CHAPTER 3. Biology and Ecology

Yellow starthistle is a winter annual widely distributed in the Central Valley and adjacent foothills of California. It is currently spreading in mountainous regions of the state below 7,000 feet elevation and in the Coast Ranges, but is less commonly encountered in the desert, high mountains and moist coastal sites. It is typically found in full sunlight and deep, well-drained soils where annual rainfall is between 10-60 inches.

Yellow starthistle competes well in both stressed conditions and more favorable environments created by disturbance (Gerlach and Rice 2003). In more favorable sites, yellow starthistle can grow larger and produce more seeds than many competing species. Its extended growing and flowering season allows it to persist within relatively closed grassland vegetation and take advantage of residual soil moisture resources not used by annual grass species (Gerlach 2000). A detailed examination of yellow starthistle biology and ecology is undertaken below.

Taxonomy and Identification

All 12 species of *Centaurea* in California are non-native and nine have purple to white flowers (Hickman 1993). The three yellow-flowered species include *Centaurea solstitialis* (yellow starthistle), *Centaurea melitensis* (tocalote, Napa or Malta starthistle), and *Centaurea sulphurea* (Sicilian or sulfur starthistle). In addition to yellow flowers, these three species also have long sharp spines associated with their flowerheads. In other western states, *Centaurea macrocephala* (bighead knapweed) also has yellow flowers but does not have long sharp spines on the flowerheads (Roché 1991c). In California, *Centaurea melitensis* is also considered invasive (Cal-IPC 2006), particularly in the southern part of the state (DiTomaso and Gerlach 2000b). However, it flowers earlier in the year, does not form such dense populations, is less vigorous, and is far less invasive than yellow starthistle.

Three yellow-flowered Centaureas. *From left to right: tocalote, Sicilian starthistle, and yellow starthistle.*

Reproduction

FLOWERING AND POLLINATION

Yellow starthistle typically begins flowering in late May and continues through September. Unlike other yellow-flowered *Centaurea* species, yellow starthistle has a very low level of self-fertilization (Barthell *et al*. 2001, Gerlach and Rice 2003, Harrod and Taylor 1995, Maddox *et al*. 1996, Sun and Ritland 1998). Thus, a significant amount of cross-fertilization insures a high degree of genetic variability within populations.

Honeybees play an important role in the pollination of yellow starthistle, and have been reported to account for 50% of seed set (Maddox *et al*. 1996). Bumblebees are the second most important floral visitor to starthistle flowers, but several other insects also contribute to fertilization of the ovules (Harrod and Taylor 1995).

In a study conducted by Barthell *et al*. (2001) on Santa Cruz Island in California, investigators found that honeybees visited yellow starthistle 33 times more than native bees. By comparison, native bees visited a native gumplant species (*Grindelia camporum*) 46 times more than honeybees. In addition, they found that when honeybees were excluded from visiting starthistle but native bees were not, the average seed head weight of yellow starthistle significantly declined. The authors concluded that honeybees and yellow starthistle may act as invasive mutualists, increasing the survivorship of each other.

TIMING OF FLOWER AND SEED DEVELOPMENT

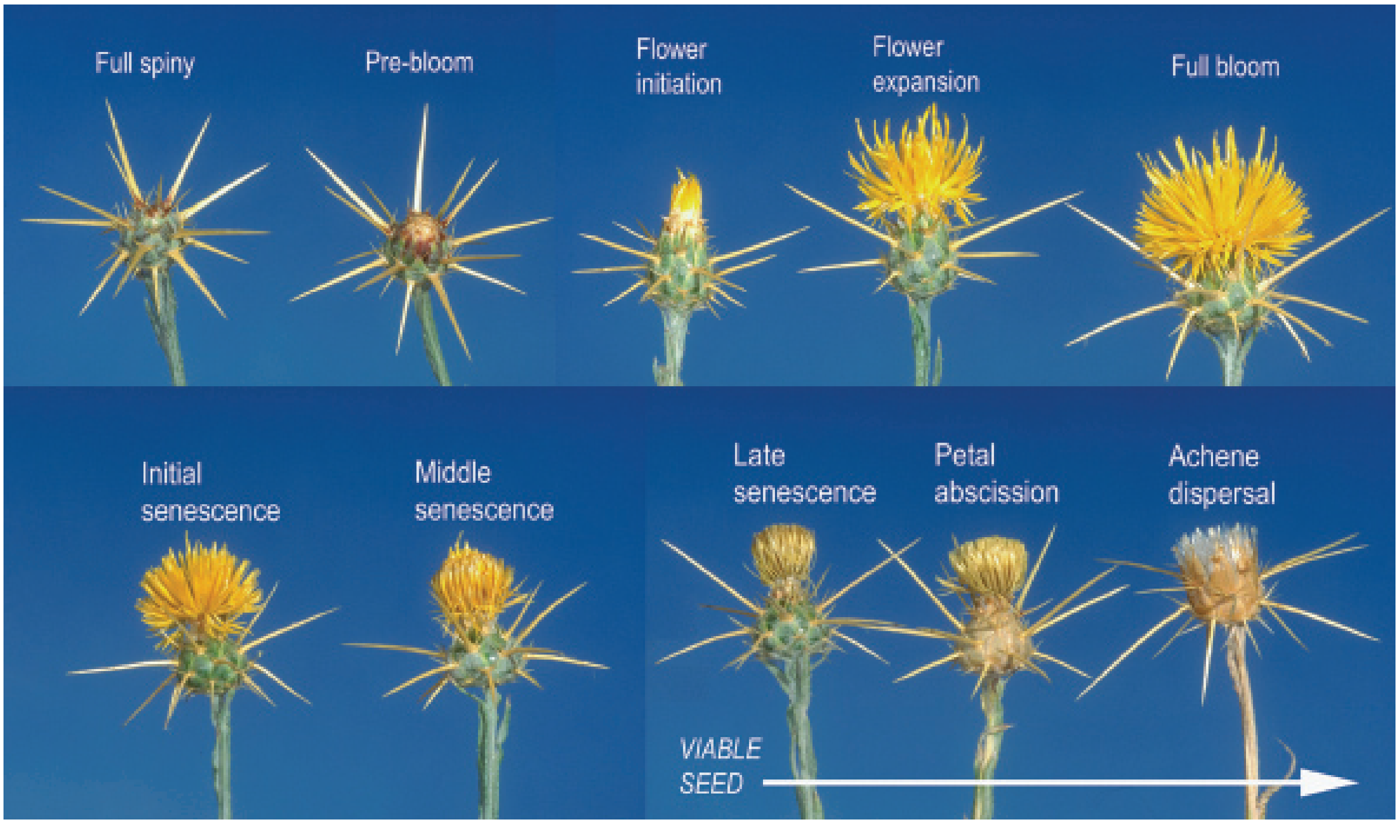
On average, seed heads require approximately 21 days to progress from pre-bloom to petal abscission (Benefield *et al*. 2001). Flowers remain in full bloom for just over two days before they began to senesce. Senescence requires an additional 14 days.

The time period from flower initiation to the development of mature viable seed is only eight days. In one study, no germinable seeds were produced until 2% of the spiny heads in a population had initiated flowering (Benefield *et al*. 2001). By the time 10% of the heads were in flower, numerous viable seeds had already been produced. 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, prescribed burning, and herbicides should be conducted before approximately 2% of the total spiny heads have initiated flowering.

SEED DISPERSAL

Unlike most other species in the genus *Centaurea*, yellow starthistle produces two morphologically distinct achenes, one type with a distinct pappus, and the other with a pappus either poorly developed or absent (Callihan *et al*. 1993). The pappus-bearing achenes are light to dark brown with tan striations throughout. By comparison, the non-pappus-bearing achenes are dark brown to black without striations. Non-pappus-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 seed head. Development of achenes occurs centripetally, from the outer non-pappus-bearing achenes to the inner pappus-bearing achenes (Maddox *et al*. 1996). Of the total achenes produced, between 75% and 90% are pappus-bearing and 10% to 25% are non-pappus-bearing (Benefield *et al*. 2001, Maddox 1981, Roché 1965).

The pappus-bearing seed are usually dispersed soon after the flowers senesce and drop their petals. However, non-pappus-bearing seeds can be retained in the seed head for a considerable period



Life stages. *A yellow starthistle flowerhead goes through predicable stages from bud through senescence. Viable seed set is the critical point for those seeking to control the plant. (Photo: J. Clark)*

Winged stems. *Before bolting, yellow starthistle develops winged stems with increased surface area that help the plant dissipate summer heat.*

Bolting. *Bolting is a stage of vigorous shoot growth during the time of greatest light availability.*

Early flowering stage—time to mow. *To prevent seed production, late-season control techniques should be used when plants are in the early flowering stage, as shown here.*

Yellow starthistle "Q-tips." *Following flowerhead senescence and seed dispersal, yellow starthistle stems retain white cottony tips into the winter.*

of time, extending into the winter (Callihan *et al.* 1993). These seeds have no wind dispersal mechanism and most simply fall to the soil just below the parent plant. With pappus-bearing seed, the pappus is not an effective long distance wind dispersal mechanism. Roché (1991a, 1992) reported that 92% of yellow starthistle seed fall within two feet of the parent plant, with a maximum dispersal distance of 16 ft over bare ground with wind gusts of 25 miles/hr. By comparison, birds such as pheasants, quail, house finches, and goldfinches feed heavily on yellow starthistle seeds and are capable of long distance dispersal (Roché 1992). Human influences, including vehicles, contaminated crop seed, hay or soil, road maintenance, and moving livestock, can also contribute to rapid and long distance spread of the seed.

Germination and Dormancy

SEED PRODUCTION AND TYPES

Average seed production per seed head ranges from about 35 to over 80 achenes (Benefield *et al*. 2001, Maddox 1981, Pitcairn *et al*. 1998c), depending upon the site. Large plants can produce over 100,000 seeds. The number of seed heads and achenes per seed head can vary dramatically and are often determined by soil moisture and other soil properties (Maddox 1981; Pitcairn *et al*. 1997; Roché 1991b).

Yellow starthistle infestations have been reported to produce 57-114 million achenes per acre (DiTomaso *et al*. 1999a, Maddox 1981, Callihan *et al*. 1993).

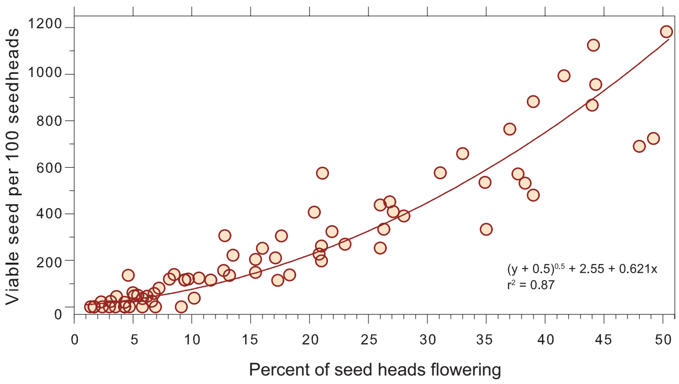


Fig. 3. Viable seed production in relation to flowering stage. *Percentage of yellow starthistle heads that are flowering can be used by managers as an indicator of seed maturation in order to time late-season treatments (Benefield* et al. *2001).*

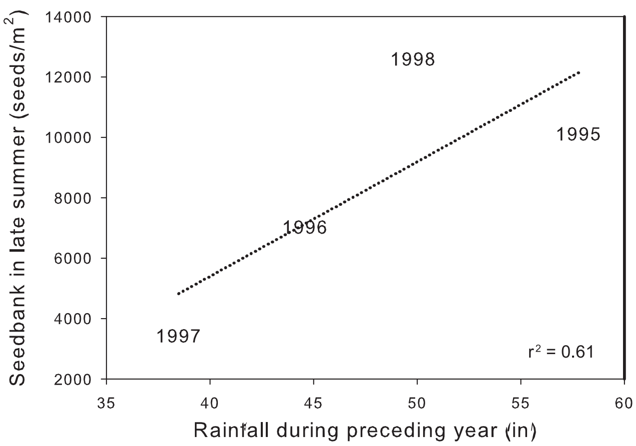


Fig. 4. Seedbank in relation to yearly rainfall. *The number of yellow starthistle seeds in the soil is positively correlated with the preceding year's rainfall, in this study at Sugarloaf Ridge State Park 1995-98 (G.B. Kyser, unpubl. data).*

GERMINATION

Over 90% of yellow starthistle achenes are germinable one week after seed dispersal (Benefield *et al*. 2001, Joley *et al*. 1997, 2003, Roché *et al*. 1997, Roché and Thill 2001, Sheley *et al*. 1983, 1993). Maximum germination of yellow starthistle achenes (nearly 100%) occurs when seeds are exposed to moisture, light and constant temperatures of 10, 15, or 20 °C, or alternating temperatures of 15:5 or 20:10 °C (Joley *et al*. 1997, Roché *et al*. 1997). At temperatures above 30 °C

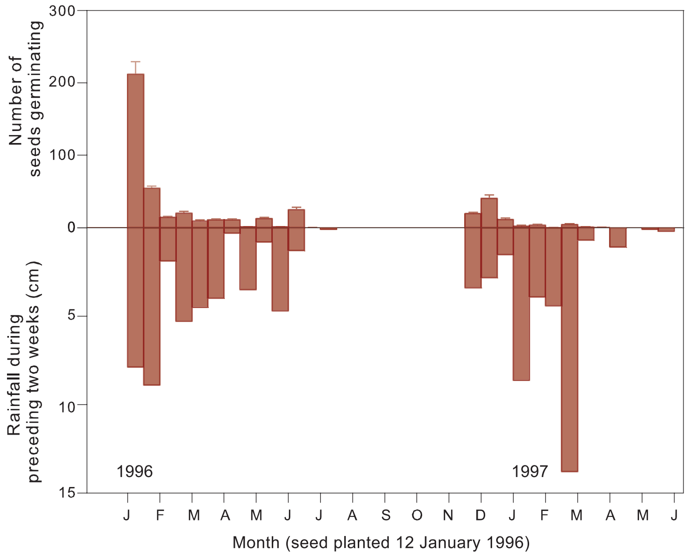


Fig. 5. Germination in relation to recent rainfall. *Germination of yellow starthistle seed shows a correlation with rainfall during the preceding two weeks (Benefield* et al. *2001).*

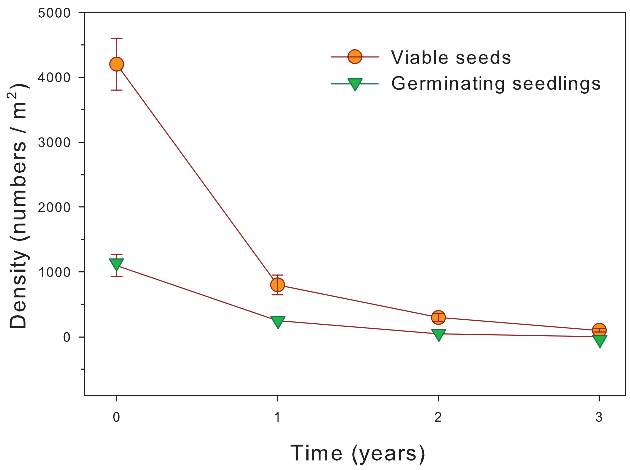


Fig. 6. Decline in seedbank. *When the introduction of new seeds is prevented, the yellow starthistle seedbank declines almost completely over three years (Joley* et al. *1992).*

germination is dramatically reduced (Joley *et al*. 1997, Roché *et al*. 1997). Yellow starthistle appears to have a light requirement for germination (Joley, unpublished data).

Because nearly all viable seeds are able to germinate at the dispersal stage, yellow starthistle may not have an innate or induced dormancy mechanism. Interestingly, achenes will germinate only within a narrow, relatively cool temperature range shortly after dispersal. This ensures that seeds do not germinate, and then dry up, following an occasional late summer thunderstorm. However, with ongoing exposure to higher temperatures and low moisture, as would occur in later summer, achenes experience an after-ripening that allows germination over a wider range of temperatures (Enloe, unpublished data).

SEASONAL GERMINATION PATTERN

Maddox (1981) and Benefield *et al*. (2001) reported that yellow starthistle seed germination was closely correlated with winter and spring rainfall events. Although emergence was highest after early season rainfall events, germination occurred throughout the rainy season. The extended germination period increases the difficulty of controlling yellow starthistle populations during the late winter and early spring, as 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 events are completed, but before viable seeds are produced. In addition, the use of preemergence herbicides applied from late fall to early spring should provide residual control extending beyond the rainy season.

SEED LONGEVITY AND SEEDBANK DEPLETION

From a land manager's perspective, it is important to know the longevity of yellow starthistle achenes in the soil seedbank.

Although some studies have suggested that seeds can survive as long as ten years in the soil (Callihan *et al*. 1989, 1993), most studies in California show a more rapid rate of depletion. In one study, yellow starthistle achenes on the soil surface were depleted by 80% after one year with no additional recruitment, and by three years only 3.9% of the original seeds had not germinated and were still viable (Joley *et al*. 1992). In another experiment, one year of prescribed summer burning in Sonoma County, California, reduced the seedbank of yellow starthistle by 74%; three consecutive years of burning, with no further seed recruitment, depleted the seedbank by 99.6% (DiTomaso *et al*. 1999a). This suggests that the longevity of viable seeds under normal field conditions in California may be shorter than previously believed. Joley *et al*. (2003) reported that nearly all achenes from the soil seedbank were depleted after four years. Microbial degradation and invertebrate predation of yellow starthistle achenes probably contribute significantly to the rapid depletion of the soil seedbank.

These recent findings indicate that yellow starthistle management programs may require only two to four years of control to dramatically reduce the soil seedbank and thus the infestation. For long-term sustainable management to be achieved, land managers must prevent achene recruitment from the remaining seedbank germinants or from new introduction of achenes from off-site sources.

Growth and Establishment

SEEDLING ESTABLISHMENT

High germination rates can result in extremely dense seedling populations. In many areas, a significant amount of self-thinning occurs and only a small fraction of seedlings reach reproductive maturity (Larson and Sheley 1994). Thus, in heavily infested areas, starthistle populations produce far more seed than are necessary to reinfest the area year after year. Seedlings are most likely to establish in soils with deep silt loam and loam with few coarse fragments (Larson and Sheley 1994).

ROOTS

Following germination, yellow starthistle allocates resources initially to root growth, secondarily to leaf expansion, and finally to stem development and flower production (Sheley *et al*. 1983, 1993, Roché *et al*. 1994). Root growth during the winter and early spring is rapid and can extend well beyond three feet in depth (DiTomaso *et al*. 2003b). Starthistle roots elongate at a faster rate and to greater depths than potentially competitive species, including weedy annual grasses and clovers (Sheley *et al*. 1993). During this same time period, rosettes expand slowly. In a study conducted in Washington by Roché *et al*. (1994), roots grew at a mean rate of 0.5 cm per day

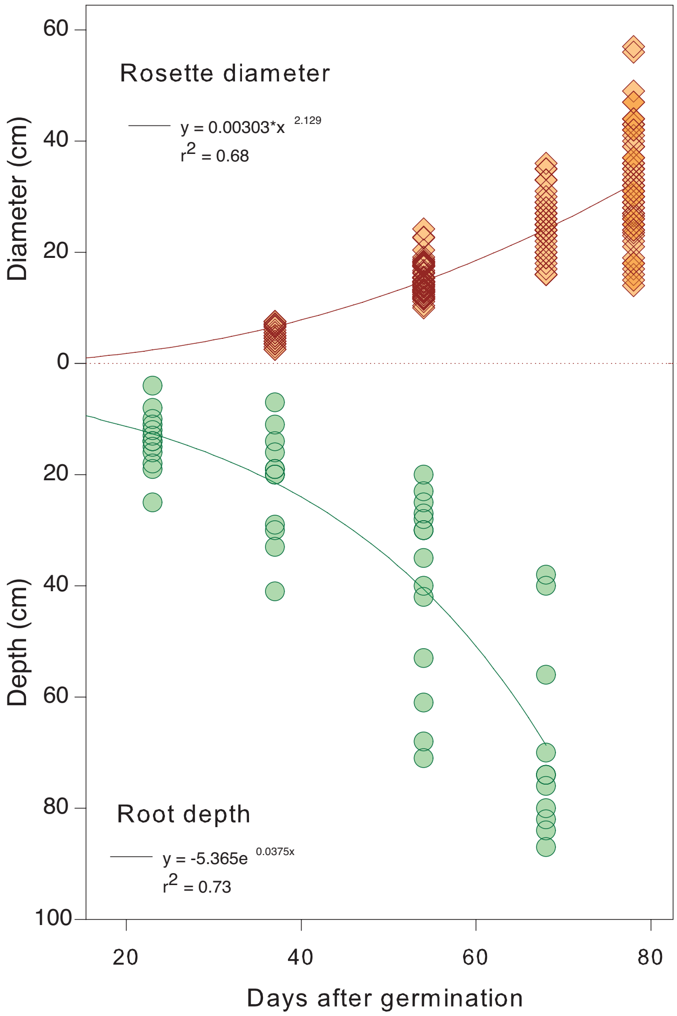
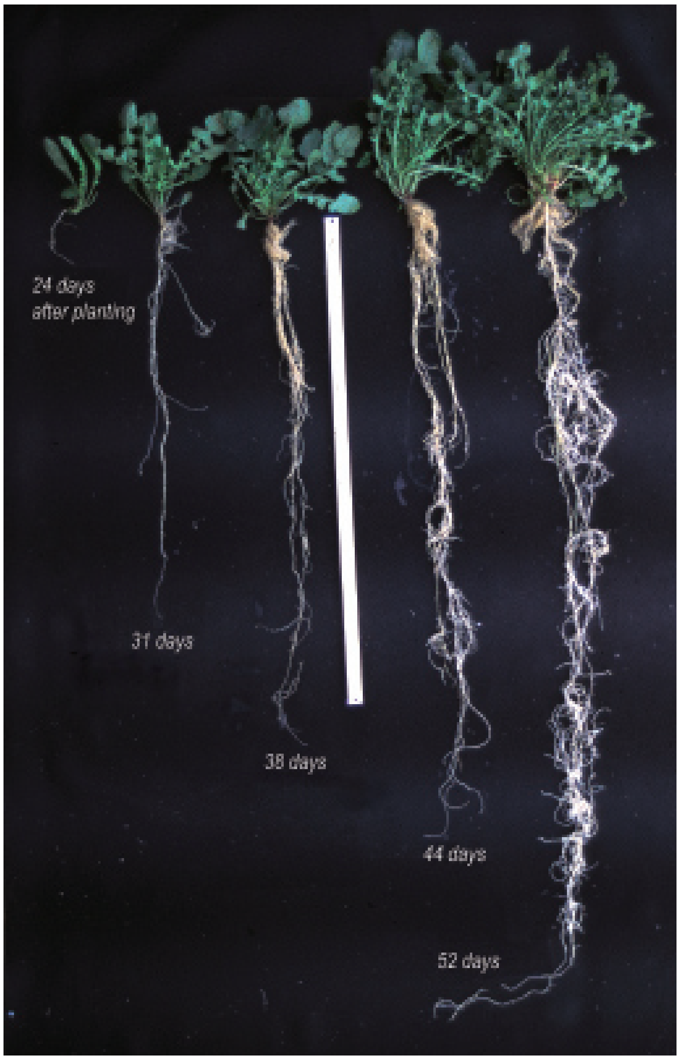


Fig. 7. Growth of roots and rosettes. *While yellow starthistle rosettes grow slowly during the winter, roots are elongating rapidly (DiTomaso* et al. *2003b).*



Root growth. *Roots of yellow starthistle plants grow deep rapidly, even in the rosette stage.*

and as fast as 2.1 cm per day; 140 days after planting, roots grew out the bottom of 123 cm long (4 ft) tubes. While root growth was rapid during the winter months, there was little above-ground rosette expansion. In another study using minirhizotron tubes in the field, DiTomaso *et al*. (2003b) showed that root depth increased exponentially with time. By 64 days after planting, roots reached depths of 0.6 m (2 ft); within 80 days (end of March), roots in most plots extended beyond 1 m. Plants grown in tubes grew roots beyond 2 m (6 ft) after two months.

Rapid germination and deep root growth in yellow starthistle extends the period of resource availability into late summer, long after seasonal rainfall has ended and shallow-rooted annual grasses have senesced. By extending the period of resource availability, competition is reduced at the reproductive stage. This can greatly benefit starthistle by ensuring ample seed production into the dry summer months (Sheley *et al*. 1993).

The potential density of yellow starthistle in a particular site can be closely associated with soil depth and thus late season water storage capacity. Roché *et al*. (1994) demonstrated a direct relationship between the number of starthistle plants per unit area and the soil moisture depth.

Shading of young rosettes can reduce root growth dramatically (Roché *et al*. 1994). In one study, roots of unshaded yellow starthistle reached a depth of 60 cm (2 ft) in 94 days; plants grown under 80% or 92% light reduction took 138 and 163 days, respectively (DiTomaso *et al*. 2003b).

Since yellow starthistle plants germinate over an extended time period beginning with the first

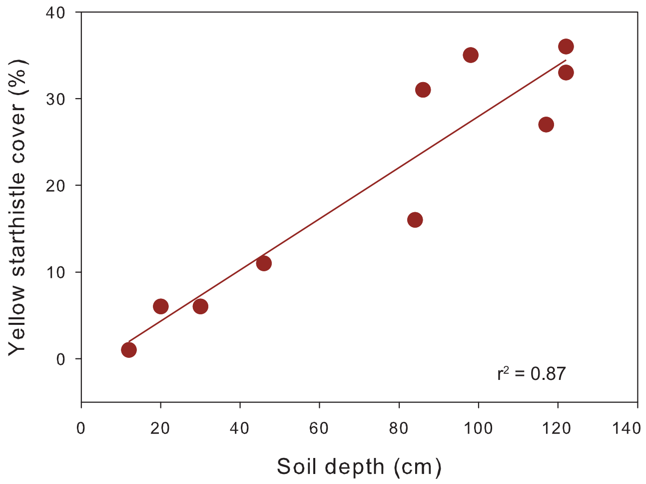


Fig. 8. Effect of soil depth. *Roché* et al. *(1994) found a positive correlation between soil depth and yellow starthistle cover.*

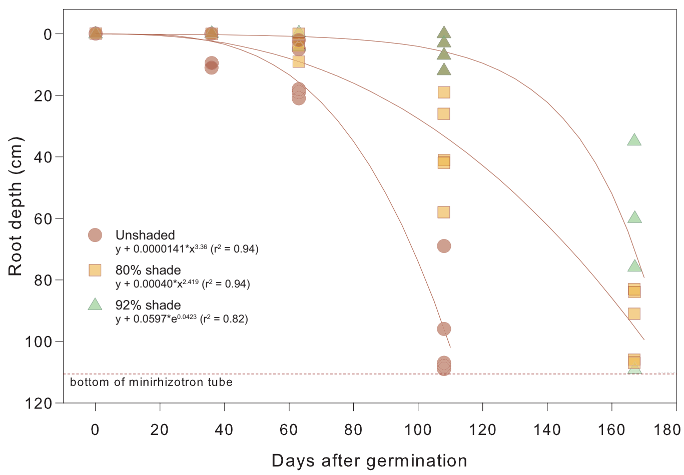


Fig. 9. Effect of shading on root growth. *Yellow starthistle seedlings show dramatically slower root growth under shaded conditions (DiTomaso* et al. *2003b).*

fall rains and ending with the last spring rain event, a typical stand of starthistle includes plants in several stages of development. Dense stands have both large canopied plants receiving full sunlight and an understory of smaller shaded plants. For these smaller plants, light suppression is a significant factor regulating root growth. The roots of larger plants exposed to full sunlight quickly grow to great depths, while roots of shaded plants in the understory occupy shallower depths for longer periods of time (DiTomaso *et al*. 2003b). Under these conditions, soil moisture is depleted from all depths in the soil profile.

SHOOTS

Seedlings that germinate in late fall or early winter pass the winter as basal rosettes. Rosettes develop slowly throughout the early spring. In the Central Valley and foothills of California, bolting typically occurs in late spring; by early to mid-summer, spines appear on developing seed heads. Around the time of bolting, yellow starthistle foliage develops pubescence and a waxy grayish coating that reflects a considerable amount of light. This reduces the heat load and the transpiration demand during hot dry summer months. Winged stems add surface area and also dissipate heat like a radiator (Prather 1994). These characteristics, as well as a deep root system, allow yellow starthistle to thrive under full sunlight in hot and dry conditions. Vigorous shoot growth coincides with increased light availability as neighboring annual species senesce and dry up. Moreover, the presence of spines on the bracts surrounding the seed head provides protection against herbivory. This is particularly important during the vulnerable flowering and seed development stages.

Senescence typically occurs in fall when moisture becomes limiting and plants are exposed to frost. Flowers can abort development before completion. Senesced stems can contain the non-pappus-bearing seeds for about a month until the spiny bracts and phyllaries fall off. Flowerhead receptacles contain fine chaff that gives the seed heads a cotton-tip appearance. In contrast, Malta starthistle (tocalote) and Sicilian (sulfur) starthistle do not have cotton-tip seed heads after senescence. Stems of yellow starthistle degrade slowly and may remain erect for a year or more.

Light, Temperature and Water Use Patterns

LIGHT

When yellow starthistle rosettes grow in full sunlight, they grow compact and flattened to the soil surface. However, in grasslands where they receive less light, rosettes grow larger leaves and develop a more erect growth form that may reach 25 cm (10 in) in height. This upright form allows them to capture more light until the reproductive shoots bolt through the senescing grass canopy in late spring (Roché *et al*. 1994).

Dense yellow starthistle seedling cover can significantly suppress the establishment of annual grasses and forbs. However, yellow starthistle rosettes are also very susceptible to light suppression; if shaded, they will produce short roots, larger leaves, more erect rosettes, and fewer flowers than plants in full sunlight (Roché and Roché 1991, Roché *et al*. 1994). Consequently, yellow starthistle does not survive well in shaded areas, and is less competitive in areas dominated by shrubs, trees, taller perennial forbs and grasses, or late season annuals. For this reason, infestations are nearly always restricted to disturbed sites or to open grasslands dominated by annuals.

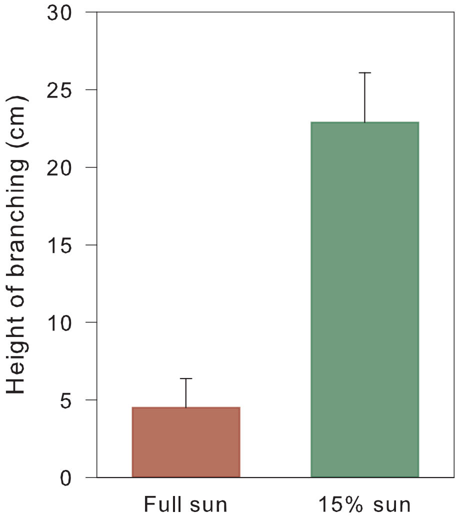


Fig. 10. Effect of shading on rosette growth. *One hundred days after germination, yellow starthistle rosettes grown in shade are elongated compared to plants grown in full sun (C.B. Benefield, unpubl. data).*

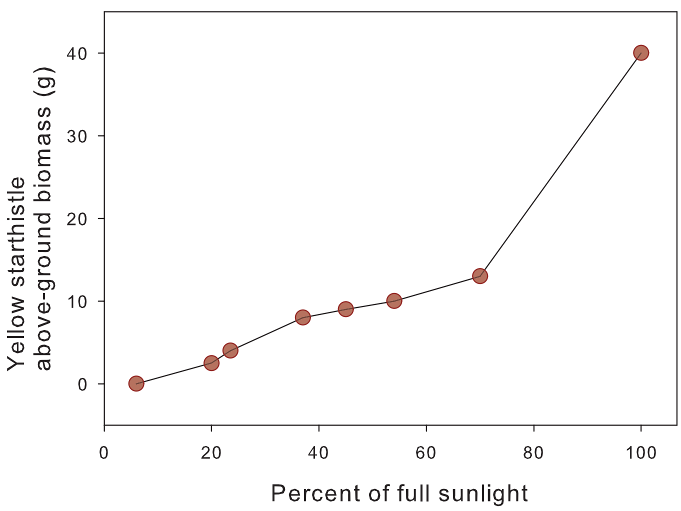


Fig. 11. Effect of sunlight on biomass production. *Yellow starthistle biomass production is strongly correlated with availability of sunlight (Roche* et al. *1994).*

TEMPERATURE

Yellow starthistle plants are insensitive to photoperiod and lack a vernalization requirement (Roché *et al*. 1997, Roché and Thill 2001). This allows late germinating plants to continue flowering as long as moisture is adequate, or until newly developing buds are killed by frost. In areas with mild winters, plants can act as biennials. However, in cold-winter areas such as eastern California or other western states, mature plants rarely survive the winter. Whereas seedlings can survive extended frost periods, mature plants are not considered to be frost tolerant. Cold hardiness appears to be lost during the transition from vegetative to reproductive phases.

WATER USE

Heavy infestations of yellow starthistle in grasslands with loamy soils can use as much as 50% of annual stored soil moisture (Gerlach, unpublished data). In deep soils on the floor of California's Central Valley, starthistle can significantly reduce soil moisture reserves to depths greater than 6.5 feet, and in foothill soils three feet deep it can extract soil moisture from fissures in the bedrock (Gerlach *et al*. 1998).

COMPETITION WITH INTRODUCED ANNUAL GRASSES

Shallow versus deep root partitioning between yellow starthistle and competing vegetation can greatly influence the susceptibility of grasslands to starthistle invasion (Brown *et al*. 1998). Since the root systems of most annual species are comparatively shallow, there is little competition for moisture between yellow starthistle and annual grasses during late spring and early summer. In addition to utilizing deep soil moisture, yellow starthistle can also survive at extremely low soil water potential as compared to annual grasses (Gerlach 2004).

Seasonal moisture can also influence the competitive advantage between yellow starthistle and annual grasses. Under dry spring conditions, early maturing annual grasses have an advantage over late season annuals, as they utilize the available moisture and complete their life cycle before the later maturing species, such as starthistle (Larson and Sheley 1994). In contrast, under moderate or wet conditions, starthistle has an advantage by continuing its growth later into the summer and fall and producing more seed.

Thus, in grassland systems, yellow starthistle would be at a competitive advantage 1) in communities dominated by annual grasses, 2) in areas with deep soil, and 3) in years with moderate to high spring rainfall (Sheley and Larson 1992). Under these conditions, yellow starthistle would mature later, have increased seed production, and have little competition for deep soil moisture. In annual grasslands, yellow starthistle would be disadvantaged by shallow soils and low spring rainfall.

COMPETITION WITH NATIVE SPECIES

The use of soil moisture by yellow starthistle is similar to that of perennial grasses (Borman *et al*. 1992). Like yellow starthistle, perennial grasses also have an extended growing season. These factors account for increased competition between yellow starthistle and perennial species, compared to annual species.

The characteristics that enable yellow starthistle to invade grasslands can threaten native species and ecosystems processes. Native species such as blue oak (*Quercus douglasii*) and purple needlegrass (*Nassella pulchra*) depend on summer soil moisture reserves for growth and survival (Gerlach *et al*. 1998). Yellow starthistle, however, uses deep soil moisture reserves earlier than blue oak or purple needlegrass. Thus, from the perspective of native species, infested sites can experience drought conditions even in years with normal rainfall (Gerlach *et al*. 1998).

Heavy yellow starthistle infestations can remove large amounts of stored soil moisture through plant transpiration (Gerlach *et al*. 1998). Most soils in California grasslands store about 12 inches of rainfall for each 3.25 ft of soil depth. In most years annual grasses reduce soil moisture reserves by about 4 inches of stored rainfall in the top 3.25 ft of soil. By comparison, yellow starthistle can reduce soil moisture levels by 8 inches of stored rainfall for each 3.25 ft of soil depth – about the same as a mature oak tree. As a result, large yellow starthistle populations transpire at least an additional 4 inches of rainfall for each 3.25 ft of soil depth during average rainfall years and about 8 inches during wet years (Gerlach *et al*. 1998).

Species shown to be the most competitive with yellow starthistle are those that occupy a similar root zone (Brown *et al*. 1998), including many native perennial grasses. Increased species diversity, particularly with overlapping community resource use patterns, can also reduce invader success (Brown *et al*. 1998, DiTomaso, unpublished data).

Management

The goal of any management plan should be not only controlling the noxious weed, but also improving the degraded community, enhancing the utility of that ecosystem, and preventing reinvasion or invasion by other noxious weed species. To accomplish this usually requires a long-term integrated management plan. Development of a management program and selection of the proper tool(s) also may depend on other factors such as weed species and associated vegetation, initial density of yellow starthistle infestation, effectiveness of the control techniques, years necessary to achieve control, environmental considerations, chemical use restrictions, topography, climatic conditions, and relative cost of the control techniques. A number of considerations can influence the choice of options, most important being the primary land-use objective. These objectives may include forage production, preservation of native or endangered plant species, wildlife habitat development, and recreational land maintenance.

There are a number of control options available for the management of yellow starthistle, including grazing, mowing, manual removal, perennial grass or broadleaf reseeding, burning, application of herbicides, and release of biological control agents. Recent emphasis has been on the development of integrated systems for the long-term sustainable management of yellow starthistle. Such systems include various combinations of control techniques. In many cases, three or more years of intensive management may be necessary to significantly reduce a yellow starthistle population. Although uncommon, it is possible to substantially reduce the infestation with one year of control. However, a more established starthistle population with a large residual seed bank usually requires a longer-term management program (DiTomaso 2000).

When developing a yellow starthistle management program, it is important to consider the advantages (benefits) and disadvantages (risks) of each approach and to judge how it may best fit into a long-term program. It is possible that several different strategies can prove successful in a given location. Successful programs incorporate persistence, flexibility, and, most importantly, prevention of new seed recruitment (DiTomaso *et al*. 2000b). Advantages, disadvantages, risks, timing, and strategic role for each control option are discussed below.