazing system is beneficial to decreasing seed production. A long-term commitment to the use of grazing management with biological control agents could reduce the density of yellow starthistle plants. On productive sites restoration efforts could be less costly after the density of yellow starthistle plants are reduced.

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Appendix

Analysis of Variance Tables

Appendix Table A1. Analysis of variance table of post-treatment density[a] of yellow starthistle plants.

Source	df	SS	MS	F-stat	P-value
Total	63	65.366			
Block	3	18.4139	6.138	12.68	0.0001
Treatment	3	19.3612	6.4537	13.33	0.0001
Error	57	27.5909	0.4841		

a=Data were not normally distributed and were transformed using the natural log for analysis.

Appendix Table A2. Analysis of variance table for mean height(cm) of yellow starthistle plants following defoliation.

Source	df	SS	MS	F-stat	P-value
Total	63	40.9440[a]			
Block	3	1.3026	0.4342	6.1224	0.0011
Treatment	3	35.5991	11.8664	167.3259	0.0001
Error	57	4.0423	0.0709		

a = Data were not normally distributed and were transformed using the natural log for analysis.

Appendix Table A3. Analysis of variance table of number of branches per yellow starthistle plant following defoliation.

Source	df	SS	MS	F-stat	P-value
Total	63	103.4894			
Block	3	26.9469	8.9823	7.11	0.0004
Treatment	3	4.5569	1.519	1.2	0.3170
Error	57	71.9856	1.2629		

Appendix Table A4. Analysis of variance table of the effects of defoliation on number of yellow starthistle seedheads per plant.

Source	df	SS	MS	F stat	P-value
Total	63	455.109			
Block	3	76.1719	25.3906	6.54	0.0085
Treatment	3	50.7969	16.9323	4.36	0.0008
Block x Treatment	9	141.891	15.7656	4.06	0.0006
Error	48	186.25	3.88021		

Appendix Table A5. Analysis of variance table of the effects of defoliation on seedhead diameter of yellow starthistle plants.

Source	df	SS	MS	F stat	P-value
Total	63	69.0000			
Block	3	4.6250	1.5417	3.52	0.0218
Treatment	3	35.3750	11.7917	26.95	0.0000
Block x Treatment	9	8.0000	0.8889	2.03	0.0558
Error	48	21.0000	0.4375		

Appendix Table A6. Analysis of variance table of the effects of defoliation on actual number of seeds per seedhead of yellow starthistle plants.

Source	df	SS	MS	F stat	P-value
Total	63	7477.8600			
Block	3	731.1720	243.7240	2.43	0.0769
Treatment	3	203.4220	67.8073	0.68	0.5715
Block x Treatment	9	1722.5200	191.3910	1.91	0.0737
Error	48	4820.7500	100.4320		

Appendix Table A7. Analysis of variance table of the effects of defoliation on the estimated[a] number of seeds per seedhead.

Source	df	SS	MS	F stat	P-value
Total	63	2687.75			
Block	3	313.625	104.542	5.24	0.0033
Treatment	3	1083.13	361.042	18.08	0.0000
Block x Treatment	9	332.5	36.9444	1.85	0.0832
Error	48	958.5	19.9687		

a = Yield was estimated using the regression equation Y = 6.22(X) - 6.21, were Y is number of seed and X is seedhead diameter(mm) (Pitcairn et al. 1998).

Appendix Table A8. Analysis of variance table for the effects of defoliation on the estimated[a] number of seeds per plant.

Source	df	SS	MS	F-stat	P-value
Total	63	38.4395[b]			
Block	3	7.1621	2.3874	6.86	0.0006
Treatment	3	5.0879	1.696	4.87	0.0049
Block x Treatment	9	9.4751	1.0528	3.02	0.0061
Error	48	16.7145	0.3482		

a = Yield was estimated using the regression equation Y = 6.22(X) - 6.21 were Y is number of seed and X is seedhead diameter(mm) (Pitcairn et al. 1998).

b = data were not normally distributed and were transformed using the natural log for analysis.

Appendix Table A9. Analysis of variance table for the estimated[a] number of seeds per square meter.

Source	df	SS	MS	F-stat	P-value
Total	63	116.196[b]			
Block	3	15.908	5.3027	5.2	0.003
Treatment	3	42.2046	14.0682	13.81	<0.0001
Error	57	58.0834	1.019		

a = Yield was estimated using the regression equation Y = 6.22(X) -6.21 were Y is number of seed and X is seedhead diameter(mm) (Pitcairn et al. 1998).

b = data were not normally distributed and were transformed using the natural log for analysis.

Appendix Table A10. Analysis of variance table of mean germination values of plumed yellow starthistle seeds from four defoliation treatments and four locations in northeastern Oregon.

Source	df	SS	MS	F-stat	P-value
Total	15	0.03191084			
Block	3	0.00949	0.003163	1.9796	0.1876
Treatment	3	0.00804	0.002679	1.6766	0.2406
Error	9	0.01438	0.001598		

Appendix Table A11. Analysis of variance of pre-dawn xylem pressure potentials (-Mpa) following five defoliation treatments of yellow starthistle plants.

Source	df	SS	MS	F-stat	P-value
Total	98	77.9518			
Block	3	11.8294	3.9431	7.89	0.0001
Treatment	4	12.8231	3.2058	6.42	0.0002
Block x Treatment	12	11.5398	0.9617	1.92	0.0435
Error	79	39.4682	0.4996		

Appendix Table A12. Analysis of variance table of soil moisture (θm) content from three depths (0-15, 15-30, 30-46cm).

Source	df	SS	MS	F-stat	P-value
Total	67	0.0965			
Depth	2	0.0010	0.0005	0.3464	0.7086
Error	65	0.0955	0.0015		

Appendix Table A13. Analysis of variance table of percent infestation of biological control agents in yellow starthistle seedheads from four locations following four defoliation treatments.

Source	df	SS	MS	F-stat	P-value
Total	63	51861.6550			
Block	3	16153.6001	5384.5334	9.23	0.0001
Treatment	3	2451.3734	817.1245	1.40	0.2520
Error	57	33256.6815	583.4506		

Appendix Table A14. Analysis of variance table of differences among number of seeds per seedhead from infested seedheads due to defoliation treatments.

Source	df	SS	MS	F-stat	P-value
Total	278	30416.23			
Treatment	3	563.75	187.9156	1.7185	0.1634
Error	273	29852.48	109.3497		