

Effect of light and density on yellow starthistle (*Centaurea solstitialis*) root growth and soil moisture use

Joseph M. DiTomaso

Corresponding author. Weed Science Program,
Department of Vegetable Crops, University of
California, Davis, CA 95616;
ditomaso@vegmail.ucdavis.edu

Guy B. Kyser

Weed Science Program, Department of Vegetable
Crops, University of California, Davis, CA 95616

Carri B. Pirosko

California Department of Food and Agriculture,
20235 Charlanne Drive, Redding, CA 96002

Yellow starthistle root growth was measured under field conditions using a minirhizotron camera system. Roots grew 1.0 to 1.3 cm d⁻¹ and quickly reached the bottom of the 100-cm tube. When plants were grown under 80 and 92% shading, roots grew 45 and 64% slower, respectively, than when plants were grown unshaded. Using a neutron probe, we evaluated the effect of yellow starthistle density on soil moisture depletion to 180 cm in the soil profile. At the end of the growing season, we also measured above-ground biomass and seedhead production. Total plant dry weight and seedhead number at the lowest density (0.6 plants m⁻²) were 43 and 97% of the maximum values, respectively, suggesting that yellow starthistle is capable of reaching near-maximum yield at low densities. Moisture depletion was density dependent, and plants in low-density plots used more soil moisture from deep in the profile than from shallow soil (30 cm) early in the season. In contrast, yellow starthistle densities > 90 plants m⁻² rapidly depleted moisture from all depths in the soil profile by preflowering growth stages. High yellow starthistle density expands the moisture depletion zone and leads to increased shallow moisture depletion. In high-density plots, soil moisture did not recharge, compared with bare-ground plots, after subnormal winter and spring precipitation. These results illustrate the importance of reducing yellow starthistle densities in grassland restoration efforts, where shallow soil moisture is critical to the establishment of seeded perennial grasses or annual forbs and where moderate to deep soil moisture is essential for the establishment and survival of transplanted shrubs and trees.

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

Key words: Invasive, light suppression, minirhizotron, neutron probe, noncrop weed, soil moisture.

The loss of native perennial vegetation throughout North America's rangelands has been accompanied by invasions of aggressive alien annual weeds (Sheley et al. 1993). In California, yellow starthistle has become one of the most widely distributed and important invasive species in rangelands, pastures, and wildlands. It is found in 56 of the 58 counties in California and infests 10 to 15% of the total surface area of the state (Pitcairn et al. 1997). In many areas, yellow starthistle forms nearly solid stands, with densities exceeding 100 plants m⁻² (Thomsen and Williams 1992).

Dense stands of yellow starthistle competitively exclude native species, decrease recreation value of lands, reduce forage production and grazing capacity, poison horses when consumed in large quantities, and hinder rangeland restoration efforts (Joley et al. 1992; Thomsen et al. 1996). Many characteristics contribute to the success of yellow starthistle in grassland. As an introduced species, starthistle lacks its native predators and pathogens. In addition, it produces numerous seeds with nonrestrictive germination requirements and is a long-lived, deep-rooted winter annual capable of exploiting late-season deep residual soil moisture not available to early-senescent shallow-rooted annuals (Larson et al. 1992).

Previous studies have shown rapid and continuous yellow starthistle root growth during winter and early spring (Roché et al. 1994; Sheley et al. 1993). Starthistle roots and radicles elongate at a faster rate and to greater depths than do potentially competitive species, such as weedy annual grasses and subterranean clovers (*Trifolium* spp.) (Sheley et al. 1993). The ability of starthistle roots to penetrate to greater soil depths

extends the period of resource availability into the dry summer months and provides a competitive advantage over shallow-rooted species (Gerlach et al. 1998).

In addition to using deep soil moisture, yellow starthistle can also survive at lower soil water potentials than annual grasses can (Gerlach 2000). Heavy infestations of starthistle in grasslands (loamy soil) use as much as 50% of annual stored soil moisture (Gerlach 2000). Reseeded perennial grasses and desirable broadleaf species in rangelands and wildlands likely will fail to establish in the absence of adequate surface soil moisture during the critical spring growing season (DiTomaso et al. 2000).

In this study, we addressed the question of whether low- and high-density stands of yellow starthistle differentially deplete available grassland soil moisture zones. The results of these findings will have important implications in restoration efforts. This study was accomplished by (1) measuring rooting depth and growth rate of yellow starthistle under full and reduced light, (2) determining the aboveground yield response of starthistle at several densities in the absence of other competing vegetation, and (3) assessing the time course of moisture depletion and recharge in response to yellow starthistle density at several soil depths.

Materials and Methods

Site Parameters

All field studies were carried out near Davis in Yolo County, CA. The site is at an elevation of 15 m and received

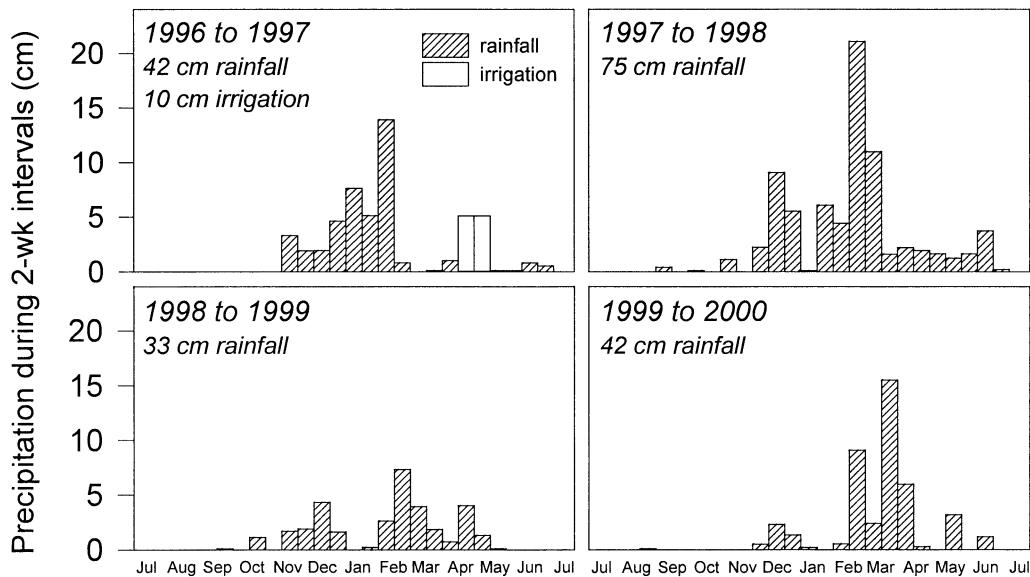


FIGURE 1. Precipitation (cm) and irrigation (in 1997) at 2-wk intervals at Davis during the experimental years 1996–2000.

42 cm of rain in the 1997 field season (July 1, 1996 to June 30, 1997), 75 cm of rain in the 1998 field season (July 1, 1997 to June 30, 1998), 33 cm of rain in the 1999 field season (July 1, 1998 to June 30, 1999), and 42 cm of rain in the 2000 field season (July 1, 1999 to June 30, 2000) (Figure 1). Average precipitation during the period from 1961 to 1990 was 45 cm. The soil is classified as a Yolo silty loam and is a deep alluvial soil typical of the Central Valley. We collected yellow starthistle achenes from a moderately sized population close to the research site. Yellow starthistle was the only species present in field trial plots because all other species were hand weeded.

Rooting Depth

We established fifteen 3- by 1-m plots on January 19, 1996. Plots were broadcast seeded with yellow starthistle (500 seed per plot) after 180-cm-long, clear acrylic minirhizotron tubes were installed at a 45° angle in the center of each plot. A $\times 100$ color camera¹ was inserted into minirhizotron tubes to observe nondestructively and record root growth over time to a 100-cm depth. We measured growth until roots reached beyond the base of the tubes. In addi-

TABLE 1. Average number of yellow starthistle (*Centaura solstitialis* L.) plants m^{-2} at five density levels in 1997, 1998, and 2000. Numbers in parentheses indicate \pm SD when not equal to zero.

Density treatment	Mean number of plants m^{-2} (\pm SD)		
	1997	1998	2000
0	0	0	0
1	0.6	0.6	0.6
2	27 (18.5)	10 (5.6)	18 (7.1)
3	93 (28.6)	479 (62.5)	60 (18.2)
4	169 (34.4)	1,504 (710.6)	116 (30.2)
Precipitation (cm) from July 1 (previous year) to June 30	52 ^a	75	42

^a Includes 10 cm of irrigation water.

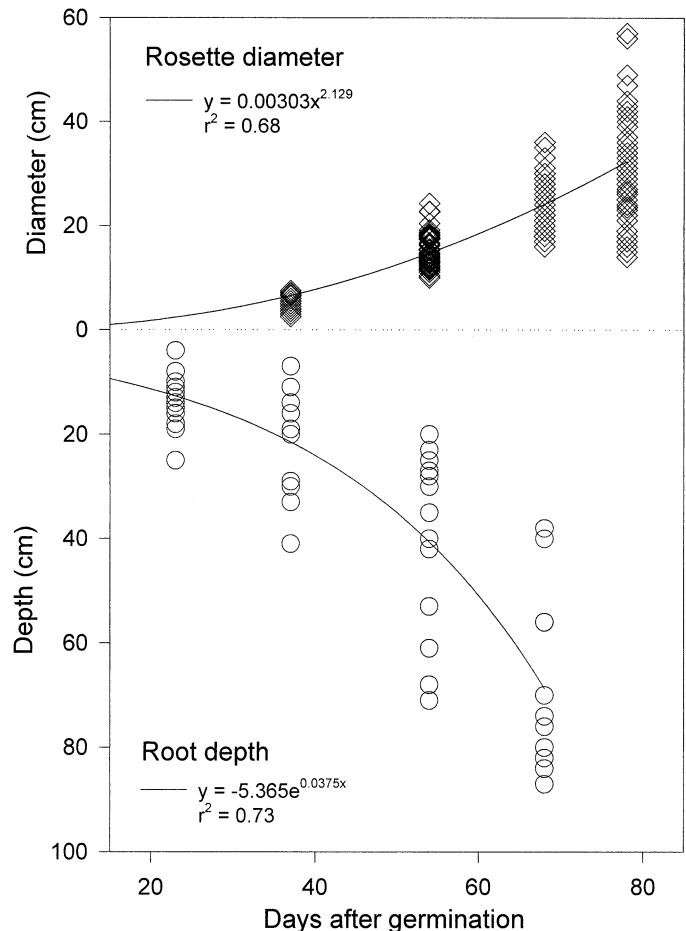


FIGURE 2. Above- and belowground growth of yellow starthistle roots and shoots for 78 d from January 19 to April 7, 1996 at Davis. Diamonds indicate individual rosette diameter, and circles represent individual root depth. Regressions are interpolated from the raw data.

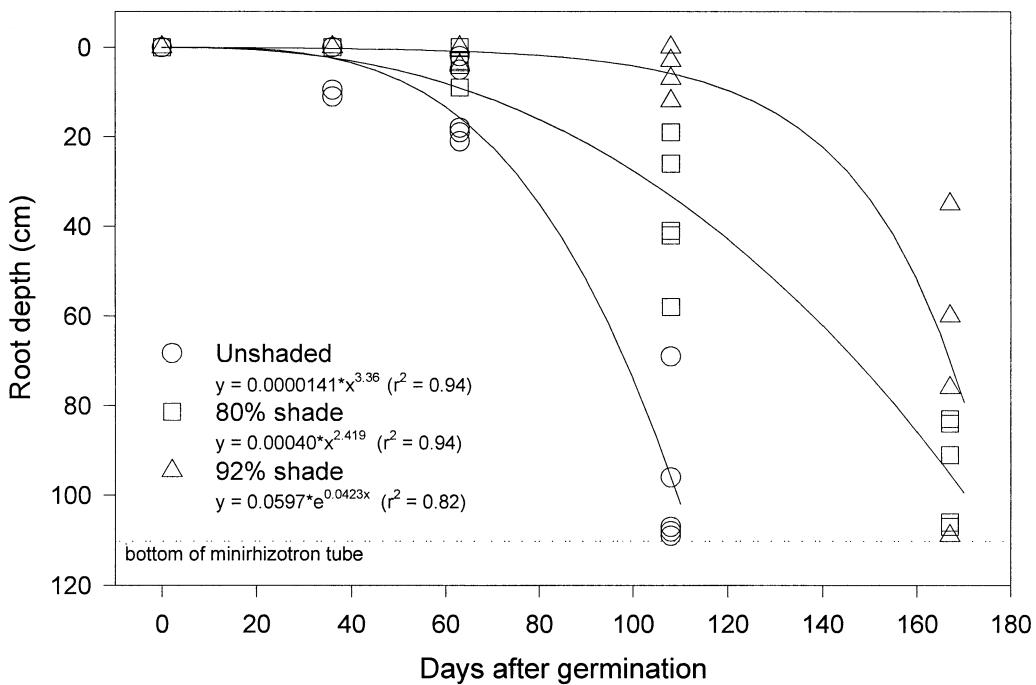


FIGURE 3. Root growth of yellow starthistle seedlings under shaded and unshaded conditions for 167 d from December 2, 1996 to May 18, 1997. Lines are plots of equations fitted by iterative nonlinear regression procedures. Each treatment produced distinct results based on repeated measures analysis.

tion, we measured aboveground rosette diameter (10 subsamples per plot measured in two directions and averaged) several times throughout the duration of the experiment. A similar root growth experiment was conducted at the same location in the winter and early spring of 1997. In the second study, we evaluated yellow starthistle root growth under three light regimes using shade cloth² to simulate plant canopy light reduction. Treatments included 80 and 92% light reduction (shade cloth) and unshaded controls (four to five replications per treatment, in randomized complete blocks). Light reduction levels were comparable with previous measurements of light suppression underneath yellow starthistle canopies in the field. Plots were seeded with yellow starthistle (December 2, 1996) and covered with shade cloth. We again used minirhizotron tubes and the camera to observe nondestructively and measure root growth for 167 d beginning with seeding of yellow starthistle.

Effect of Density on Biomass, Seedhead Production, and Soil Moisture Depletion

We established 20 to 25 circular, 4-m-diam plots in 1997, 1998, and 2000. We installed polyvinyl chloride tubes with a hand auger in the center of each plot to a depth of 180 cm. Plots were broadcast seeded with yellow starthistle and subsequently thinned to five densities (four to five replicates each, in randomized complete blocks). Plants were uniformly spaced in a constant pattern in all plots. At the two lower densities, 0 and 0.6 plants m^{-2} , we hand weeded the plots to prevent subsequent seedling establishment. At the highest density, we allowed plants to grow, and all species other than starthistle were removed. In these plots the final yellow starthistle density for the three highest density levels varied depending on year (Table 1). Plots at the third and fourth highest densities were maintained by periodic manual hoeing. In 1998, rainfall was 67% above normal, and densities

at the two highest levels were much higher than those in 1997 and 2000. Because of lack of spring rainfall in April 1997, we added an additional 10 cm of sprinkler-irrigated water to all plots (Figure 1). Plots were not irrigated in 1998 or 2000.

A neutron probe³ was used to measure the effects of five yellow starthistle densities on soil moisture availability at six depths (30, 60, 90, 120, 150, and 180 cm) at approximately 2-wk intervals (only representative dates are presented) throughout the 1997, 1998, and 2000 growing seasons and once on March 16, 1999. On each recording date, three 30-s readings were taken at each depth. The neutron probe measures subsurface soil volumetric water content by emitting high-energy neutrons that are slowed by the presence of hydrogen in water. A reduction in the reflected signal indicates increased soil moisture content. Tubes were capped to prevent moisture entry.

We also recorded phenological development throughout the growing season. Toward the end of each season, in August (initial plant senescence), we measured individual and total dry weight biomass and seedhead numbers per unit area in each plot. Biomass samples and seedhead estimates were selected from portions of each plot that were most representative of the plot as a whole. In each low-density plot (0.6 plants m^{-2}), a 1.5- m^2 sample was harvested. To avoid edge effects in the higher-density plots, we sampled a 0.85- m^2 section inside a 2.1- m^2 wedge for each plot.

Analysis

We used iterative procedures to fit nonlinear regression equations to yellow starthistle seedling root growth and rosette diameter data. Because the rate of early plant growth is a positive feedback function, it was initially assumed that power or exponential functions would most accurately describe the data.

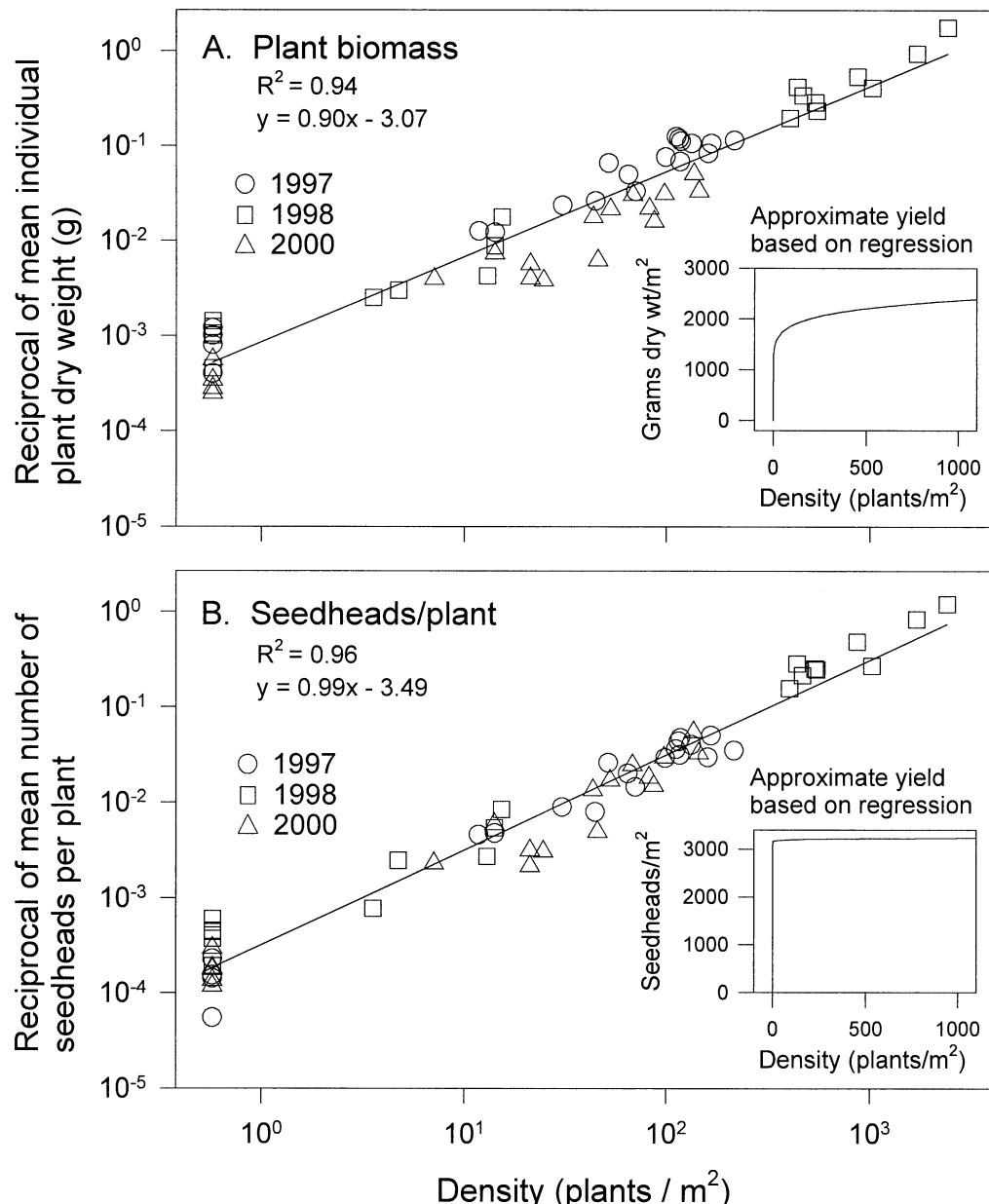


FIGURE 4. Reciprocal yield of yellow starthistle (A) dry weight and (B) seedhead number, plotted as a function of the log of density (plants m^{-2}). Data points represent means for each individual plot. Linear regressions were derived from combined data for 1997, 1998, and 2000. Inserts within each figure were based on regressions found in the analysis of reciprocal yield, and yield data are plotted as a function of density.

Soil moisture profiles under each planting density of yellow starthistle were separated for each date using multiresponse permutation procedures (MRPPs) (Mielke et al. 1981). MRPP is a nonparametric technique that allows comparison between each series of values as a unit. In this case, we treated each moisture profile as an object with six measurements (a soil water value for each depth); the four to five replicates of each planting density were treated as a group. The measurements characterizing each moisture profile were used to calculate its geometric distance from the other profiles. MRPP compared distances within groups with distances among groups and calculated the likelihood of such distances occurring by chance. Initially, all five profiles were compared for each date. Significant differences ($\alpha \leq 0.05$) were found among groups on all dates. We ran pairwise comparisons between each pair of profiles for each

date, and letter symbols were assigned to indicate significant differences.

Results and Discussion

Root and Rosette Growth

All measures of root growth were taken under field conditions during seedling and rosette stages, before bolting. During these developmental phases, most of the carbohydrate resources were being allocated belowground to root growth. Power or exponential functions described the data most accurately. Root length increased exponentially with time, and by 68 d after germination, roots reached an average depth of 65 cm (Figure 2). Within 80 d of planting (mid-April), roots in most plots extended beyond the depth

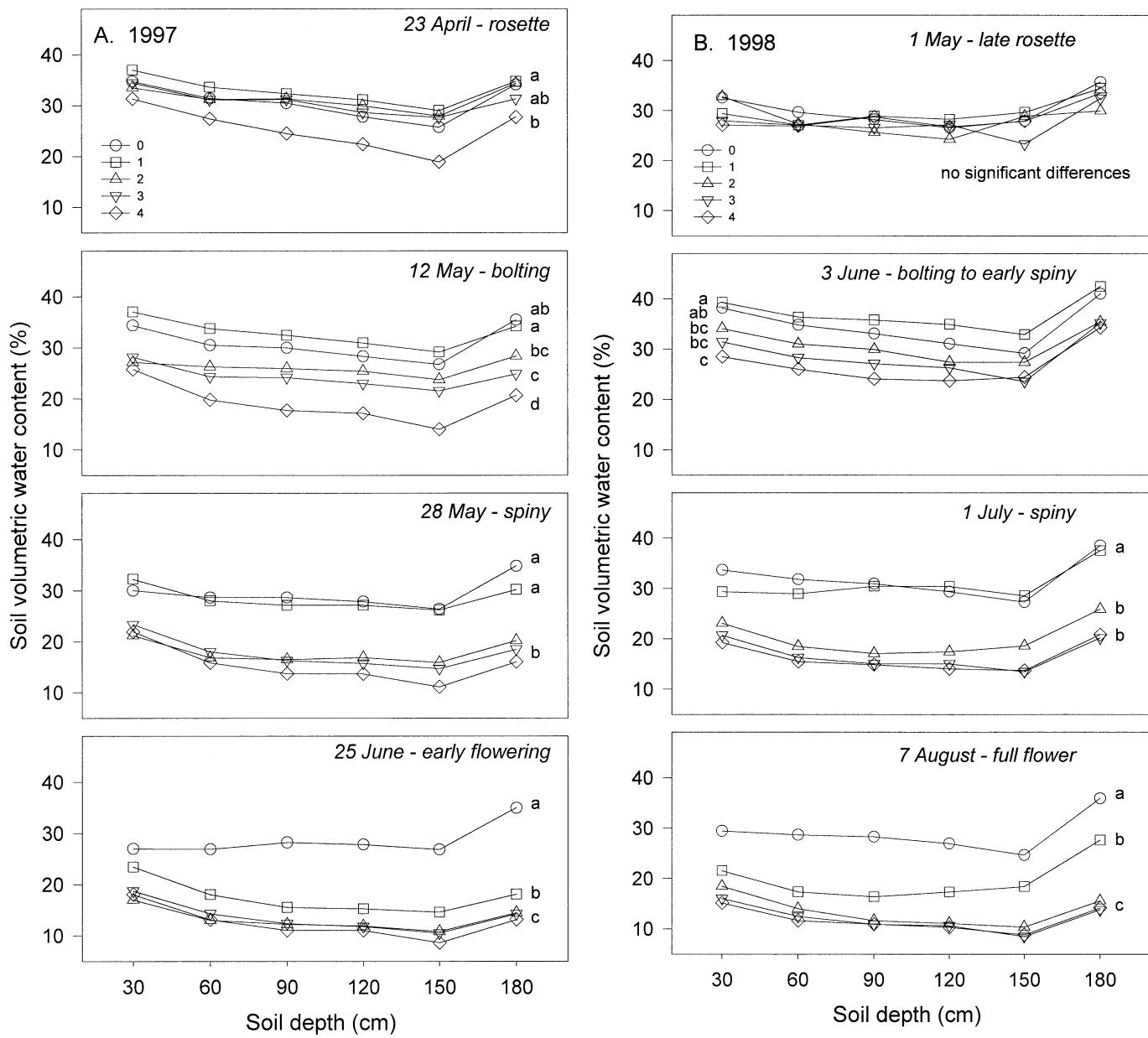


FIGURE 5. Soil volumetric water content at 30-cm intervals to 180-cm depth at several yellow starthistle densities and times in (A) 1997, (B) 1998, and (C) 2000. Density levels correspond with those presented in Table 1 and range from 0 (bare ground) to 4 (highest density). Differences between lines were determined using multiresponse permutation procedures. Moisture profiles followed by the same letter are not different at the 5% confidence level.

of the acrylic tubes. Average rate of root growth across the length of the study was 1.3 cm d^{-1} . Rosette diameter also increased exponentially, but rosettes had not produced flowering stems by the last measurement date. Root growth in our study was similar to that in other studies conducted in root tubes or boxes. Roché et al. (1994) and Sheley et al. (1993), for example, demonstrated yellow starthistle root growth at mean rates of 1.1 and 1.7 cm d^{-1} , respectively. They also showed little aboveground rosette growth during winter months, when roots were growing rapidly.

On the basis of our previous work (Benefield et al. 2001), in which yellow starthistle germinated over the entire rainy season, we hypothesized that later-germinating seedlings would be shaded by older and larger rosettes and would not be exposed to maximum available sunlight during the rosette phase. Thus, we postulated that light suppression

might influence yellow starthistle root growth. To test this, we used a minirhizotron system to measure the rate of root growth in shaded and unshaded plots.

Reduced root growth correlated with increased shading (Figure 3). Based on the derived equations for growth, roots of yellow starthistle required 96, 143, and 165 d to reach a 65-cm depth in the unshaded, 80% shaded, and 92% shaded plots, respectively. The rate of root growth in the unshaded treatment (0.98 cm d^{-1}) was similar to that shown in Figure 2. The mean rate of root growth under 80 and 92% shading was 0.54 and 0.35 cm d^{-1} , respectively. Consequently, root growth was delayed by as much as 1.5 mo under 80% light reduction and by over 2 mo with 92% light reduction. Roots eventually reached the bottom of the minirhizotron tubes despite substantial (92%) shading.

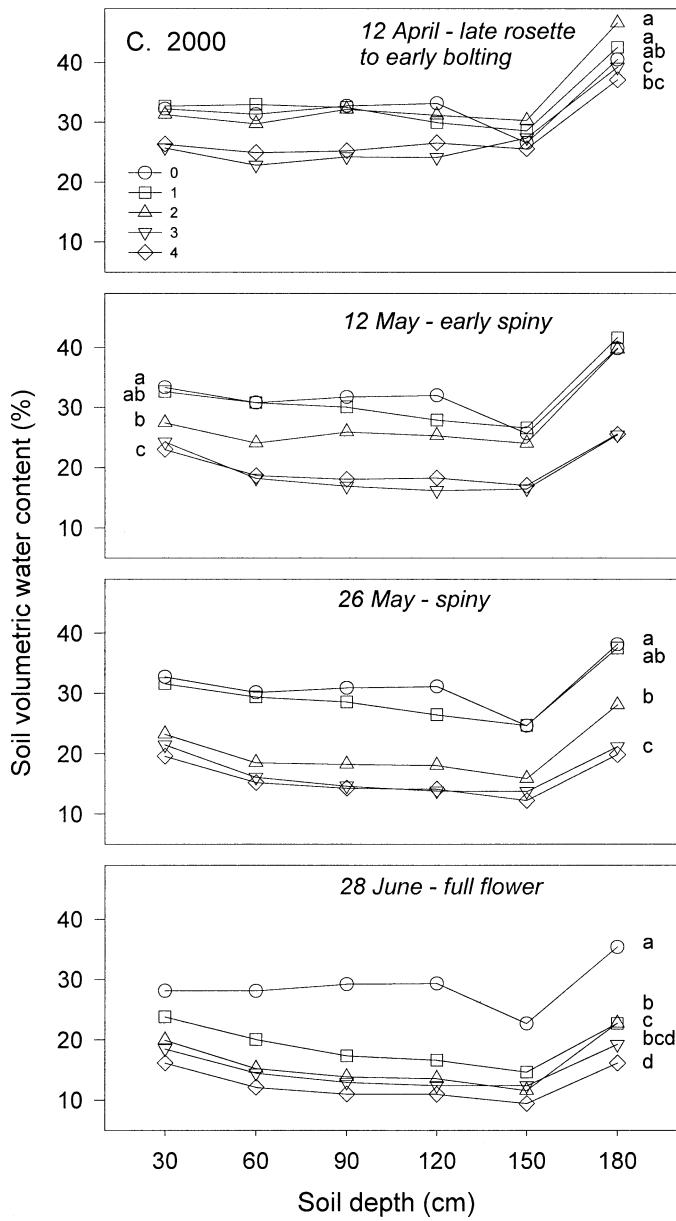


FIGURE 5. Continued.

Effect of Density on Biomass and Seedhead Production

No differences in phenological development were observed among plants growing at various densities in 1997, 1998, and 2000. Analysis of reciprocal yield (Watkinson 1980) of both yellow starthistle biomass (dry weight) and seedhead count vs. the log of density for the 3 yr combined showed a strong negative correlation between individual starthistle plant yield and planting density (Figures 4A and 4B). Both yield measures produced robust linear regressions: $r^2 = 0.94$ for dry weight and $r^2 = 0.96$ for seedhead number. On the basis of the regressions found in the analysis of reciprocal yield, we also plotted yield data as a function of density (inserts of Figures 4A and 4B). Even at the lowest density ($0.6 \text{ plants m}^{-2}$), biomass and seedhead numbers were estimated to be 43 and 97%, respectively, of the maximum values within the range of densities in this study. The density giving 50% of the maximum value for biomass was

estimated to be $2.4 \text{ plants m}^{-2}$. These results support theories describing the law of constant final yield and plasticity of weedy annuals with increasing density (Harper and Gajic 1961; Kira et al. 1956) and indicate that yellow starthistle has the potential to reach near-maximum yield potential at very low densities in the absence of competition.

Effect of Density on Soil Moisture Depletion

The neutron probe measures soil volumetric water content. In this experiment, we compared soil moisture depletion in yellow starthistle plots with that in bare-ground plots (zero density). Thus, we made the assumption that soil moisture depletion in yellow starthistle plots is due to plant uptake rather than evaporation from the soil surface. Reductions in soil volumetric water content over time are considered to be synonymous with plant water use.

Water-use patterns of yellow starthistle were density dependent. One month after irrigation in April 1997, all plant foliage was in the rosette stage of development. At this time, only the highest-density plots had significantly depleted soil moisture compared with bare-ground plots (Figure 5A). By the time plants were in the bolting and spiny (flowerheads producing expanding spines) stage in mid to late May, all densities, except the lowest one ($0.6 \text{ plants m}^{-2}$), had significantly diverged from those of the bare-ground plots, and this depletion was seen at all soil depths (for phenological stages, see Benefield et al. 2001). In most grassland areas of California, annual grasses and native forbs typically progress through their reproductive stages during mid to late spring. Although the deep root system of yellow starthistle allows it to use soil water at much greater depths than in the case of most annuals (Sheley and Larson 1994, 1995), dense stands of yellow starthistle also would deplete shallow soil moisture reserves (30 cm). This likely would lead to significant competition with desirable annual species during a critical period in their life cycle. However, at the lowest yellow starthistle density, there was no significant difference in water depletion compared with bare-ground plots until late June, when starthistle was in the early flowering stage, and this was due to increased depletion of soil moisture at depths of 60 cm or greater. Plots at the three highest densities showed similar soil moisture depletion patterns by the early flowering stage in late June.

Results in 2000 (Figure 5C) were very similar to those in 1997. Total precipitation in both years was identical (42 cm), although plots received an additional 10 cm of irrigated water in April 1997. In 1998, however, California experienced a very wet and warm spring (El Niño), with precipitation far above (167%) the normal levels (Figure 1). As a result, the vegetative growth phase appeared to extend longer in 1998, and the phenological development of yellow starthistle was delayed compared with 1997 and 2000. We reported similar results with barb goatgrass (*Aegilops triuncialis* L.) in 1997 and during the El Niño season of 1998 (DiTomaso et al. 2001). In 1998, bolting occurred at the end of May, and the spiny stage was initiated around July 1. In comparison, bolting occurred in mid-May in 1997 and at the end of April in 2000, and the spiny stage began at the end of May in both 1997 and 2000. Nevertheless, the pattern of water use relative to phenology in 1998 was similar to that in both 1997 and 2000 (Figure 5B). By the spiny

stage, the water-use patterns for all densities except the lowest were higher ($\alpha \leq 0.05$) than those in bare-ground plots.

Although aboveground biomass and seedhead numbers for yellow starthistle did not differ greatly between the lowest density and all other higher densities (Figure 4), clear differences were measured in soil water-use patterns (Figure 5). Consequently, initial infestations at low density have the potential to produce high numbers of seeds without significantly affecting water use of shallow-rooted annual species. At these low densities, yellow starthistle primarily depletes deeper soil moisture early in the growing season (≥ 60 cm). However, in subsequent years the expanding seedbank of yellow starthistle would undoubtedly increase population density. At these higher densities, soil moisture would be depleted from all depths in the soil profile throughout the season. Using a similar experimental procedure, Borman et al. (1992) showed that soil volumetric moisture in a yellow starthistle-infested grassland site in southern Oregon was depleted at all soil depths from 15 to 60 cm. Although they did not report starthistle density at this site, it was the dominant species. As a result, they concluded that yellow starthistle was responsible for the lower soil moisture content at depths of 30 cm and below.

We have hypothesized that high yellow starthistle densities expand the water-use profile through intraspecific competition between early-germinating, rapidly establishing yellow starthistle seedlings (deep rooting) and seedlings germinating later in the season that were shaded by the early germinators (shallow rooting). Sheley and Larson (1997) found that intraspecific competition in yellow starthistle was twice as influential as interspecific competition with the annual grass downy brome (*Bromus tectorum* L.). Under these high-density conditions, competition for moisture with shallow-rooted annual species would likely increase, thus affecting forage capacity of annual grass-dominated rangelands and grasslands. In support of this, clopyralid applied to a heavily infested yellow starthistle site ($> 1,000$ plants m^{-2}) in late winter (February or March) produced a significantly higher desirable annual grass forage yield compared with untreated plots (DiTomaso et al. 1999). However, similar applications made toward the end of the rainy season (May), at the early bolting stage of yellow starthistle, resulted in no additional annual grass forage compared with untreated plots. These findings support the view that higher yellow starthistle densities have the capacity to extract soil moisture from the entire soil profile and compete with shallow-rooted annual species as well as deep-rooted annuals and perennials.

After the 1998 growing season, we measured soil water content the following March (1999) in the 1998 highest-density and bare-ground plots at six depths from 30 to 180 cm. During that year (July 1, 1998 to June 30, 1999), precipitation was 73% of the yearly average. Even in the absence of vegetation, the soil volumetric water content was statistically lower at soil depths of 120 cm and below in the 1998 high-density plots (Figure 6). In contrast, moisture recharge in the bare-ground plots was similar to the values obtained in other years at all soil depths. The inability of soil moisture to recharge in a heavily infested yellow starthistle site can severely hamper restoration efforts, where shallow soil moisture is critical in the early establishment of seeded perennial grasses and desirable annual forbs, and moderate to deep soil moisture is essential for the establish-

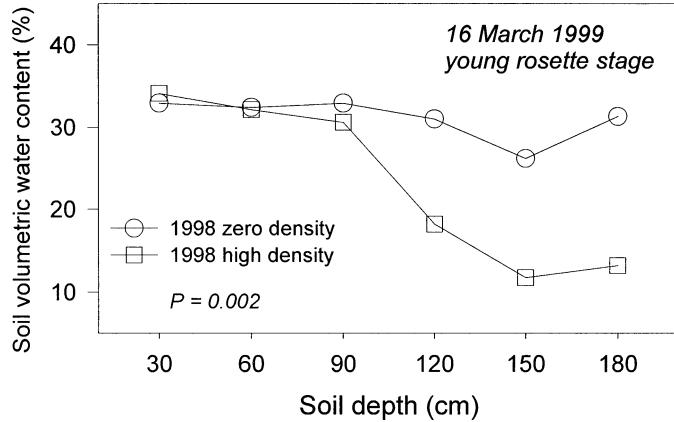


FIGURE 6. Soil volumetric water content in March 1999 at 30-cm intervals to 180-cm depth in bare-ground plots and plots previously planted (1998) with a high density ($1,504$ plants m^{-2}) of yellow starthistle. Plots at time of measurement lacked vegetation, and curves represent moisture recharge from fall and winter precipitation. Lines were found to be significantly different ($P = 0.002$) using multiresponse permutation procedures.

ment and survival of pole-planted native shrubs and trees such as oaks (*Quercus* spp.). In effect, yellow starthistle infestations can create drought conditions even in years with normal rainfall. Gerlach (2000) calculated that depletion of soil moisture by yellow starthistle on invaded sites is equivalent to a loss of 15 to 25% of mean annual precipitation. In terms of economic loss, he estimated that the value of lost water ranged between \$16 and \$75 million per year in the Sacramento River watershed alone.

Because yellow starthistle plants germinate during an extended period (Benefield et al. 2001), beginning with the first fall rains and ending with the last spring rain, the resulting canopy would consist of plants in several stages of development. In dense stands of yellow starthistle, both large canopied plants receiving full sunlight and an understory of smaller shaded plants are often observed. We have demonstrated that intracanopy light suppression is a significant factor regulating root growth (Figure 3). Roché et al. (1994) reported a high correlation between percentage of full sunlight and yellow starthistle height, biomass, and reproductive capacity. They found that yellow starthistle seedlings under reduced light produced larger leaves and more erect rosettes but significantly fewer flowers, less biomass, and shorter roots. A 25% reduction of full sunlight reduced flower production by 82% and biomass by 65%. For this reason, yellow starthistle rarely invades shaded sites and is primarily a problem in open grassland (Roché et al. 1994). On the basis of our previous findings, we hypothesize that roots of larger plants exposed to full sunlight grow quickly to great depths, whereas roots of shaded plants underneath the yellow starthistle canopy occupy shallower depths for longer periods. Under these conditions, soil moisture is rapidly depleted from all depths in the soil profile. Initial control measures must significantly reduce plant densities and cover before revegetation efforts can be considered. In another study, DiTomaso et al. (2000) were successful in establishing drill-seeded pubescent wheatgrass [*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey] in areas treated with clopyralid for control of yellow starthistle. In contrast, drill-seeded pubescent wheatgrass was unable to establish in uncontrolled yellow starthistle-infested areas.

Thus, reseeding of perennial grasses in yellow starthistle-infested grasslands will require initial control efforts to allow establishment of perennials to use available surface moisture during the vulnerable period in late spring.

Sources of Materials

¹ ×100 color camera, Bartz Technology Corp., 116 'A' East Yonanoli Street, Santa Barbara, CA 93101.

² Sudden shade, DeWitt Co., 905 S. Kingshighway, Sikeston, MO 63801.

³ CPN 503DR hydroprobe moisture neutron depth gauge, Boart Longyear Co., 2830 Howe Road, Martinez, CA 94553-4000.

Acknowledgments

We thank Jenny Drewitz, Kevin Karabian, and Alison Stanton for their field assistance. We are also grateful to Dr. Dave Spencer of the USDA Invasive Plant Laboratory at UC Davis for the use of the minirhizotron equipment and to Mike Mata of the Department of Land Air and Water Resources at UC Davis for the use of the neutron probe.

Literature Cited

- Benefield, C. B., J. M. DiTomaso, G. B. Kyser, and A. Tschohl. 2001. Reproductive biology of yellow starthistle: maximizing late-season control. *Weed Sci.* 49:83–90.
- Borman, M. M., D. E. Johnson, and W. C. Krueger. 1992. Soil moisture extraction by vegetation in a Mediterranean/Maritime climatic regime. *Agron. J.* 84:897–904.
- DiTomaso, J. M., K. L. Heise, G. B. Kyser, A. M. Merenlender, and R. J. Keiffer. 2001. Carefully timed burning can control barb goatgrass. *Calif. Agric.* 55:47–53.
- DiTomaso, J. M., G. B. Kyser, S. B. Orloff, and S. F. Enloe. 2000. Integrated strategies offer site-specific control of yellow starthistle. *Calif. Agric.* 54:30–36.
- DiTomaso, J. M., G. B. Kyser, S. B. Orloff, S. F. Enloe, and G. A. Nader. 1999. New growth regulator herbicide provides excellent control of yellow starthistle. *Calif. Agric.* 53:12–16.
- Gerlach, J. D., Jr. 2000. A Model Experimental System for Predicting the Invasion Success and Ecosystem Impacts of Non-Indigenous Summer-flowering Annual Plants in California's Central Valley Grasslands and Oak Woodlands. Ph.D. dissertation. University of California, Davis, CA. 102 p.
- Gerlach, J. D., A. Dyer, and K. J. Rice. 1998. Grassland and foothill woodland ecosystems of the Central Valley. *Fremontia* 26:39–43.
- Harper, J. and D. Gajic. 1961. Experimental studies of the mortality and plasticity of a weed. *Weed Res.* 1:91–104.
- 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.
- Kira, T., H. Ogawa, K. Hozumi, K. Yoda, T. Asahira, and K. Shinozaki. 1956. Intraspecific competition among higher plants V-VIII. *J. Inst. Polytch. Osaka City Univ. Ser. D.* 7:1–94.
- Larson, L. L., G. L. Kiemnec, and M. L. McInnis. 1992. Effects of water and salt stress on yellow starthistle germination and root growth. *Knapweed* 6(2):1–4.
- 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.
- Pitcairn, M. J., R. A. O'Connell, and J. M. Gendron. 1997. Yellow starthistle: survey of statewide distribution. Pages 53–56 in D. M. Woods, ed. *Biological Control Program Annual Summary*, 1996. Sacramento, CA: California Department of Food Agriculture, Plant Health and Pest Prevention Services.
- Roché, B. F., Jr., C. T. Roché, and R. C. Chapman. 1994. Impacts of grassland habitat on yellow starthistle invasion. *Northwest Sci.* 68:86–96.
- Sheley, R. L. and L. L. Larson. 1994. Comparative growth and interference between cheatgrass and yellow starthistle seedlings. *J. Range Manag.* 47:470–474.
- Sheley, R. L. and L. L. Larson. 1995. Interference between cheatgrass and yellow starthistle at three soil depths. *J. Range Manag.* 48:392–397.
- Sheley, R. L. and L. L. Larson. 1997. Cheatgrass and yellow starthistle growth at three soil depths. *J. Range Manag.* 50:146–150.
- Sheley, R. L., L. L. Larson, and D. E. Johnson. 1993. Germination and root dynamics of range weeds and forage species. *Weed Technol.* 7: 234–237.
- Thomsen, C. D. and W. A. Williams. 1992. Controlling yellow starthistle with livestock grazing in California. *Knapweed* 6(3):1–3.
- Thomsen, C. D., W. A. Williams, M. P. Vayssières, C. E. Turner, and W. T. Lanini. 1996. *Yellow Starthistle Biology and Control*. University of California DANR Publ. No. 21541. 19 p.
- Watkinson, A. R. 1980. Density dependence in single-species populations of plants. *J. Theor. Biol.* 83:345–357.

Received January 15, 2002, and approved August 21, 2002.