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Reproductive biology of yellow starthistle: maximizing late-season control

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Field studies at three sites and growth chamber experiments were conducted to determine the reproductive potential, flower phenology, seed viability and germination, and overall seedbank longevity of yellow starthistle in the Central Valley of California. At the three study sites, seedheads contained an average of between 65 and 83 achenes. Overall, 85% of the achenes were the interior pappus-bearing type, and the remaining 15% were the outer nonpappus-bearing type. Germinable seed did not initially develop until the late corolla senescence stage 8 d after flower initiation. Seed germination and viability 1 wk after dispersal were similar (86 and 91%, respectively). Comparison in flower phenology in 1996 and 1997 indicated that development from initial anthesis to achene dispersal more closely corresponded to days, rather than thermal units. In the field, germinable seed was produced when more than 2% of the total seedheads had initiated anthesis. To minimize seed production with late-season control methods, such as prescribed burning, mowing, or herbicide treatment, management strategies should be timed before the plant population has advanced beyond the 2% flower initiation stage. Over 84% of the seed germinated under growth chamber conditions 1 wk after seedheads reached the dispersal stage. This indicates that most yellow starthistle seed had little or no after-ripening requirements. In a field experiment, yellow starthistle seed germination corresponded to seasonal rainfall. A total of 44 and 39% of the pappus-bearing and nonpappus-bearing seed, respectively, germinated after one growing season. Of seed recovered from the soil after the first growing season, 88 and 81% of the pappus-bearing and nonpappus-bearing seed, respectively, was either damaged or degraded. From projected values based on recovered and germinated seed, it was estimated that over 97% of the total seed was removed from the soil seedbank after two growing seasons. These findings should assist land managers in developing long-term yellow starthistle management strategies.

Nomenclature: Yellow starthistle, *Centaurea solstitialis* L. CENSO.

Key words: Flower phenology, reproduction, seedbank, seedling emergence, seed germination, seed longevity, seed production, CENSO.

Yellow starthistle (*Centaurea solstitialis*) is a member of the Asteraceae (sunflower) family and was first introduced into California from Spain, in some cases via South America, in the mid- to late-1800s as a contaminant of alfalfa [*Medicago sativa* (L)] seed (Gerlach 1997). Today it is considered the most widely distributed noncrop weed in California, occurring in 56 of 58 counties and infesting between 15 and 22% of the state's surface area (Balciunas and Villegas 1999; Pitcairn et al. 1997; White 1999). The competitive abilities of yellow starthistle typically lead to the exclusion of many desirable species in pastures and rangelands, state and national parks, wildlands, and industrial sites, including roadsides and disturbed urban lands. As a result, yellow starthistle reduces native plant diversity, decreases recreation value of land, reduces forage production and grazing capacity, and can poison horses when consumed in large quantities (Callihan et al. 1995).

Among the methods for control of yellow starthistle, the most widely practiced techniques include mowing, livestock grazing, prescribed burning, biological control, and herbicides (DiTomaso et al. 1999c; Thomsen et al. 1994). Understanding the biology of yellow starthistle is key to developing a successful control program (Thomsen et al. 1994). Proper timing is critical to both the efficacy of most of these control options and to the minimization of seed production.

Yellow starthistle infestations have been reported to produce 125 to 250 million achenes ha^{-1} (DiTomaso et al. 1999a; Maddox 1981). Unlike most other species within the genus *Centaurea,* yellow starthistle produces dimorphic achenes, one type with a distinct pappus, and the other with a pappus either poorly developed or absent (Callihan et al. 1992). The pappus-bearing achenes are light to dark brown with tan striations throughout. By comparison, the nonpappus-bearing achenes are dark brown to black without striations. Nonpappus-bearing achenes occur in a single ring around the periphery of the head, whereas pappus-bearing achenes occur in many rings in the center of the seedhead. Development of achenes occurs centripetally, from the outer nonpappus-bearing achenes to the inner pappus-bearing achenes (Maddox et al. 1996).

The successful development of a long-term management program for yellow starthistle will depend upon an understanding of seedbank size and dynamics. The objectives of this study were to determine the (1) reproductive potential of yellow starthistle, (2) reproductive phenology and flowering stage when seed becomes viable and germinable, (3) effects of late-season control timing on achene production, and (4) germination timing and influence of achene degradation on seedbank longevity.

Materials and Methods

Site Parameters

Field studies were conducted at two sites in Davis, Yolo County, CA: adjacent to the University Airport (site A, 1996 and 1997) and along Putah Creek south of Interstate 80 (site B, 1999). Davis is in the northern half of California's Central Valley at 38.53°N, 121.78°W, and 18 m elevation. The study site received 56 cm rain in 1995/1996, 38 cm rain in 1996/1997, and 33 cm rain in 1998/1999 (field season, July 1 to June 30). The soil is classified as a Yolo Silty Loam and is a deep alluvial soil typical of the northern Central Valley. A third site was established in San Benito County (1999), in gently sloping coastal foothills 6.5 km south of the east entrance to Pinnacles National Monument. The San Benito County site is in the interior Coast Range in the center third of the state at 36.50°N, 121.08°W, and 500 m elevation. It received 27 cm of rain in 1998/1999. The soil is classified as a San Benito Clay Loam and is a deep alluvial soil typical of the central Coast Range.

The Davis sites were chosen as representing typical Central Valley yellow starthistle infestations; these sites were also convenient for extensive phenology measurements. The San Benito County site was added later for comparison with the results obtained from Davis. All yellow starthistle achenes were collected from a source near each experimental site. All experiments reported in this study were replicated twice in randomized complete block designs.

Timing of Seedhead Development

Thirty full-spiny seedheads (one seedhead per plant within a 200-m^2 area) were randomly tagged at each site, and the transition of each phenological stage was recorded over 4 wk from late June to mid-July 1996 and 1997. Ten phenologically distinct seedhead developmental stages were identified, ranging from full spiny to achene dispersal (Table 1). Phenological stages were easily distinguished without the need of a hand lens.

Seed Viability and Germination

Thirty to 100 seedheads from five reproductive stages (initial, middle, and late senescence; petal abscission; and achene dispersal; Table 1) were collected by clipping individual heads from several randomly selected plants within a 100-m^2 area at two sites in Yolo County, site A in 1996 and site B in 1999, and one site in San Benito County in 1999. Because insect biocontrol agents are widespread in California and all agents target yellow starthistle seedheads (Balciunas and Villegas 1999), only uninfested seedheads were used for viability and germination analyses. This was typically represented by 5 to 30 seedheads per phenological stage. The number of pappus and nonpappus-bearing achenes was determined from seedheads just before achene dispersal. Seedheads were allowed to dry for 1 wk under ambient conditions to simulate postcutting seed maturation following mowing. Achenes were carefully removed with tweezers 1 wk after clipping. Through visual evaluation, filled (swollen

TABLE 1. Ten distinct stages in yellow starthistle seedhead phenology.

Stage	No.	Description
Full spiny	1	Late bud; spines fully expanded
Prebloom	2	Florets appressed and barely protruding from apex of seedhead; white top
Flower initiation	3	Florets just protruding from bracts, straight up and down
Flower expansion	4	Florets opening, expanding downward; outside florets at 45° from vertical
Full bloom	5	All florets fully open and uniform in color, lemon yellow; outside florets at 90° from vertical
Initial senescence	6	Florets fully open but beginning to oxidize
Middle senescence	7	Florets continue oxidizing, becoming orange/brown; outside florets begin to close toward vertical
Late senescence	8	Florets further oxidized and nearly vertical, pale yellow/white; phyllaries green
Petal abscission	9	Florets completely oxidized; phyllaries browning
Achene dispersal	10	Florets abscise; phyllaries brown; pappus-bearing seeds disperse

throughout, no concave sides), partially filled (slightly swollen with concave sides), and unfilled (thin and flat) seed of the two achene types, pappus-bearing and nonpappus-bearing, was separated and counted from individual flowers of each stage. Pappus-bearing and nonpappus-bearing achenes were collected and combined from five seedheads in each flowering stage (approximately 200 seeds collected per flowering stage). Seed (1999 study sites only) was soaked in distilled water in petri dishes ($<$ 100 seeds/dish) for 12 to 24 h in the dark. The seed was then placed in petri dishes containing 1.0% tetrazolium (TZ) solution in the light at room temperature for up to 24 h. Seed that did not stain was considered nonviable. In germination tests, seed from individual seedheads was placed in 9-cm plastic petri dishes (pappus-bearing and nonpappus-bearing seed on separate dishes) on saturated Whatman filter paper 1 wk after clipping. Dishes were placed in a growth chamber and exposed to a fluctuating light (278 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux) and temperature (14/10 h at 25/20 C light/dark). Roché et al. (1997) previously reported a germination optimum for yellow starthistle at 25 C. Germination, defined as protrusion of the radicle through the testa, was recorded daily for 2 wk.

Time Course of Seed Production

In Yolo County (site A), 75 plants in various stages of flowering were sampled over a 200-m^2 area within 1 mo in 1996. In each plant, total counts of seedheads in the spiny stage (preanthesis), flowering seedheads, and phenological stage of development of individual flowering seedheads were recorded. Values obtained in the growth chamber germination studies for each flowering stage were used to estimate field seed production per plant. From these data, an approximation of the total number of germinable seed per 100 spiny seedheads was determined at increasing percent yellow starthistle flowering.

Seedbank Depletion

Yellow starthistle (1,000 achenes) was sown in the Yolo County study site A 1 cm deep in each of twelve 1- by 1-m areas contained by wooden frames (germination frames) in fall 1996. Six germination frames were sown with 1,000 pappus-bearing achenes and six with 1,000 nonpappus-bearing achenes. The study site was maintained weed-free by frequent hand weeding. The site was not irrigated, and precipitation levels were monitored every 2 wk for 18 mo. The frames were covered with a fine mesh cloth from midsummer through early fall to prevent wind-blown seed recruitment. Emerged seedlings in late fall, winter, and spring were counted in each frame every 2 wk and removed. Prior to the first fall rains in 1997, the top 10 cm of soil from three frames of each achene type were removed, washed and sieved with U.S. standard sieve series no. 20 (0.85 mm). Ungerminated and damaged or decayed achenes were counted using a stereomicroscope. Decayed seed was defined as achenes with intact seed coats but decomposed endosperm and embryos. Partial predation or seed coat cracking were used to distinguish damaged achenes. Seedling germination counts were again recorded in the six undisturbed frames (three with pappus-bearing and three with nonpappus-bearing seed) the following (1997) growing season.

Data Analysis

Phenological Development of Flowers and Seed

Roché et al. (1997) reported that accumulated thermal units could be used to predict early phenology in yellow starthistle. For the Davis population of yellow starthistle, a lower developmental threshold of 9 C provided the most reliable prediction of the interval between germination and flowering (data not shown). In calculating thermal unit accumulation between flowering head stages, a 9 C threshold was used with a single sine approximation and no upper cutoff. Thermal units were based on air temperature 1.5 m above the soil surface. Total transition times and thermal unit accumulation (degree days) for seedheads were compared in 1996 and 1997 using *t* tests.

Total seed produced per seedhead was compared at different sites and years using a one-way analysis of variance (ANOVA) followed by mean separation with a Tukey test.

Seed Viability and Germination

Percent germination of seed from seedheads was compared at several stages of development using a one-way ANOVA, followed by separation of means using a LSD test. A separate analysis was performed for each sampling site.

Seed tested for viability was grouped by seed type, seedhead stage, and site. Frequency of viable and nonviable seed was recorded within each group. A three-way contingency table was developed for each site, and an overall chi-square analysis was used to detect highly significant interactions between factors. This was followed by a series of two-way chi-square analyses to detect differences in viability for each seed type between adjacent seedhead stages. Because this necessitated numerous independent two-way analyses, the threshold of significance was lowered to $P < 0.005$.

Time Course of Seed Production

A linear regression was performed to estimate germinable seed per 100 seedheads vs. percent flowering. In order to meet requirements for normality and homoscedasticity, a square root transformation was made of seed count data [$y' = (y + 0.5)^{0.5}$].

Seedbank Depletion

Multiresponse permutation procedures, or MRPP (Mielke et al. 1981), were used to make comparisons of season-long germination patterns in pappus seed field plots with those in nonpappus seed plots. MRPP is a nonparametric technique that allows comparisons among each series of values as a unit. End of season germination totals and rates of seed recovery were compared using *t* tests.

Visual comparisons were made between rains and germination of seed in 1,000-seed plots. No attempt was made to quantify this relationship.

TABLE 2. Days and thermal units in each yellow starthistle seedhead phenology stage (± SE).

Flower phenology	Days 1996	Days 1997	Days Mean	Days since flowering	Degree days 1996	Degree days 1997	Degree days Mean
Prebloom	2.9 ± 0.2	2.8 ± 0.2	2.8	—	29.4 ± 3.0	26.7 ± 1.9	28.03
Flower initiation	0.9 ± 0.0	0.9 ± 0.0	0.9	—	12.3 ± 1.0	9.5 ± 0.5	10.91
Flower expansion	1.2 ± 0.1	1.9 ± 0.1	1.6	0.9	18.0 ± 1.0	22.6 ± 2.2	20.32
Full bloom	2.3 ± 0.1	1.9 ± 0.1	2.1	2.5	37.5 ± 2.2	26.6 ± 2.3	32.02
Initial senescence	0.9 ± 0.1	1.2 ± 0.1	1.0	4.6	13.5 ± 1.3	16.2 ± 1.3	14.88
Middle senescence	2.9 ± 0.2	2.2 ± 0.2	2.6	5.6	43.0 ± 2.8	36.8 ± 2.4	39.89
Late senescences[a]	7.3 ± 0.2	8.4 ± 0.3	8.1	8.2	110.6 ± 2.6	125.2 ± 4.2	117.9
Petal abscission	3.3 ± 0.2	1.4 ± 0.2	2.4	16.3	43.9 ± 2.2	19.6 ± 2.5	31.71
Total (prebloom to petal abscission)	21.4 ± 0.4	20.5 ± 0.4	21.0		304.5 ± 4.3	282.0 ± 5.0	293.3
	NS[b]				P = 0.001		
Total (flower initiation to start of late senescence)	8.2 ± 0.2	8.1 ± 0.3	8.2		124.3 ± 3.3	111.7 ± 3.2	118.0
	NS				P = 0.008		

[a] Seed germination typically occurred at late senescence stage and later.
[b] No significant difference.

TABLE 3. Seed counts (± SE) per yellow starthistle seedhead.[a]

Year	Study site	Total count	Mean	
			Pappus	Nonpappus[b]
		seeds seedhead^{-1}	% of total	
1996	Yolo Co. site A	73.8 ± 3.6 ab	91.0 ± 1.1 a	9.0
1997	Yolo Co. site B	82.6 ± 4.5 a	86.1 ± 2.1 ab	13.9
1999	Yolo Co. site B	72.2 ± 1.5 b	82.5 ± 2.5 ab	17.5
1999	San Benito Co.	65.0 ± 2.2 b	79.7 ± 1.8 b	20.3

[a] Values followed by the same letter are not significantly different (P = 0.05).
[b] Standard error values and significance are the same as presented for pappus seed.

Results and Discussion

Phenological Development of Flowers and Viable Seed

Transition times did not differ between the 2 yr but degree day accumulation was significantly lower in 1997 (Table 2). This suggests that seedhead development may depend more on time than on thermal accumulation.

On average, seedheads required approximately 21 d to progress from prebloom to petal abscission in both 1996 and 1997 (Table 2). Flowers remained in full bloom for just over 2 d before they began to senesce. Senescence required an additional 14 d, with the late senescence stage requiring the longest transition time (7 to 9 d).

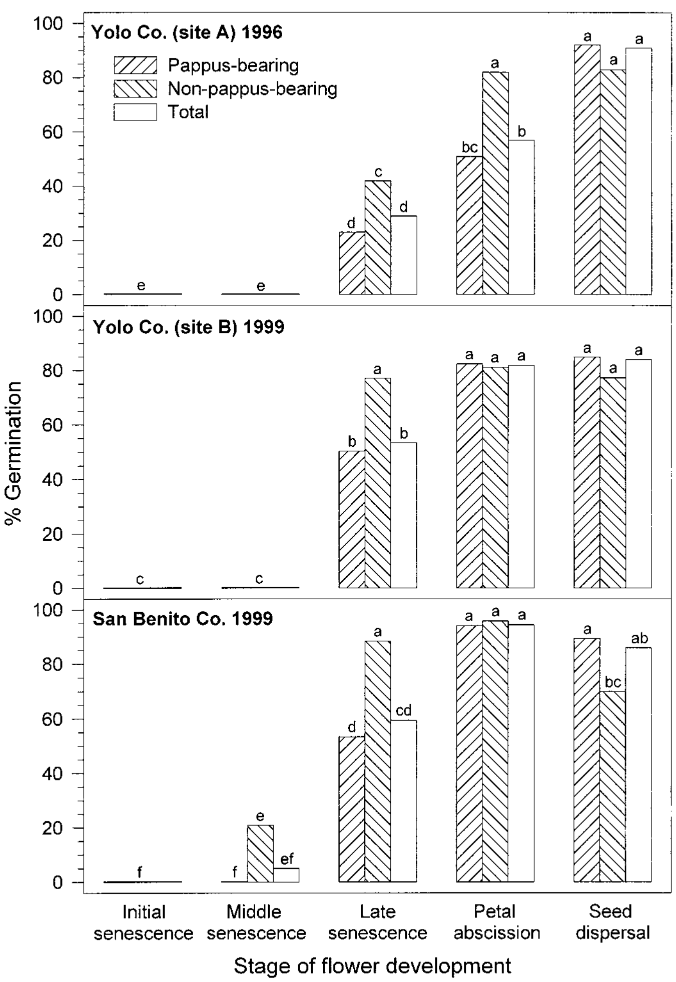

FIGURE 1. Percent germination of yellow starthistle seed from five flower phenology stages in 1996 (Yolo County site A) and 1999 (Yolo County site B and San Benito County). Within each site, bars labeled with the same letter are not significantly different (LSD test, P < 0.05).

Average seed production per seedhead ranged between 65 and 83 achenes among sites and years (Table 3). Several authors have suggested that the number of achenes per seedhead can vary dramatically and are often determined by soil moisture and other soil properties (Maddox 1981; Pitcairn et al. 1997; Roché 1991). In other areas of California (Mendocino, Contra Costa, and Yolo counties), Maddox (1981) reported 38 and 43 achenes per seedhead.

Of the total achenes produced, 80 to 91% were pappus bearing and 9 to 20% were nonpappus bearing (Table 3). Maddox (1981) also reported other populations to consist of 75 to 90% pappus-bearing achenes. Similarly, Roché (1965) reported 75% pappus-bearing yellow starthistle achenes in Idaho.

No germinable seed was found before the late senescence stage of flower development in both Yolo County sites in 1996 and 1999 (Figure 1). In the San Benito County site in 1999, only 5% of the total seed in the middle senescence stage germinated, and all were nonpappus bearing. By the late senescence stage, germination rates had increased to 60% in San Benito County, 29% at site A in Yolo County (1996), and 53% at site B in Yolo County (1999). The viability of seed collected at the San Benito and Yolo (site B) County study sites in 1999 was determined using 1.0% TZ. Few pappus-bearing seeds were viable at flower developmental stages earlier than late senescence (Figure 2). In contrast, over 50% of nonpappus-bearing seed was viable at the middle senescence stage at both sites. Viability increased as flowerheads developed, reaching a peak of 87.6 and 95.2% at the dispersal stage in the San Benito County and Yolo County sites, respectively. At this same stage of development, germination rates at the San Benito County and Yolo County sites were 87.6 and 84%, respectively (Figure 1). Thus, nearly all viable seed was able to germinate by the dispersal stage, suggesting that yellow starthistle may not have an innate or induced dormancy mechanism or an ecologically significant after-ripening period.

Seedheads at the middle senescence stage or earlier contained only partially filled or unfilled seed at all sites and years. Although a proportion of partially filled seed was viable and capable of germinating, the rapid increase in germination rate corresponded to initiation of seed fill in the late senescence stage (data not shown). Germination of both achene types significantly increased from the late senescence to the achene dispersal stage in 1996 and 1999. Between late senescence and seed dispersal, the mean (SE) percent

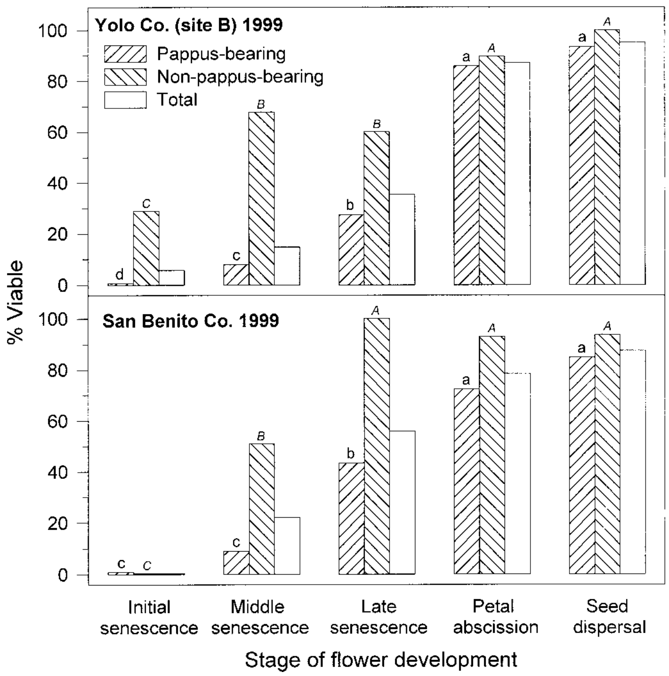

FIGURE 2. Viability of yellow starthistle seed from five flower phenology stages in 1999; data from San Benito County and Yolo County site B. Within each site and each seed type, bars labeled with the same letter are not significantly different (separation by chi-square tests, $P < 0.005$). Analysis was performed on original seed frequency data, not on percentages.

filled seed increased from 25.3% (8.6) to 93.2% (1.9), whereas average germination increased from 47.3% (9.6) to 87.0% (2.1). Maddox et al. (1996) also reported a consistent increase in the mean number of germinating achenes with advancing phenological stage.

Although germinable seed did not typically develop until the late senescence stage 8 d after flower initiation, some seed was viable even at the initial senescence stage 5 d after flower initiation (Table 2). Consequently, to prevent significant seed production, late-season management options should be conducted at very early stages of flower development.

Compared to pappus-bearing achenes, a significantly higher percentage of nonpappus-bearing achenes germinated in the late senescence stage at all sites and years (Figure 1). However, at the time of achene dispersal, germination rates of the two achene types were similar. These findings likely reflect the centripetal maturation of achenes within the seedheads. This is also supported by the higher percentage of viable seed (Figure 2) and filled seed in nonpappus-bearing achenes compared to pappus-bearing achenes at earlier stages of development. By the late senescence stage, over 97% of nonpappus-bearing seed was completely filled, whereas less than 50% of pappus-bearing seed was completely filled in Yolo County (site A [1996] and site B [1999]) and San Benito County sites (1999) (data not shown).

Over 90% of the seed was germinable 1 wk after seed dispersal. Sheley et al. (1983) reported 100% germination of mature seed 96 h after seed dispersal. Nearly complete germination of yellow starthistle within 1 wk of dispersal suggests that the majority of yellow starthistle seed has no substantial after-ripening requirements. In contrast with these findings, Joley et al. (1992) noted a significant increase in the rate of germination from 67% initially to 98% 1 mo postharvest in achenes either buried (5 cm) or under laboratory storage and suggested that yellow starthistle may have a short after-ripening period.

Time Course of Seed Production

The proper timing for late-season management practices of yellow starthistle was investigated by estimating total germinable seed production at various percentages of total seedheads in flower. Estimates of total germinable seed was accomplished by evaluating 75 plants over 30 d in Yolo County (site A). In each plant, the number of spiny flowerheads was counted, including those in preanthesis and at each stage of phenological development (see Table 1). By extrapolating the data obtained in germination studies for that site (Figure 1), estimates were made of total germinable seed production per 100 spiny seedheads. No germinable seed was produced until 2% of the spiny heads had initiated anthesis (Figure 3). By 10% flowering, an estimated 100 germinable seeds were produced per 100 flowerheads. Achene production increased exponentially as percent flow-

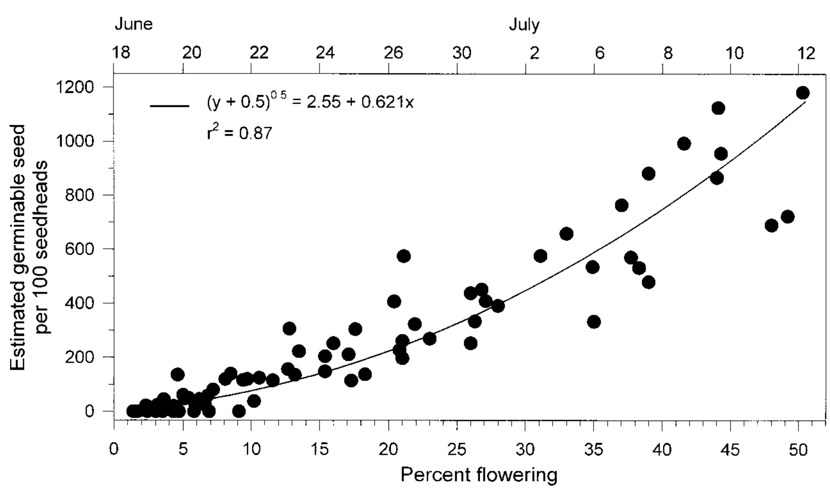

FIGURE 3. Estimated production of germinable yellow starthistle seed by plants in various degrees of flowering. Each point represents counts from a single plant with at least 100 spiny (preanthesis) or flowering seedheads.

TABLE 4. Field germination and survival (± SE) of two seed types of yellow starthistle in 1,000-seed plots.

Parameter	Dates determined	Pappus seed	Nonpappus seed	Analysis	P
First season					
Germination pattern		Higher initial rate	Lower initial rate	MRPP[a]	0.014
Mean total germination (no. seeds)	Jan–Sept 1996	436 ± 45	390 ± 41	*t* test	NS[b]
Dead seed recovered from soil (no. seeds)	Oct 1996	225 ± 15	149 ± 19	*t* test	0.006
Live seed recovered from soil (no. seeds)	Oct 1996	32 ± 15	35 ± 5	*t* test	NS
Proportion of dead seed in total seed recovered		0.875	0.810		
Second season					
Germination pattern		—	—	MRPP	NS
Mean total germination (no. seeds)	Nov 1996–July 1997	69 ± 7	94 ± 10	*t* test	0.023

[a] Multiple response permutation procedure.
[b] No significant difference.

ering progressed. Thus, to prevent seed production, it is most practical to gauge timing of late-season control practices around flower initiation, as this stage is easily recognized. Effective long-term control may be compromised if control practices are delayed too long after flower initiation, allowing production of viable seed. Therefore, to prevent new achene recruitment, late-season control options such as tillage, mowing (Benefield et al. 1999), prescribed burning (DiTomaso et al. 1999a), and herbicides (DiTomaso et al. 1999b) should be conducted before approximately 2% of the total spiny heads have initiated flowering.

Seedbank Depletion

Yellow starthistle infestations have been reported to produce as many as 250 million achenes ha^{-1} annually (Callihan et al. 1992). This level of achene production results in a large seedbank that may require many years to deplete. To develop a long-term management program, it is essential to understand the longevity of the seedbank under field conditions.

In earlier studies, Joley et al. (1992) and Callihan et al. (1993) investigated yellow starthistle achene longevity in the soil by burying nylon mesh packets containing pappus-bearing and nonpappus-bearing achenes at various depths. In a study conducted in Idaho, Callihan et al. (1993) reported no effects of burial depth on achene longevity and showed that the average longevity of nonpappus-bearing and pappus-bearing achenes was 6 and 10 yr, respectively. Even after 6 yr of burial, 9% of the pappus-bearing seed germinated after achenes were retrieved and planted in petri dishes. In a similar study in California, Joley et al. (1992) found significant differences in achene longevity at various soil depths. After burying seed in bags for 1 yr, they reported 88% viability in seed planted 5 cm deep, but only 4% viable seed remaining in bags 1 cm deep. Consequently, there is some confusion as to longevity of yellow starthistle achenes under typical field conditions. The discrepancy between these two studies may be due to ecotypic variability among populations from Idaho and California, various differences in edaphic or climatic conditions that could influence the rate of microbial degradation, or invertebrate predation of the achenes.

In the same study, Joley et al. (1992) dispersed yellow starthistle achenes on the soil surface. After 1 yr, they reported 80% depletion in the seedbank, and by 3 yr only 3.9% of the original seed had not germinated and were still viable. They attributed this rapid decline in the seedbank to germination, achene mortality, and predation. In addition, 1 yr of prescribed summer burning in Sonoma County, CA, reduced the seedbank of yellow starthistle by 74% and 3 consecutive yr of burning, with no further seed recruitment, depleted the seedbank by 99.6% (DiTomaso et al. 1999a). This suggests that the longevity of viable seed under normal field conditions in California may be shorter than previously believed.

Despite what appears to be a rapid depletion of the yellow starthistle seedbank under typical California conditions, no studies have yet separated the contribution of achene degradation and germination to yellow starthistle seedbank dynamics. To address this, 1,000 achenes of each type were planted in weed-free soil containers. Both emergence and degradation were monitored for 18 mo. In the first year, 44% of pappus-bearing and 39% of nonpappus-bearing achenes germinated from January to June 1996 (Table 4). At the end of the first season (October 1996), soil from half of the plots was collected and the achenes were elutriated. Although an average of 564 achenes was expected, the average recovery was only 257 achenes. Of those achenes recovered, 88% of the pappus-bearing achenes and 81% of the nonpappus-bearing achenes were damaged or degraded by microbial or insect activity. After 1 yr, germination and seed recovery accounted for only 69% (pappus bearing) and 57% (nonpappus bearing) of the original 1,000 seeds sown. Unrecovered seed was speculated to have been lost to bird or rodent predation. In the second season, beginning with the first rains in November 1997 and extending until July 1, an additional 7% of pappus-bearing and 9% of nonpappus-bearing seed germinated in the remaining six plots. Thus, of the seed that emerged over the 2-yr period, the vast majority germinated in the first year. These results support the findings of both Joley et al. (1992) and DiTomaso et al. (1999a), suggesting that yellow starthistle achenes are relatively short-lived under California soil and climatic conditions. Furthermore, under these conditions, microbial deg-

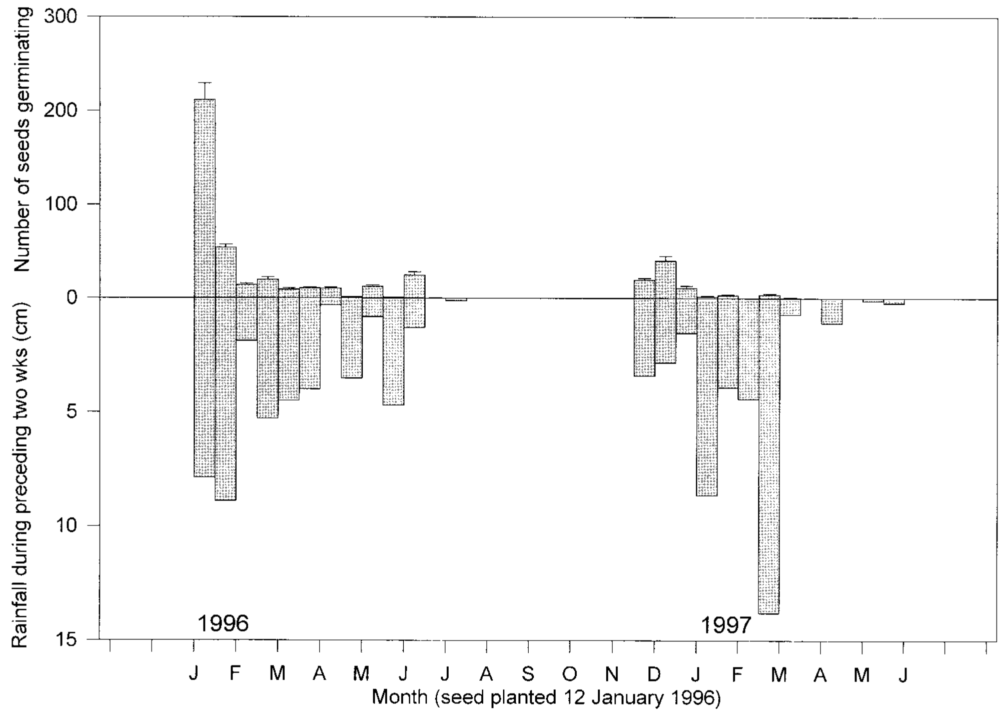

FIGURE 4. Correspondence of yellow starthistle germination in 1,000-seed field plots with precipitation. Error bars represent sample standard error.

radation and invertebrate predation of yellow starthistle achenes probably contribute significantly to the rapid depletion of the soil seedbank. This indicates that yellow starthistle management programs may require only 2 to 3 yr of effective control to dramatically reduce the soil seedbank and infestation. In support of this, DiTomaso et al. (1999a) demonstrated that 3 consecutive yr of prescribed burning reduced yellow starthistle seedbanks by 99.6% and vegetative cover by 91%. For long-term sustainable management to be achieved, land managers will be required to prevent achene recruitment from the remaining seedbank germinants or from new introduction of dispersed achenes from off-site sources.

The overall rate of germination was not statistically different for pappus-bearing and nonpappus-bearing achenes by the end of the season. Interestingly, germination rates for pappus-bearing achenes were significantly higher than for nonpappus-bearing achenes during the first 2 mo after sowing (Table 4). This difference was reversed by March 1996. This is in contrast to germination results presented in Figure 1. In the growth chamber, there were no significant differences in germination percentages between pappus-bearing and nonpappus-bearing seed at all sites and years. As a possible explanation, Roché (1965) found that nonpappus-bearing seed has a higher temperature requirement for germination. This could account for the increased germination of pappus-bearing seed in January and February. By the end of each growing season, however, there was no statistical difference between total germination of the two seed types. Although achene dimorphism is likely to be an adaptation for dispersal, particularly among annual species (Olivieri and Berger 1985), there was no significant difference in soil longevity between the two seed types in this study.

Maddox (1981) reported that yellow starthistle seed germination was closely correlated with winter and spring rainfall. Similarly, a correlation between rainfall and yellow starthistle germination was demonstrated in both 1996 and 1997 (Figure 4). Although germination occurred throughout the rainy season, emergence was highest after early-season rainfall. The extended timing of germination increases the difficulty of controlling yellow starthistle populations during the late winter and early spring because subsequent germination often results in significant infestations. Consequently, effective late-season control strategies, such as mowing, tillage, prescribed burning, or postemergence herbicides, should be conducted after seasonal rainfall is completed but before viable seed is produced. In addition, the use of preemergence herbicides applied from late fall to early spring should provide residual control extending beyond the rainy season.

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Literature Cited

Balciunas, J. and B. Villegas. 1999. Two new seed head flies attack yellow starthistle. Calif. Agric. 53(2):8–11.

Benefield, C. B., J. M. DiTomaso, G. B. Kyser, S. B. Orloff, K. R. Churches, D. B. Marcum, and G. A. Nader. 1999. Control of yellow starthistle with mowing: effects of timing, repeated cuttings, and growth form. Calif. Agric. 5(2):17–21.

Callihan, R. H., T. S. Prather, and F. E. Northam. 1992. Recolonization strategies and longevity of yellow starthistle achenes in soil. Knapweed 6(3):3–4.

Callihan, R. H., T. S. Prather, and F. E. Northam. 1993. Longevity of yellow starthistle achenes in soil. Weed Technol. 7:33–35.

Callihan, R. H., L. Smith, and E. L Michalson. 1995. Yellow Starthistle Management for Small Acreages. Moscow, ID: University of Idaho College of Agriculture Current Infomation Ser. CIS 1025. 4 p.

DiTomaso, J. M., G. B. Kyser, and M. S. Hastings. 1999a. Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. Weed Sci. 47:233–242.

DiTomaso, J. M., G. B. Kyser, S. B. Orloff, S. F. Enloe, and G. A. Nader. 1999b. New growth regulator herbicide provides excellent control of yellow starthistle. Calif. Agric. 53(2):12–16.

DiTomaso, J. M., W. T. Lanini, C. D. Thomsen, T. S. Prather, C. E. Turner, M. J. Smith, C. L. Elmore, M. P. Vayssieres, and W. A. Williams. 1999c. Pest Notes: Yellow Starthistle. Oakland, CA: University of California Division of Agriculture and Natural Resources Publ. 7402. 4 p.

Gerlach, J. D., Jr. 1997. The introduction, dynamics of geographic range expansion, and ecosystem effects of yellow star-thistle (*Centaurea solstitialis*). Proc. Calif. Weed Sci. Soc. 49:136–141.

Joley, D. B., D. M. Maddox, D. M. Supkoff, and A. Mayfield. 1992. Dynamics of yellow starthistle (*Centaurea solstitialis*) achenes in the field and laboratory. Weed Sci. 40:190–194.

Maddox, D. M. 1981. Introduction, Phenology, and Density of Yellow Starthistle in Coastal, Intercoastal, and Central Valley Situations in California. Albany, CA: USDA ARS ARR-W-20. 33 p.

Maddox, D. M., D. B. Joley, D. M. Supkoff, and A. Mayfield. 1996. Pollination biology of yellow starthistle (*Centaurea solstitialis*) in California. Can. J. Bot. 74:262–267.

Mielke, P. W., K. J. Berry, P. J. Brockwell, and J. S. Williams. 1981. A class of nonparametric techniques based on multiresponse permutation procedures. Biometrika 68:720–724.

Olivieri, I. and A. Berger. 1985. Seed dimorphism for dispersal: physiologic, genetic and demographical aspects. Pages 413–429 *in* P. Jacquard, ed. Genetic Differentiation. Dispersal in Plants. Berlin: Springer Verlag.

Pitcairn, M. J., R. A. O'Connell, and J. M. Gendron. 1997. Yellow starthistle: survey of statewide distribution. Pages 53–56 *in* Biological Control Program Annual Summary, 1996. Sacramento, CA: California Department of Food Agriculture, Division of Plant Industry.

Roché, B. F. 1965. Ecologic Studies of Yellow Starthistle (*Centaurea solstitialis* L.). Ph.D. dissertation. University of Idaho, Moscow, ID, pp. 78–89.

Roché, B. F. 1991. Achene dispersal in yellow starthistle (*Centaurea solstitialis* L.). Northwest Sci. 66:62–65.

Roché, C. T., D. C. Thill, and B. Shafii. 1997. Reproductive phenology in yellow starthistle (*Centaurea solstitialis*). Weed Sci. 45:763–770.

Sheley, R. L., D. L. Zamora, C. Huston, R. H. Callihan, and D. C. Thill. 1983. Seed and Seedling Root Growth Characteristics of Several Populations of Yellow Starthistle. Research Progress Report of the Western Society of Weed Science, pp. 62–63.

Thomsen, C. D., M. Vayssieres, and W. A. Williams. 1994. Grazing and mowing management of yellow starthistle. Proc. Calif. Weed Conf. 46:228–230.

White, J. 1999. Can integrated methods stop starthistle? Calif. Agric. 53(2):7.

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