

Soil water dynamics differ among rangeland plant communities dominated by yellow starthistle (*Centaurea solstitialis*), annual grasses, or perennial grasses

Author(s): Stephen F. Enloe, Joseph M. DiTomaso, Steve B. Orloff, and Daniel J. Drake

Source: Weed Science, 52(6):929-935. 2004.

Published By: Weed Science Society of America

DOI: 10.1614/WS-03-156R

URL: <http://www.bioone.org/doi/full/10.1614/WS-03-156R>

BioOne (www.bioone.org) is an electronic aggregator of bioscience research content, and the online home to over 160 journals and books published by not-for-profit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Soil water dynamics differ among rangeland plant communities dominated by yellow starthistle (*Centaurea solstitialis*), annual grasses, or perennial grasses

Stephen F. Enloe

Corresponding author. Department of Plant Sciences, University of Wyoming, Laramie, WY 82071; sfenloe@uwyo.edu

Joseph M. DiTomaso

Department of Vegetable Crops, University of California, Davis, CA 95616

Steve B. Orloff

Daniel J. Drake

University of California Cooperative Extension, Yreka, CA 96097

California's interior grasslands have undergone dramatic changes during the last two centuries. Changes in land-use patterns and plant introductions after European contact and settlement resulted in the conversion of perennial-dominated grasslands to exotic annual grasses. More recently, the annual grasslands have been heavily invaded by the deeply rooted late-maturing forb yellow starthistle. This series of invasions and conversions has changed the community structure and phenology of the grasslands. We hypothesized that these changes have resulted in significant differences in soil water-use patterns in the grasslands. We studied soil water depletion and recharge patterns of three grassland community types dominated by perennial grasses, annual grasses, or yellow starthistle with contrasting phenology and rooting depths for 4 yr. Soil moisture measurements were taken every month from March to December in 1998, 1999, and 2000 and every other month in 2001. Measurements were taken with a neutron probe at depths of 30 to 150 cm at 30-cm intervals. The results indicate that the yellow starthistle community maintained a significantly drier soil profile than the annual grass community. The perennial grass community maintained an intermediate soil water content that was not significantly different from either of the other two communities. Significant time by community and depth by community interactions indicated that the yellow starthistle community continued depleting soil moisture later into the season and at deeper depths than the other grass communities. This study demonstrates the effect of plant invasion on soil water recharge and depletion patterns in California grasslands.

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

Key words: California annual grasslands, ecosystem changes, plant invasions.

Although it is not a new phenomenon, the issue of biological invasion has recently come to the forefront of ecological attention (Mack et al. 2000; Sakai et al. 2001). Although a majority of introduced species only have minor effects or fail to establish at all (Williamson and Fitter 1996), many invaders are capable of causing severe alterations in community structure and ecosystem services (Braithwaite and Lonsdale 1989; D'Antonio and Vitousek 1992). Throughout western North America, plant invasions coupled with increased disturbance have resulted in the replacement of vast areas of native perennial grasses with Eurasian and Mediterranean annual grasses (Beatley 1966; Burcham 1956; Stewart and Hull 1949; Talbot et al. 1939). Invasive grasses have been especially notorious for changing ecosystems through altered fire cycles (D'Antonio 2000). In addition, recruitment of perennial grass seedlings is often limited in the presence of invasive annual grasses that strongly compete for light and are effective at rapidly depleting available water in the upper 30 cm (Dyer and Rice 1999; Gordon and Rice 1992; Holmes and Rice 1996). This combination of factors limits perennial grass recruitment, and a low sere vegetational composition may be maintained for many years (White 1966).

Although the annual grass life-history strategy in California's Mediterranean climate is very successful in suppressing perennial grass recruitment, an exotic forb with a deep taproot and long annual phenology has readily invaded the

annual grasslands. Yellow starthistle is a member of the Asteraceae family native to the Mediterranean that has invaded more than 4.8 million ha in California (Pitcairn et al. 1998). Similar to winter annual grasses, yellow starthistle seeds rapidly germinate after the first autumn rains (Maddox 1981). Seedlings form rosettes during winter and develop a deep taproot by early spring (DiTomaso et al. 2003). Plants bolt in late spring, and flowering and seed production occur during summer and early fall, well after annual grasses have senesced. Dense yellow starthistle cover has been correlated with reduced native plant diversity (DiTomaso et al. 1999a). Yellow starthistle has one of the longest life cycles of any annual plant in California.

Sheley and Larson (1995) demonstrated strong differences in rooting depth between cheatgrass (*Bromus* spp.) (shallow rooted) and yellow starthistle (deep rooted) and suggested it as the mechanism for resource partitioning between the two species. Although actual soil water content was not quantified, predawn xylem water potentials indicated yellow starthistle plants to be under significantly less water stress than cheatgrass because of continued water uptake from a deeper root system.

Because these invasions and conversions from perennial grasses to annual grasses to yellow starthistle result in differing community structure, phenology, and potential resource partitioning (Sheley and Larson 1995), our objective was to determine whether changes in soil water-use patterns

also have occurred. We examined this by creating and maintaining the three distinct plant communities (a perennial grass community, an annual grass community, and a yellow starthistle community) and the following patterns of soil water use by depth and time for 4 yr.

Materials and Methods

The study site was located in the annual grasslands of the Shasta Valley in Northern California at an altitude of 800 m with an annual precipitation of 46 cm. The Mediterranean-type climate of the site is characterized by hot dry summers and cool wet winters, with approximately 85% of the precipitation falling between October and April. The soil series is a Dotta gravelly loam (fine-loamy, mixed, mesic Pachic Argixerolls) with low to moderate available water capacity (0.11 cm cm^{-1}) (Bowers et al. 1997).

The native vegetation supported in the area previously consisted of *Achnatherum* spp., *Ceanothus* spp., Idaho fescue (*Festuca idahoensis*), and bluebunch wheatgrass (*Pseudoroegneria spicata*). However, the current composition of the grassland study site is a low sere community of early-maturing shallow-rooted annual grasses and forbs primarily from the Mediterranean and Eurasia, including downy brome (*Bromus tectorum* L.), hare barley (*Hordeum murinum* L.), feral rye (*Secale cereale* L.), redstem filaree [*Erodium cicutarium* (L.) L'Her. ex Ait.], and tumble mustard (*Sisymbrium altissimum* L.). The early-spring perennial bulbous bluegrass (*Poa bulbosa* L.), which was introduced as a forage species (Vinall and Westover 1928), is also common. During the last 30 yr, the deep-rooted late-maturing exotic forb yellow starthistle has begun to dominate large areas of annual grasslands throughout the valley. Although the exact composition of the annual grassland type varies throughout the interior grasslands of California, this pattern of successive invasion has been very typical throughout the state (Gerlach et al. 1998).

We hypothesized that with these changes in plant communities, subsequent changes in soil water-use patterns have occurred concomitantly. To test this, we created three plant community types, which were yellow starthistle dominated, annual grass dominated, or perennial grass dominated. Each community type was established on its own separate 15- by 15-m plot in a randomized complete block design with four blocks in total. Before initiation of the study, the entire field site was covered by a dense stand of yellow starthistle. Plots selected to represent yellow starthistle communities were left as is, and no treatments were applied. Plots selected to represent annual grass communities were treated with the herbicide clopyralid at 70 g ae ha^{-1} in March 1997. Clopyralid is a selective herbicide that controls plants in specific dicot families including the Asteraceae and is very effective on yellow starthistle but has no effect on grasses (DiTomaso et al. 1999b). In the plots where yellow starthistle was controlled with clopyralid, the annual grasses rapidly reasserted dominance in the community and maintained 50 to 90% cover. Repeated clopyralid applications at 105 g ha^{-1} were necessary in March 1998 and 1999 to control yellow starthistle recruitment from the soil seedbank. No herbicide applications were necessary in 2000 or 2001.

Plots selected to represent perennial grass communities required seeding to establish a perennial grass stand. Seeding

preparation consisted of a broadcast application of glyphosate at 330 g ae ha^{-1} on February 26, 1997, to control resident annual vegetation and to provide a window for perennial grass seedling emergence without intense interspecific competition. All herbicide applications were made with a tractor-mounted boom sprayer delivering 187 L ha^{-1} at 0.2 MPa pressure. Pubescent wheatgrass (*Thinopyrum intermedium* Host. Barkworth and Dewey) Nevski var. 'Luna' was seeded on March 6, 1997, with a no-till drill to a depth of 1.3 cm in 20-cm rows at a rate of 13.4 kg ha^{-1} (220 seeds m^{-2}). Plots seeded to wheatgrass also were treated with clopyralid at the same times and rates as the annual grass plots. Pubescent wheatgrass is not native to California but was used as a surrogate for a native perennial grass community because of its similarities in phenology and growth characteristics to the native creeping wildrye [*Leymus triticoides* (Buckley) Pilger] and its proven ability to readily establish with range revegetation techniques (Kay and Street 1961).

We allowed the grass community plots to establish for 1 yr before beginning soil moisture readings. In January 1998, we installed one polyvinylchloride (PVC) pipe (5-cm diameter) vertically to a depth of 150 cm in the center of each plot, by boring a 5-cm-diam hole with a handheld soil auger. Each pipe was carefully installed to prevent caving of the sides of the hole. Caps were placed on each pipe to prevent precipitation from collecting in the pipes. Beginning in March 1998, soil moisture readings were taken with a neutron hydroprobe¹ monthly between March and December. Monthly readings were taken for three consecutive years (1998, 1999, and 2000) with bimonthly readings taken in 2001. At each sample time, readings were taken at depths of 30, 60, 90, 120, and 150 cm. Neutron probe calibration for the specific soil type was done by concurrent gravimetric soil moisture determinations when an additional set of pipes was installed specifically for this purpose. We were unable to install PVC pipes to a depth of 150 cm in the center of three plots, so additional pipes were installed to collect data from depths with missing values within each community type. These additional data were used in the final analysis.

Because the study was conducted on a private ranch, the area was grazed each fall during the months of November and December. During this time, cattle primarily grazed dry standing forage from the previous spring and summer. Pubescent wheatgrass generally initiated regrowth with the onset of the fall and winter rains but grew little throughout the winter and did not appear to be affected by grazing. No spring or summer grazing occurred during the course of the study.

Statistical Analyses

Neutron probe data were transformed to percent volumetric water content by fitting the data to a calibration curve with the following equation:

$$V_w = 26.872(\text{CPM}_{\text{actual}}/\text{CPM}_{\text{baseline}}) - 5.4515, \quad [1]$$

$$(R^2 = 0.8836, n = 34)$$

where V_w is the percent volumetric water content, $\text{CPM}_{\text{actual}}$ is the neutron probe reading for any sample taken, and $\text{CPM}_{\text{baseline}}$ is the neutron probe reading taken as a baseline reading before beginning sampling.

Transformed data were subjected to a factorial repeated-

TABLE 1. Univariate repeated-measures tests of hypotheses for between- and within-subject effects.^a

Source	DF	SS	MS	F value	Adjusted Pr > F
Community	2	5,491.45	2,745.72	3.03	0.0986
Error	9	8,154.35	906.03		
Year	2	1,601.60	800.80	14.68	0.0005
Year by community	4	470.43	117.60	2.16	0.1332
Error (year)	18	981.58	54.53		
Depth	4	13,327.45	3,331.86	29.55	< 0.0001
Depth by community	8	1,861.46	232.68	2.06	0.0773
Error (depth)	36	4,059.63	112.76		
Time of sampling	8	15,300.46	1,912.55	261.75	< 0.0001
Time of sampling by community	16	905.08	56.56	7.74	0.0005
Error (time of sampling)	72	526.09	7.30		
Year by depth	8	401.12	50.14	5.37	0.0009
Year by depth by community	16	157.59	9.84	1.05	0.4158
Error (year by depth)	72	672.45	9.33		
Year by time of sampling	16	1,373.36	85.83	17.16	< 0.0001
Year by time of sampling by community	32	280.65	8.77	1.75	0.0951
Error (year by time of sampling)	144	720.45	5.00		
Depth by time of sampling	32	1,946.04	60.81	17.42	< 0.0001
Depth by time of sampling by community	64	282.27	4.41	1.26	0.2698
Error (depth by time of sampling)	288	1,005.34	3.49		
Year by depth by time of sampling	64	486.13	7.59	9.06	< 0.0001
Year by depth by time of sampling by community	128	194.41	1.51	1.81	0.0037
Error (year by depth by time of sampling)	576	482.65	0.83		

^a Abbreviations: DF, degrees of freedom; SS, sum of squares; MS, mean square.

measures analysis of variance.² Between-subject factors included plant community type (yellow starthistle, annual grass, or pubescent wheatgrass) and block. Within-subject factors included depth (30, 60, 90, 120, and 150 cm), year (1998, 1999, and 2000), and time of sampling (nine sampling dates from March to December). In the initial analysis, there were no significant block effects, and the data were reanalyzed with block suppressed and the block degrees of freedom pooled into the error term. Planned contrasts were constructed to determine differences in water content between community types by depth, time of sampling, and year. Huynh–Feldt adjusted P-values were used to determine differences at the $P < 0.1$ level of significance. Data are reported as percent volumetric water content unless otherwise specified. A lack of precipitation during 2001 (46% of normal) resulted in complete mortality of all yellow starthistle plants at the site. Therefore, the limited 2001 data

were excluded from the analysis but are presented graphically with the main data.

Results

Across plant communities, there were highly significant year, depth, and time of sampling effects on soil water content, and the interactions between year, depth, and time of sampling were highly significant (Table 1). Annual precipitation patterns differed both in timing and intensity during the course of the study (Figure 1). The 1998 hydrologic year (October 1, 1997, to September 30, 1998) was characterized by well above average precipitation (147% of the annual total), with 305 mm falling between March and August (242% of normal for this period). The 1999 hydrologic year exhibited a different pattern. The annual precipitation cumulative total was 119% above average, and the timing was different because most of the precipitation occurred during winter and early spring, with only 26 mm falling between March and August (20% of normal for this period). The 2000 hydrologic year was generally similar to the 50-yr average in terms of both precipitation timing and intensity, with 98% of the annual total and 115% of normal for the period March to August. The 2001 hydrologic year was characterized by a severe drought, with 46% of the annual total and 55% of normal between March and August.

Pooled across year, depth, and time of sampling, the total quantity of water (cm H₂O per 150-cm soil) in each community type indicated that the yellow starthistle community maintained a significantly drier soil water content (18.3%) compared with the annual grass community (22.8%) (Table 2). This equated to a difference of 6.6 cm less soil water in the yellow starthistle community compared with the annual

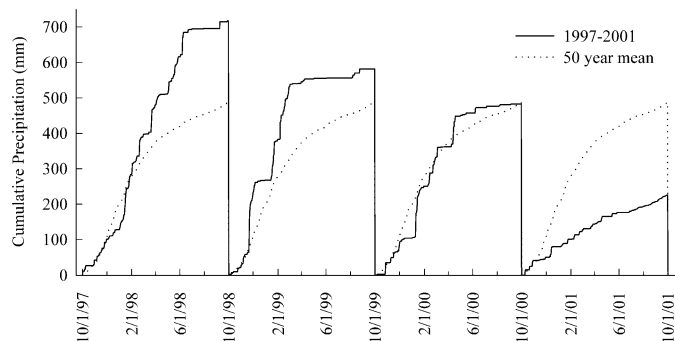


FIGURE 1. Annual cumulative precipitation (October 1 to September 30) for the years 1998–2001. Solid line = actual data; dotted line = 50 yr mean.

TABLE 2. Plant community soil water content averaged across depth, time of sampling, and year.

Community	Water content (mean \pm SE)	Total soil water content ^a
	%	cm 150 cm soil depth ⁻¹
Yellow starthistle	18.35 \pm 0.24	27.52 b
Annual grass	22.76 \pm 0.24	34.14 a
Wheatgrass	19.74 \pm 0.28	29.61 ab

^a Means followed by the same letter are not significantly different ($P < 0.1$).

grass community (Table 2). The perennial grass community had an intermediate water content (19.7%) that was not significantly different from either of the other communities.

Soil water content by depth also varied between plant communities (Table 1). The yellow starthistle community differed in its pattern of water content by depth from either the perennial or annual grass community by using more water from the deepest soil depth measured (Figure 2). Although the perennial grass community appeared to be more similar to the yellow starthistle community in water content at the shallower depths, contrasts indicated that the pattern of water use by each of the grass communities did not significantly differ (Figure 2).

Plant communities differed in soil water content through time (Table 1), with water depletion greater for yellow starthistle than grass communities (Figure 3). Contrasts indicated that yellow starthistle used more water between April and August than the annual grass community and more water between April and October than the perennial grass community. By subtracting the maximum recharge in April from the maximum depletion in October for each community, an estimate of the total water use is calculated. This is a conservative estimate that does not take into account early-season water use that is replaced by additional precipitation. The yellow starthistle community used 15.8 cm of water, the annual grass community used 9.9 cm, and the perennial grass community used 11.8 cm. By dividing each community's water use by the cumulative annual precipitation averaged across the 3 yr (1998–2000), which equals

68.6 cm, the percentage of precipitation used by each plant community is obtained. The yellow starthistle community used 23.1%, the annual grass community used 14.5%, and the perennial grass community used 17.2% of the mean annual cumulative precipitation. This estimate for yellow starthistle precipitation use is similar to the estimate by Gerlach (2000) of 25% of the mean annual rainfall from studies conducted in the Sacramento Valley in Northern California.

A weak year by time of sampling by community interaction also was observed (Table 1). This indicated that the pattern of water use between plant communities during the time of sampling period was different between years. Contrasts revealed that the difference was between the yellow starthistle and the annual grass communities. The perennial grass community did not differ significantly from either of the others. The key difference among years appears to lie in the annual grass community response in 1998 (Figure 4). In 1998, precipitation was well above average and the wet season was extended to early July (Figure 1). This reduced the apparent annual grass spring water use because soil water was recharged from precipitation and the spring depletion curve did not fall as sharply in 1998 as it did in 1999 and 2000. In addition, precipitation that fell after the annual grasses began to senesce caused higher soil water content in mid and late summer.

Precipitation was very low in 2001 (Figure 1), and there was subsequently little to no soil water recharge (Figure 4). The little precipitation that did fall failed to infiltrate beyond 30 cm, and the deeper soil remained dry. Yellow star-

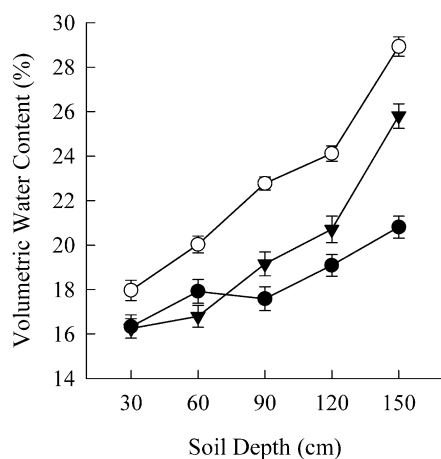


FIGURE 2. Plant community percent soil volumetric water content (mean \pm standard error) by depth averaged across time of sampling and year. Closed circles = yellow starthistle, open circles = annual grasses, and closed triangles = pubescent wheatgrass. Plant community by depth contrasts: yellow starthistle vs. annual grasses ($F = 3.33$, $P = 0.0262$), yellow starthistle vs. pubescent wheatgrass ($F = 2.59$, $P = 0.0621$), and annual grasses vs. wheatgrass ($F = 0.27$, $P = 0.8738$).

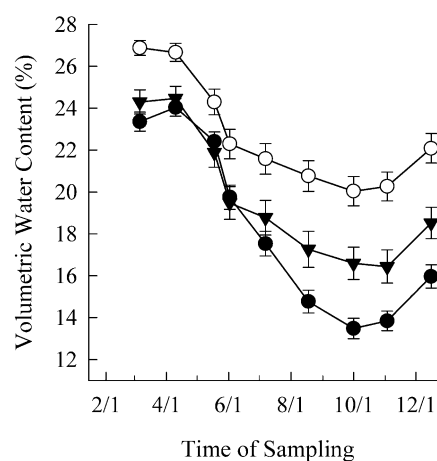


FIGURE 3. Plant community percent soil volumetric water content (mean \pm standard error) by time of sampling, averaged across depth and year. Closed circles = yellow starthistle, open circles = annual grasses, and closed triangles = pubescent wheatgrass. Plant community by time of sampling contrasts: yellow starthistle vs. annual grasses ($F = 14.38$, $P < 0.0001$), yellow starthistle vs. wheatgrass ($F = 7.47$, $P = 0.0031$), and annual grasses vs. wheatgrass ($F = 1.37$, $P = 0.2782$).

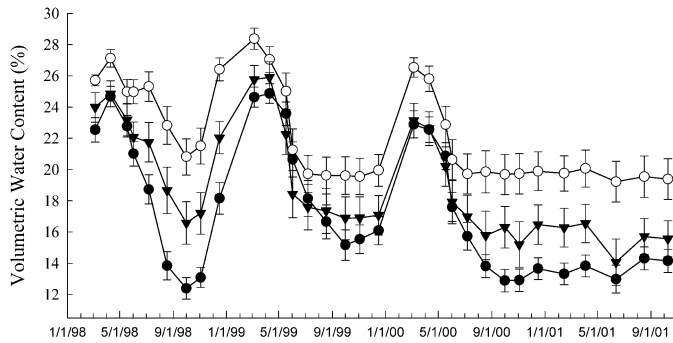


FIGURE 4. Percent volumetric soil water content (mean \pm SE) by time of sampling and year between plant communities averaged across depth. Closed circles = yellow starthistle, open circles = annual grasses, and closed triangles = pubescent wheatgrass. Plant community by time of sampling by year contrasts: yellow starthistle vs. annual grasses ($F = 2.77$, $P = 0.0272$), yellow starthistle vs. wheatgrass ($F = 1.56$, $P = 0.1873$), and annual grasses vs. wheatgrass ($F = 0.92$, $P = 0.4780$). Because of the severe drought and subsequent yellow starthistle mortality, the limited data collected in 2001 is excluded from the analyses.

thistle seedlings and rosettes were not able to establish a deep root system in the dry soil below 30 cm, and complete mortality occurred by June in all yellow starthistle community plots. The annual grass community survived to reproduction, which occurred by mid-May. The pubescent wheatgrass community was the most robust of the three in 2001, but it also went dormant earlier in the summer than normal. As observed with bimonthly neutron probe readings in 2001, the pubescent wheatgrass community reduced soil water content to a level close to that resulting from reduction by the yellow starthistle community, which had never recharged during the winter months as it had in previous years.

A highly significant year by depth by time of sampling by community interaction also was observed (Table 1). This indicated that the pattern of water use between plant communities during the time of sampling period was different by depth between years. This amount of data would be very difficult to interpret if placed on one graph. Therefore, Figure 5 is separated into five graphs by each depth. Contrasts indicated that the overall pattern of soil water content according to the year by depth by time of sampling by community interaction was significantly different between each plant community. Greater differences between the yellow starthistle and the annual grass community were observed at depths of 90 to 150 cm compared with the 30- and 60-cm depths, especially during the summer months. The perennial grass community was generally intermediate between the other two communities at the deeper depths and was very similar to the yellow starthistle community at the 30- and 60-cm depths. Differences between communities were often greatest in late summer and early fall and least in the early spring (Figure 5).

Discussion

The data presented here indicate substantial differences in soil water dynamics among three important plant communities in the California grasslands. Because plant invasions have altered community structure and phenology, our

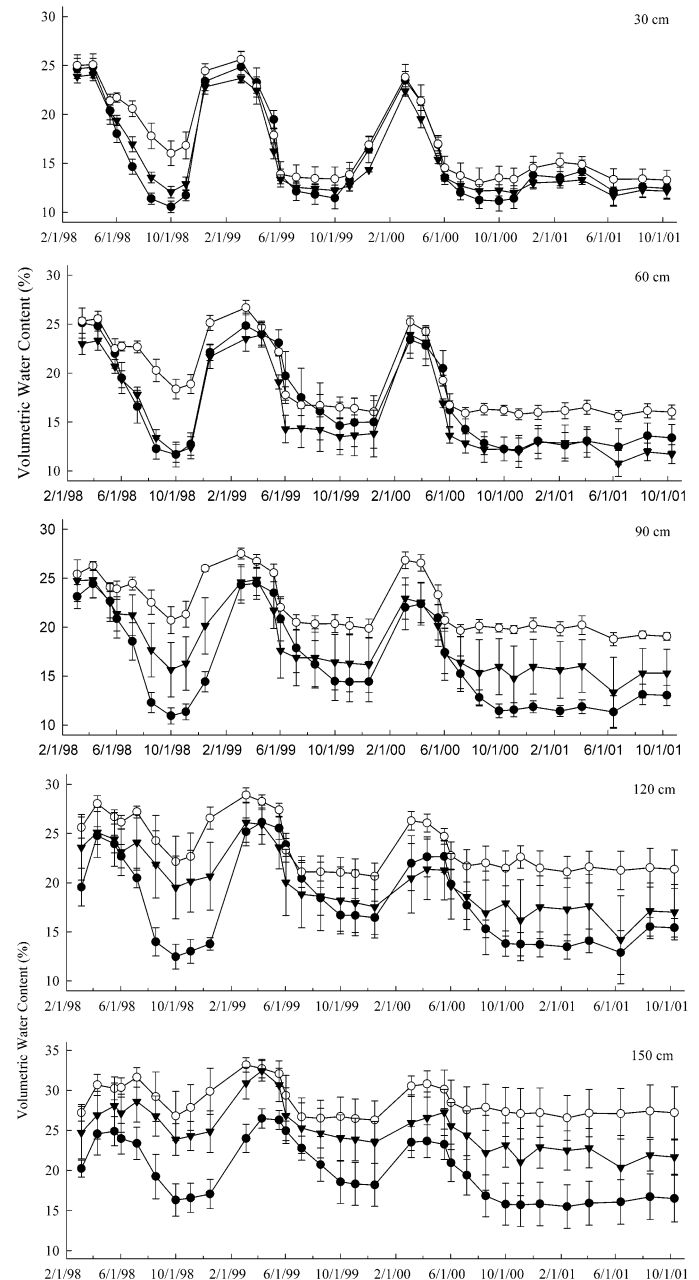


FIGURE 5. Plant community percent volumetric soil water content (mean \pm SE) by time of sampling, depth, and year. Closed circles = yellow starthistle, open circles = annual grasses, and closed triangles = pubescent wheatgrass. Plant community by time of sampling by depth by year contrasts: yellow starthistle vs. annual grasses ($F = 1.89$, $P = 0.0130$), yellow starthistle vs. wheatgrass ($F = 1.83$, $P = 0.0177$), and annual grasses vs. wheatgrass ($F = 1.72$, $P = 0.0301$). Because of the severe drought and subsequent yellow starthistle mortality, the limited data collected in 2001 are excluded from the analyses.

data indicate that changes in soil water dynamics also have occurred.

Although the perennial grass community generally exhibited an intermediate water-use pattern between the yellow starthistle community and the annual grass community, which was statistically more similar to the annual grass community, other researchers have shown greater water-use differences between perennial and annual grasses. Holmes and Rice (1996) found lower late-season soil water potentials in

perennial grass plots composed of blue wildrye (*Elymus glaucus*) and purple needlegrass (*Nassella pulchra*) compared with annual grass plots composed of false brome (*Brachypodium distachyon*) and hedgehog dogtailgrass (*Cynosurus echinatus*). Furthermore, they suggested that the invasion and conversion of native perennial grasses to exotic annual grasses might have resulted in increased soil moisture content at deeper depths. Similarly, Borman et al. (1992) demonstrated that perennial grass plots dominated by the native perennial grass Idaho fescue had lower end-of-season soil water contents than plots dominated by hedgehog dogtailgrass. Differences in soil properties and the annual grass species composition between the Shasta Valley location and these studies may have been responsible for the differences. The gravelly loam soil at this location in the Shasta Valley is characterized by a low to moderate water-holding capacity (0.11 cm cm⁻¹). Soils with higher water-holding capacity would allow for possible greater differentiation of water depletion patterns between communities. Furthermore, hedgehog dogtailgrass was not present in the annual grass composition at the Shasta Valley study site. For our study, a greater sample size may have yielded significant differences between the grass communities.

The differential patterns of soil water use between the yellow starthistle community and the grass communities were much clearer than the patterns between the grass communities. The data show similar patterns of soil water use between yellow starthistle and the grass communities both during spring season and at shallower depths. However, yellow starthistle's deep taproot and longevity throughout the summer clearly separate it from the grass communities and cause significantly lower total soil water content than that in the annual grass community. This would suggest that controlling yellow starthistle on a landscape scale may potentially increase soil water content. Oak woodland and shrubland converted to annual grasses and legumes have been shown to affect the watershed hydrology (Burgy 1968; Lewis 1968; Veihmeyer 1953). Higher soil water content, increased runoff, increased streamflow, and the conversion of some intermittent streams to perennial streams have occurred with the type conversion (Burgy 1968).

Another highly fascinating result of this study was the complete mortality of the yellow starthistle during the drought of 2001. With no soil water recharge occurring after the summer of 2000, yellow starthistle essentially created conditions highly unfavorable for the next generation's survival. This pattern of large, high-density stands of yellow starthistle for 1 yr followed by short, low-density stands has been observed in California grasslands but never attributed to soil water use. This carryover effect could have significant implications for restoration of yellow starthistle-infested grasslands. Even if yellow starthistle is successfully controlled just before restoration efforts, success may be limited because of the previous year's impact of yellow starthistle on soil water availability. This also would be much more likely in dry years after wet years, where soil water recharge is limited.

Hamilton (1997) suggested that the structure of the pristine California grasslands may have been more of a complex mosaic of shrubs, perennial grasses, and forbs than a vast open grassland. Although certain perennial grasses alone have been shown to strongly suppress yellow starthistle, in-

corporation of deeply rooted summer forbs or shrubs into perennial grassland restoration projects may be beneficial for further suppressing yellow starthistle by using more water from deeper depths in the soil profile. However, this needs to be addressed with additional research.

Sources of Materials

¹ CPN 503DR, Campbell Pacific Nuclear International, 2830 Howe Road, Martinez, CA 94553.

² SAS, v. 6.12, Statistical Analysis Systems Institute, SAS Campus Drive, Cary, NC 27513-2414.

Acknowledgments

We thank the University of California Statewide Integrated Pest Management Project for financial support. We thank Neal Willits for statistical assistance and John Randall and Anna Sher for critical reviews of the manuscript.

Literature Cited

- Beatley, J. C. 1966. Ecological status of introduced brome grasses (*Bromus* spp.) in desert vegetation of Southern Nevada. *Ecology* 47:548–554.
- 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.
- Bowers, W. O., R. L. Snyder, S. B. Southard, and B. J. Lanini. 1997. Water Holding Characteristics of California Soils. Davis, CA: University of California Leaflet 21463. 92 pp.
- Braithwaite, R. W. and W. M. Lonsdale. 1989. Alien vegetation and native biota in tropical Australia: the spread and impact of *Mimosa pigra*. *Biol. Conserv.* 48:189–210.
- Burcham, L. T. 1956. Historical backgrounds of range land use in California. *J. Range Manage.* 9:81–86.
- Burgy, R. H. 1968. Hydrological Studies and Watershed Management on Brushlands. Annual Report No. 8. Davis, CA: California Department of Water Resources and University of California Water Resources Center. 22 p.
- D'Antonio, C. M. 2000. Fire, plant invasions, and global change. Pages 65–93 in H. A. Mooney and R. J. Hobbs, eds. *Invasive Species in a Changing World*. Washington, DC: Island.
- D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annu. Rev. Ecol. Syst.* 23:63–87.
- 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.* 53:12–16.
- DiTomaso, J. M., G. B. Kyser, and C. B. Pirosko. 2003. Effect of light and density on yellow starthistle (*Centaurea solstitialis*) root growth and soil moisture use. *Weed Sci.* 51:334–341.
- Dyer, A. R. and K. J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* 80:2697–2710.
- Gerlach, J. D. 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. thesis. University of California, Davis, CA. 102 p.
- Gerlach, J. D., A. R. Dyer, and K. J. Rice. 1998. Grassland and foothill woodland ecosystems of the central valley. *Fremontia* 26:39–43.
- Gordon, D. R. and K. J. Rice. 1992. Partitioning of space and water between two California annual grassland species. *Am. J. Bot.* 79:967–976.
- Hamilton, J. G. 1997. Changing perceptions of pre-European grasslands in California. *Madrone* 44:311–333.
- Holmes, T. H. and K. J. Rice. 1996. Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. *Ann. Bot.* 78:233–243.
- Kay, B. L. and J. E. Street. 1961. Drilling wheatgrass into sprayed sagebrush in Northeastern California. *J. Range Manage.* 14:271–273.

- Lewis, D. C. 1968. Annual hydrologic response to watershed conversion from oak woodland to annual grassland. *Water Resour. Res.* 4:59–72.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10:689–710.
- Maddox, D. M. 1981. Introduction, Phenology, and Density of Yellow Starthistle in Coastal, Intercoastal, and Central Valley Situations in California. Oakland, CA: USDA-ARS, ARR-W-20, pp. 1–33.
- Pitcairn, M. J., R. A. O'Connell, and J. M. Gendron. 1998. Yellow starthistle: survey of statewide distribution. Pages 64–66 in D. M. Woods, ed. *Biological Control Program Annual Summary, 1997*. Sacramento, CA: California Department of Food and Agriculture, Plant Health and Pest Prevention Services.
- Sakai, A. K., F. W. Allendorf, J. S. Holt, et al. 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* 32:305–332.
- Sheley, R. and L. Larson. 1995. Interference between cheatgrass and yellow starthistle at three soil depths. *J. Range Manage.* 48:392–397.
- Stewart, G. and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.)—an ecological intruder in Southern Idaho. *Ecology* 30:58–74.
- Talbot, M. W., H. W. Biswell, and A. L. Hormay. 1939. Fluctuations in the annual vegetation of California. *Ecology* 20:394–402.
- Veihmeyer, F. J. 1953. Use of water by native vegetation versus grasses and forbs on watersheds. *Trans. Am. Geophys. Union* 34:201–212.
- Vinall, H. N. and H. L. Westover. 1928. Bulbous bluegrass, *Poa bulbosa*. *J. Am. Soc. Agron.* 20:394–399.
- White, K. L. 1966. Old-field succession on Hastings reservation, California. *Ecology* 47:865–868.
- Williamson, M. and A. Fitter. 1996. The varying success of invaders. *Ecology* 77:1661–1666.

Received November 22, 2003, and approved June 10, 2004.