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Instability in a grassland community after the control of yellow starthistle (*Centaurea solstitialis*) with prescribed burning

Guy B. Kyser
Corresponding author. Weed Science Program, Department of Vegetable Crops, University of California, Davis, CA 95616; gbkyser@ucdavis.edu

Joseph M. DiTomaso
Weed Science Program, Department of Vegetable Crops, University of California, Davis, CA 95616

An open grassland at Sugarloaf Ridge State Park, Sonoma County, CA, was burned during three consecutive summers (1993–1995) to control yellow starthistle. By 1996, the yellow starthistle seedbank, seedling density, and mature vegetative cover were reduced by 99, 99, and 91%, respectively, and the plant community had greater diversity and species richness, particularly of native forbs. After the cessation of the prescribed burning after 1995, the community was monitored for 4 yr to determine if the reduced yellow starthistle population represented a stable state or if the population would quickly recover. The yellow starthistle seedbank rose dramatically over 4 yr. Seedling counts and summer vegetative cover also rose, though less rapidly. Total forb cover, particularly native species, total plant cover, and plant diversity decreased significantly after cessation of the burning. Grass cover did not show any strong trends, and year-to-year variation in the grass cover appeared to be more important than the treatment effects. In the absence of some overall changes in management, e.g., periodic prescribed burning, herbicide treatments, or revegetation, it may not be possible to establish and maintain a stable state with a low population of yellow starthistle in annual grasslands in California.

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

Key words: Diversity, species richness, stability, fire, rangeland.

Recurrent fire has played an important role in the development of many ecosystems (Hatch et al. 1991), including the California grasslands (Heady 1972). Native plant species may depend on fire to reduce competition, remove thatch, cycle nutrients, and scarify seeds. Plant communities in fire-dependent ecosystems typically show increased diversity after fires and reduced diversity after long periods of fire suppression (Kruger 1983). Fire suppression also has led to the encroachment of shrubs into grasslands (e.g., Cable 1973; Looman 1979; Ralph 1980; Trollope 1982). Changes in community dynamics caused by the suppression of regular burning may be a factor in the invasion of California grasslands by exotic weeds.

One such invader is yellow starthistle, which infests rangeland, wildland, and roadsides. Approximately 42% of California townships, representing 17 million ha, reported infestations in 1997 (Pitcairn et al. 1998). Yellow starthistle infestations decrease native plant and animal diversity (Sheley and Larson 1994), lower the yield and the quality of rangeland forage, and reduce the recreational and economic value of infested land.

A number of management tools, including herbicides and mechanical techniques, can provide effective control of yellow starthistle (Benefield et al. 1999; DiTomaso et al. 1999b). Properly timed prescribed burning can reduce yellow starthistle populations in California grasslands, as well as stimulate the growth of forbs and legumes (DiTomaso et al. 1999a).

Some researchers have postulated that multiple stable states (plant community types) may be possible for a given rangeland. The rangeland may transition from one state to another after a significant event, such as disturbance, change in management practices, or climate shift. Westoby et al. (1989) presented this concept in their state-and-transition model; George et al. (1992) described it as a ball and cup to reflect the energy input required to move a system out of a stable state. In California grassland, burning can facilitate the transition from a relatively stable community dominated by yellow starthistle, introduced forbs, and annual grasses to a diverse community of mixed annual and perennial grasses and native annual forbs with a small yellow starthistle component. The latter community is more desirable for both economic and aesthetic reasons. It also supports greater native plant diversity and total plant diversity. However, the duration of its stability is unknown, given the absence of further management and the continued presence of a source of yellow starthistle propagules.

Sugarloaf Ridge State Park is in the northern California Coast Range in Sonoma County, CA, at an elevation of 300 to 800 m. It is a blue oak (*Quercus douglasii* L.) foothill woodland interspersed with grassland and chaparral (Munz and Keck 1959). As a lightly managed, low-elevation mixed habitat, it is representative of much of northern California's foothill rangeland and recreation land. Historically, fire intervals in this part of the state have ranged between 2 and 10 yr (Finney and Martin 1992). Yellow starthistle invaded the grasslands of Sugarloaf Ridge in the 1980s after 60 yr of fire suppression. Parts of the park were burned during three consecutive summers (1993 to 1995) to control yellow starthistle. During this time the yellow starthistle seedbank and seedling populations in burned sites dropped to less than 0.5% of that of the adjacent unburned sites (DiTomaso et al. 1999a). This corresponded to a 91% reduction in the yellow starthistle vegetative cover during the summer after

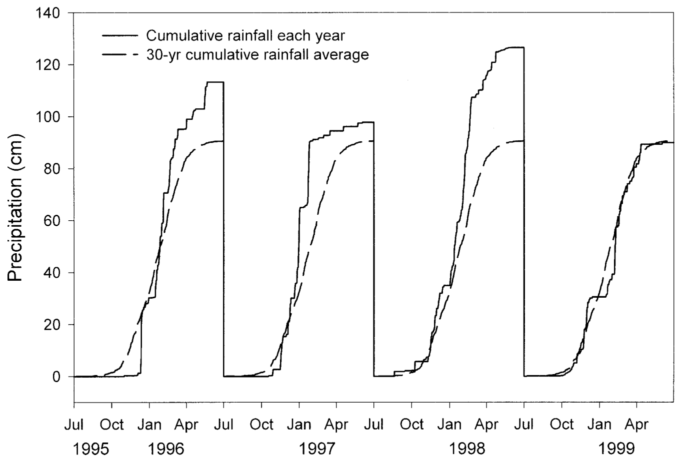

FIGURE 1. Cumulative yearly precipitation from St. Helena, 1995–1999, compared with the 30-yr mean annual precipitation. The precipitation year is July 1 to June 30.

the third year of burning. The fires also removed a heavy layer of thatch, thus increasing light exposure at the soil surface and allowing the upper layer of the soil to warm quickly in spring. The effects of three consecutive years of burning were increased growth of desirable vegetation, particularly native legumes and perennial grasses. The objectives of this study were to determine if this significant reduction in yellow starthistle could be maintained without further management and to evaluate the stability of the plant community composition after prescribed burning.

Materials and Methods

Preliminary Burning

Prescribed burns were conducted on 14 ha of land during 1993, 1994, and 1995. Burns were conducted in early July of each year, after senescence of most grass and broadleaf species but before yellow starthistle produced seed. Adjacent grasslands (10 ha) were left unburned as a control. The burns resulted in nearly complete mortality of yellow starthistle. Details on the conduct and parameters of the burns were reported in DiTomaso et al. (1999a) and Hastings and DiTomaso (1996a, 1996b). All sampling reported here was conducted between 1996 and 2000, after the completion of the 3-yr burn treatment.

Precipitation

Rainfall totals were obtained from the closest available weather station (St. Helena, 9 km away). During the first and third years of the study (precipitation years 1995–1996 and 1997–1998) precipitation was considerably above average (Figure 1). During the second year (1996–1997) precipitation was slightly above average. During the fourth year (1998–1999) precipitation was approximately average, culminating in a spring drought (almost no rainfall after February).

Monitoring Community Change

Both burned and unburned sites were monitored for 4 yr after the final year of prescribed burning. Three 0.25-ha sampling areas were selected within the burned site and three within the adjacent unburned control. The six sampling areas were all in open grassland on hillsides sloping moderately toward south to southwest. All sampling was conducted within these areas. All species encountered are reported in Table 1.

Vegetative Cover and Diversity

Surveys for vegetative cover and plant diversity were taken in late April to early May at peak flower of most species but before bolting of yellow starthistle. Point–intercept readings were made along three 15-m transects (50 points, 30-cm intervals) randomly placed within each sampling area. Plant species intercepting each point were recorded and used to determine vegetative cover. Plant diversity was calculated from point–intercept data using the Shannon index (Brower et al. 1998; Shannon 1948).

Species Richness

Species richness was measured in late April to early May, at the same time as was vegetative cover and diversity. Species present were recorded in 15 independent, randomly placed quadrats per sampling area. Five geometrically increasing quadrat sizes were used (0.0625, 0.25, 1, 4, and 16 m^2) with three replicates per size.

Seedbank and Seedling Density

The yellow starthistle seedbank was estimated after seed dispersal in the fall. Five soil samples (plugs 5 cm in diameter by 5 cm deep) were taken from each sampling area in October or November. Seeds were extracted from soil samples using a water–air elutriator (Wiles et al. 1996) and were counted under a stereomicroscope. Seeds were ruptured under the stereomicroscope in order to determine if they contained a moist endosperm, i.e., apparently viable. Only apparently viable seeds were counted.

Yellow starthistle seedling densities were estimated in March, when plants were in the seedling to small-rosette stage. Seedlings were counted in 10 randomly thrown 20-cm rings per sampling area. Seed and seedling counts are presented as mean value per square meter.

Data Analysis

Analysis was conducted with two goals: (1) detection of directional change (year to year) in the plant community in the previously burned site, and (2) direct comparison of the previously burned and unburned sites within each year. For an initial overall analysis, the vegetative cover was categorized into yellow starthistle, annual grasses, perennial grasses, introduced forbs, and native forbs. We distinguish between annual grasses and perennial grasses because of their different functional roles in the plant community. Most annual grasses were introduced, and most perennial grasses were native. Among the forbs were very few perennial, so the categories of introduced and native were more useful. In this article, forbs include all vascular plants other than grasses, e.g., broadleaf plants including legumes and members of the *Liliaceae*. Cover values were compared within and between years using multiresponse permutation procedures (MRPP),[1]

Table 1. Species found in transect and quadrat surveys. Abbreviations preceded by # are Bayer code names from the Composite List of Weeds, Weed Science 32, Supplement 2. Common names are from the Composite List of Weeds or from Hickman (1993). Native or introduced status is from Hickman (1993). Abbreviations: AG, annual grass; PG, perennial grass; F, forb.

Species	Family	Common name	Abbreviation[a]	Native	Introduced	Category	Years recorded 1996	1997	1998	1999
Achillea millefolium	Asteraceae	Common yarrow	# ACHMI	×		F	×	×	×	×
Agoseris heterophylla	Asteraceae			×		F	×	×		×
Aira caryophyllea	Poaceae	Silver hairgrass	# AIRCA		×	AG	×	×	×	×
Anagallis arvensis	Primulaceae	Scarlet pimpernel	# ANGAR		×	F	×	×	×	×
Astragalus gambelianus	Fabaceae			×		F	×	×	×	
Avena fatua	Poaceae	Wild oats	# AVEFA		×	AG	×	×	×	×
Brachypodium distachyon	Poaceae				×	AG	×	×	×	×
Briza minor	Poaceae	Little quakinggrass	# BRZMI		×	AG	×	×	×	×
Brodiaea elegans	Liliaceae	Harvest brodiaea		×		F	×	×	×	×
Bromus carinatus	Poaceae	California brome		×		PG		×	×	
Bromus diandrus	Poaceae	Ripgut brome	# BRODI		×	AG	×	×	×	×
Bromus hordeaceus	Poaceae	Soft brome	# BROMO		×	AG	×	×	×	×
Bromus tectorum	Poaceae	Downy brome	# BROTE		×	AG			×	
Calochortus luteus	Liliaceae			×		F	×	×	×	×
Calystegia sp.	Convolvulaceae	Morning-glory		×		F			×	
Carduus pycnocephalus	Asteraceae	Italian thistle	# CRUPY		×	F		×	×	×
Centaurea melitensis	Asteraceae	Tocalote	# CENME		×	F	×	×		
Centaurea solstitialis	Asteraceae	Yellow starthistle	# CENSO		×	F	×	×	×	×
Centaurium sp.	Gentianaceae			×		F			×	
Cerastium glomeratum	Caryophyllaceae	Mouse-ear chickweed	# CERGL		×	F	×	×	×	×
Chlorogalum pomeridianum	Liliaceae	Soap plant	# CHLPO	×		F	×	×	×	×
Clarkia purpurea	Onagraceae		CLApur	×		F	×	×	×	×
Clarkia sp.	Onagraceae			×		F	×	×	×	
Cynosurus echinatus	Poaceae	Hedgehog dogtailgrass	# CYXEC		×	AG	×	×	×	×
Daucus pusillus	Apiaceae	Southwestern carrot	# DAUPU	×		F	×	×	×	×
Dichelostemma congestum	Liliaceae	Ookow		×		F	×	×	×	
Elymus glaucus	Poaceae	Blue wildrye		×		PG	×	×	×	×
Epilobium brachycarpum	Onagraceae		EPIbra	×		F	×	×	×	
Eremocarpus setigerus	Euphorbiaceae	Turkey mullein	# ERMSE	×		F	×	×		×
Eriogonum sp.	Polygonaceae	Wild buckwheat		×		F				×
Erodium cicutarium	Geraniaceae	Redstem filaree	# EROCI		×	F	×	×	×	×
Eschscholzia californica	Papaveraceae	California poppy	# ESHCA	×		F	×	×	×	×
Festuca rubra	Poaceae	Red fescue	# FESRU	×		PG	×	×	×	×
Galium aparine	Rubiaceae	Catchweed bedstraw	# GALAP	×		F	×	×	×	×
Galium divaricatum	Rubiaceae	Lamarck's bedstraw			×	F	×	×	×	×
Gastridium ventricosum	Poaceae	Nit grass			×	AG	×	×	×	
Geranium dissectum	Geraniaceae	Cutleaf geranium	# GERDI		×	F	×	×	×	×
Geranium sp.	Geraniaceae					F			×	
Gilia tricolor	Polemoniaceae	Bird's eyes		×		F	×	×	×	
Hemizonia congesta	Asteraceae			×		F		×	×	
Heterocodon rariflorum	Campanulaceae			×		F	×	×	×	×
Hordeum brachyantherum	Poaceae		# HORBR	×		PG	×	×		×
Hypochaeris glabra	Asteraceae	Smooth cat's-ear	# HRYGL		×	F	×	×	×	×
Hypochaeris radicata	Asteraceae	Rough cat's-ear	# HRYRA		×	F			×	
Juncus effusus	Juncaceae		# IUNEF	×		F	×	×	×	
Lactuca serriola	Asteraceae	Prickly lettuce	# LACSE		×	F	×	×	×	×
Lathyrus cicera	Fabaceae	Wild pea	# LTHCI		×	F	×	×	×	×
Linanthus bicolor	Polemoniaceae			×		F	×	×	×	×
Lolium perenne	Poaceae	Perennial ryegrass	# LOLPE		×	PG	×	×	×	×
Lomatium utriculatum	Apiaceae			×		F	×	×	×	×
Lotus purshianus	Fabaceae			×		F	×	×	×	
Lotus wrangelianus	Fabaceae		LOTwra	×		F	×	×	×	×
Lupinus nanus	Fabaceae	Lupine		×		F	×	×	×	×
Madia gracilis	Asteraceae	Slender tarweed		×		F	×	×	×	×
Medicago polymorpha	Fabaceae	California burclover	# MEDPO		×	F	×	×	×	
Melica californica	Poaceae	California melic		×		PG	×	×	×	
Micropus californicus	Asteraceae	Slender cottonweed		×		F	×	×	×	×
Microseris douglasii	Asteraceae			×		F	×	×	×	
Nassella pulchra	Poaceae	Purple needlegrass	NASpul	×		PG	×	×	×	×
Orthocarpus sp.	Scrophulariaceae			×		F		×	×	
Petrorhagia nanteuilii	Caryophyllaceae		PETnan		×	F	×	×	×	×

Table 1. Continued.

Species	Family	Common name	Abbreviation[a]	Native	Intro-duced	Cate-gory	Years recorded 1996	1997	1998	1999
Plagiobothrys nothofulvus	Boraginaceae	Popcornflower		×		F	×	×	×	
Plantago erecta	Plantaginaceae			×		F	×	×	×	×
Poa secunda	Poaceae			×		PG		×	×	×
Polycarpon tetraphyllum	Caryophyllaceae	Four-leaved allseed			×	F	×	×	×	
Rumex pulcher	Polygonaceae				×	F			×	
Sanicula bipinnata	Apiaceae	Poison sanicle		×		F	×	×	×	×
Sidalcea diploscypha	Malvaceae	Checker mallow	SIDdip	×		F	×	×	×	
Silene gallica	Caryophyllaceae	English catchfly	# SILGA		×	F	×	×	×	×
Sisyrinchium bellum	Iridaceae	Blue-eyed grass		×		F	×	×	×	×
Sonchus oleraceus	Asteraceae	Common sowthistle	# SONOL		×	F	×	×	×	×
Stachys sp.	Lamiaceae	Hedge nettle		×		F			×	
Taeniatherum caput-medusae	Poaceae	Medusahead	# ELYCM		×	AG		×	×	
Torilis arvensis	Apiaceae	Hedgeparsley	# TOIAR		×	F	×	×	×	×
Trifolium albopurpureum	Fabaceae			×		F	×	×	×	
Trifolium bifidum	Fabaceae			×		F	×	×		
Trifolium depauperatum	Fabaceae			×		F	×	×	×	
Trifolium dubium	Fabaceae	Small hop clover	# TRFDU		×	F				×
Trifolium gracilentum	Fabaceae		TRFgra	×		F	×	×	×	×
Trifolium hirtum	Fabaceae	Rose clover			×	F	×	×	×	×
Trifolium microdon	Fabaceae		TRFmic	×		F	×	×	×	×
Triodanis biflora	Campanulaceae	Small venuslookingglass	# TJDBI	×		F	×	×	×	
Triphysaria versicolor	Scrophulariaceae			×		F	×	×	×	
Vicia lutea	Fabaceae				×	F	×	×	×	
Vicia sativa	Fabaceae	Common vetch	# VICSA		×	F	×	×	×	×
Vicia villosa	Fabaceae	Hairy vetch	# VICVI		×	F	×	×	×	×
Vulpia myuros	Poaceae	Rattail fescue	# VLPMY		×	AG	×	×	×	×

[a] Abbreviations such as CLApur are non-BAYER names by the authors for this table.

a nonparametric technique for the comparison of predetermined groups (Mielke et al. 1981). MRPP was used in a manner similar to multiple analysis of variance to compare sites using all cover data together.

In a more detailed analysis, we compared responses for vegetative cover categories (yellow starthistle, annual grasses, perennial grasses, total grasses, introduced forbs, native forbs, total forbs, and total plant cover), diversity, and yellow starthistle seed and seedling densities. For year-to-year comparisons, values from burned sampling areas were expressed as a percentage of the respective mean values from the unburned sampling areas in the same year. This approach was intended to remove fluctuations in response variables caused by yearly climatic variation, analogous to using a concomitant variable in the analysis of covariance. These percentages were compared across years, for burned sites only, using MRPP. First, all years were compared. If this analysis detected significant differences among years, then the years were compared pairwise.

Actual values for vegetative cover categories, diversity, and yellow starthistle seed and seedling densities were compared between previously burned and unburned plots within years using a Kruskal–Wallis[2] test (nonparametric test for three or more groups), followed by pairwise Mann–Whitney *U* tests[2] (nonparametric test for two unpaired groups). Species richness curves (number of species per quadrat vs. quadrat size) were developed for total number of grass species, forb species, and all plant species in each year, allowing visual comparison of richness in burned vs. unburned sampling areas. Each pair of species richness curves was tested for differences using MRPP.

Indicator species analysis (ISA)[1] was used to characterize postfire community trends by tracking the occurrence of individual species. In ISA, an indicator value is calculated for each species on the basis of frequency and abundance, and the likelihood of the indicator value differences occurring by chance is estimated by performing a Monte Carlo test (1,000 repetitions in our analysis) (Dufrêne and Legendre 1997). We performed ISA comparing burned vs. unburned sampling areas within each year and then made a visual assessment of the year-to-year changes.

Results and Discussion

Vegetative Cover—Overall Analysis

Overall analysis of the vegetative cover categories (spring cover of yellow starthistle, annual grasses, perennial grasses, introduced forbs, and native forbs) found no difference between years in the unburned site. This indicates that year-to-year climatic variation alone was not sufficient to produce major community shifts. In the previously burned site, each year was different from every other year (with the exception of 1997 compared with 1999), suggesting that the burn treatment introduced some degree of instability. Relatively low amounts of spring precipitation in 1997 and 1999 may have suppressed the potential differences in vegetative cover.

Within-year analysis of the vegetative cover categories showed that vegetation in the burned site differed from that in the unburned site in all years, except 1998. To a rough approximation, the plant community had reverted to its unburned condition 3 yr after the final burn.

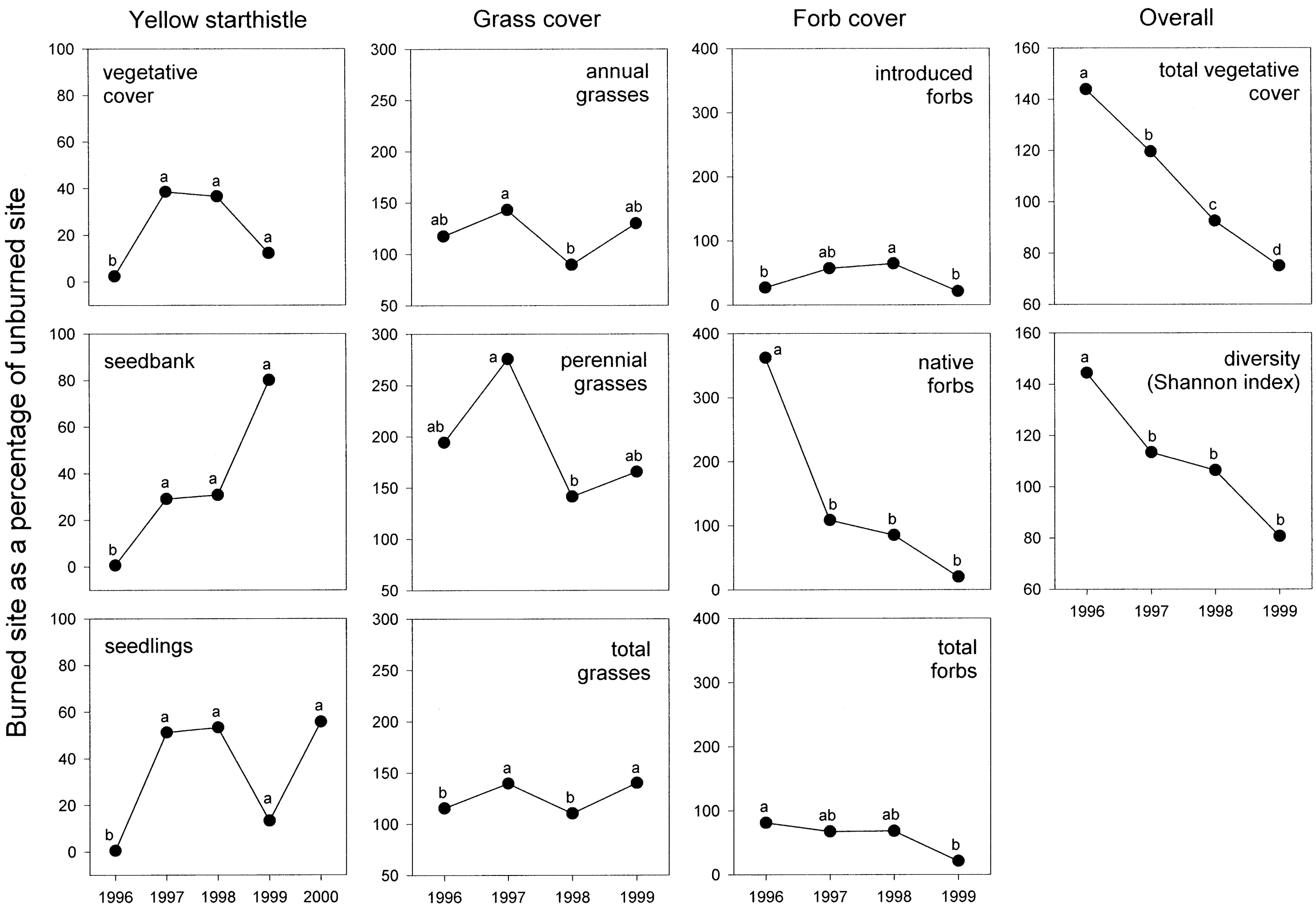

FIGURE 2. Changes in vegetative cover in previously burned sampling areas as a percentage of unburned sampling areas in the same year. Within each series, symbols labeled with the same letter represent values that are not significantly different (Mann–Whitney *U* test, P ≤ 0.05).

Year-to-Year Differences

In the previously burned site, the yellow starthistle seedbank population density increased from 0.5% of the value in the unburned site (1996) to 80% (1999) (Figure 2). The yellow starthistle seedling population increased from 0.4% in 1996 to 56% by 2000, with a dip during the spring drought year of 1999. The yellow starthistle vegetative cover in summer increased from 2.4% in 1996 to a peak of 38% during 1997 and then dropped to 17% in 1999. Because the yearly weather patterns influence both early seedling mortality and vegetative growth of yellow starthistle, the seedbank may be the most reliable indicator of the yellow starthistle population levels. In this case, the seedbank increased over the duration of the study.

The grass vegetative cover did not show any important trends. However, the cover of both annual and perennial grasses was highest during 1997 and lowest during the wet year of 1998. The native forb cover in the burned site showed a strong decline, from 362% of the unburned site in 1996 to 20% in 1999. The total forb cover also declined, from 81 to 21%. Introduced forbs did not show any consistent trend. The total plant cover and Shannon diversity in the burned site decreased consistently over the course of the study (144 to 75 and 144 to 81%, respectively).

ISA did not reveal any overall trends, although there were differences in the response of certain species to burn cessation (Figure 3). For example, yellow starthistle and ripgut brome (*Bromus diandrus* Roth) retained higher indicator values (relative frequency × relative abundance) on the unburned site; redstem filaree [*Erodium cicutarium* (L.) L'Her. ex Ait.] and purple needlegrass (*Nassella pulchra* A. Hitchc.) retained higher values on the burned site. Some introduced annual grasses, such as wild oat (*Avena fatua* L.) and little quakinggrass (*Briza minor* L.), with higher initial values in the burned site shifted toward higher values in the unburned site in later years. In contrast, the introduced annual grass soft brome [*Bromus hordeaceus* L., sensu Am. auctt.] showed an opposite trend.

Within-Year Differences

In all years, the previously burned site had lower yellow starthistle cover compared with the unburned site (Table 2). Yellow starthistle seed and seedling counts were initially lower in the burned site, but by 1999 seed counts were not different (Table 3). Seedling counts were consistently lower in burned sampling areas compared with unburned areas but were not significantly different in 1998 or 2000. This may be because of dry spring weather during 1997 and 1999, resulting in limited survival of yellow starthistle, reduced seed production, and suppression of the differences in seedling populations in the following years.

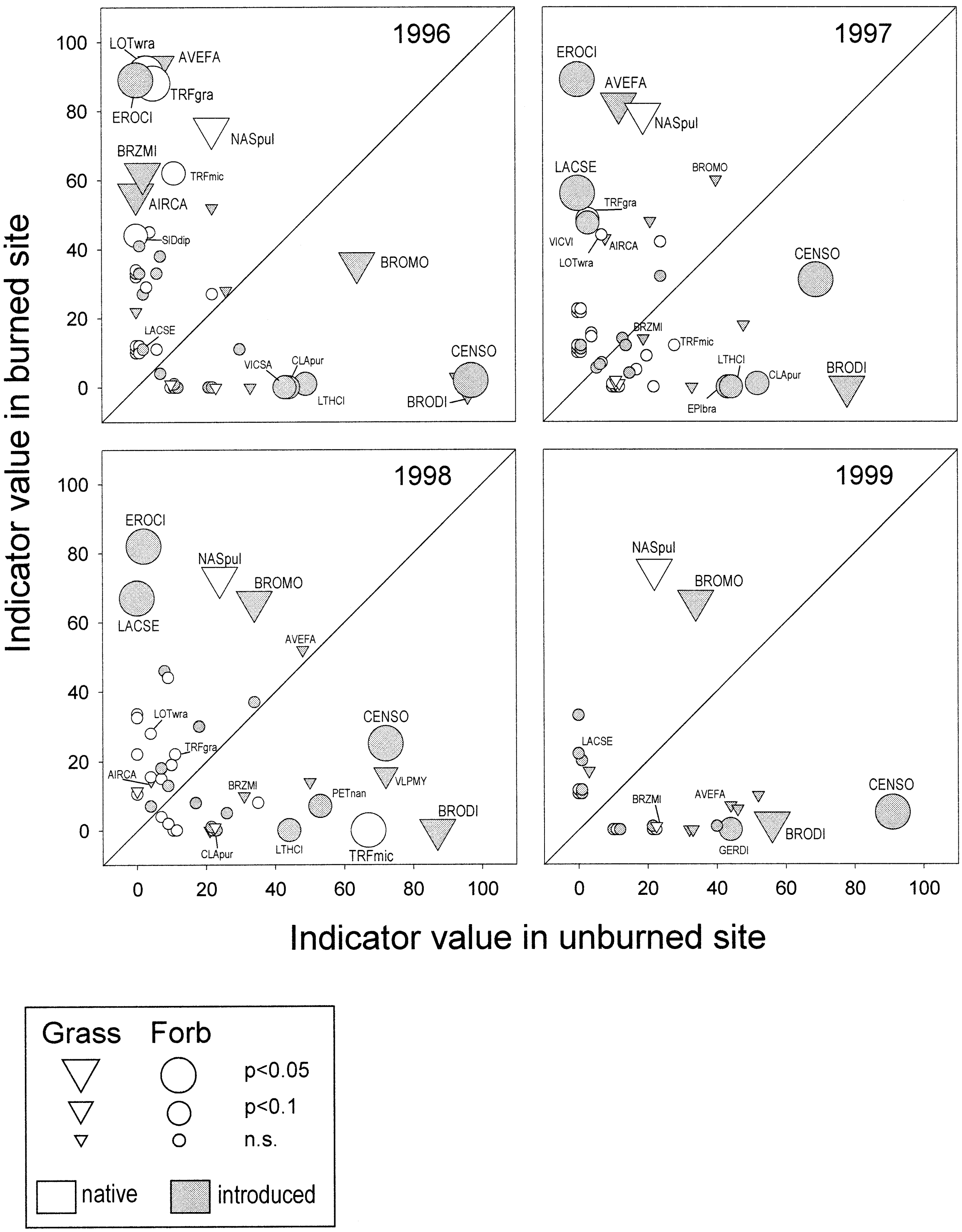

FIGURE 3. Indicator species analysis of species differences between previously burned and unburned sites. Indicator values were calculated from species relative frequency and relative abundance. The diagonal line represents equal frequency and abundance in burned and unburned sites, e.g., species above the diagonal were more frequent and abundant in the burned site. Symbol size represents the significance of a species' indicator value difference between burned and unburned sites. Species with $P < 0.05$ for at least 1 yr are labeled throughout. Species with $P < 0.1$ are labeled for each year. Abbreviations are included in Table 1.

Like yellow starthistle, the cover of other introduced forbs was consistently lower in burned sampling areas (Table 2). In 1996 the native forb cover was higher in the burned site, but differences were not significant in the following years. By 1999 the cover of native forbs had dropped to 0.5% (20% of the mean for the unburned site). As with the across-year analysis, the grass cover did not show any trends. Total plant cover and diversity were higher in the burned

TABLE 2. Relative vegetative cover and plant diversity in spring (late April to mid-May). Mean values ± standard deviation. Shannon index values were calculated for individual transects without inclusion of the yellow starthistle (*Centaurea solstitialis*) component. Asterisk indicates that the value in the burned sampling area is significantly different from the value in the unburned sampling area in the same year ($P \leq 0.05$, Mann–Whitney test).

Sampling areas	Year	Yellow starthistle	Annual grasses	Perennial grasses	Total grasses	Introduced forbs	Native forbs	Total forbs	Total cover, all species	Plant diversity without yellow starthistle
		% relative cover							%	Shannon index
Unburned	1996	29.0 ± 5.6	45.1 ± 10.1	10.7 ± 12.8	55.8 ± 6.2	36.9 ± 11.0	7.1 ± 6.1	44.0 ± 6.3	215.3 ± 19.7	1.55 ± 0.18
	1997	25.8 ± 5.2	32.3 ± 5.5	16.6 ± 12.8	48.8 ± 11.1	37.0 ± 14.8	9.5 ± 8.2	46.5 ± 10.7	175.8 ± 15.5	1.64 ± 0.11
	1998	29.1 ± 4.9	30.5 ± 5.5	20.6 ± 14.1	51.1 ± 8.6	40.3 ± 5.2	8.6 ± 3.4	48.9 ± 8.6	258.7 ± 37.0	1.73 ± 0.08
	1999	31.5 ± 13.6	36.8 ± 14.1	14.9 ± 11.2	51.7 ± 9.2	36.0 ± 15.3	2.5 ± 2.6	38.5 ± 12.9	141.1 ± 15.9	1.34 ± 0.13
Burned	1996	0.7 ± 0.8*	52.9 ± 13.8	11.5 ± 8.2	64.4 ± 6.5	9.9 ± 4.7*	25.7 ± 11.1*	35.6 ± 6.5	309.8 ± 26.6*	2.24 ± 0.14*
	1997	9.9 ± 5.7*	46.1 ± 6.5*	21.9 ± 2.3	68.1 ± 8.8*	21.0 ± 5.1*	10.3 ± 4.4	31.3 ± 9.5	210.0 ± 10.3*	1.86 ± 0.11*
	1998	10.7 ± 10.5*	27.3 ± 4.1	29.1 ± 5.1	56.4 ± 5.2	25.9 ± 18.0	7.3 ± 3.9	33.3 ± 14.3	239.1 ± 24.3	1.84 ± 0.13
	1999	3.9 ± 3.5*	47.7 ± 12.6	24.6 ± 11.8	72.3 ± 6.8*	7.5 ± 7.4*	0.5 ± 0.8	8.0 ± 8.1*	105.8 ± 9.8*	1.08 ± 0.28

TABLE 3. Yellow starthistle (*Centaurea solstitialis*) seed and seedling counts. Mean values ± standard deviation. Asterisk indicates that the value in the burned sampling area is significantly different from the value in the unburned sampling area in the same year ($P \leq 0.05$, Mann–Whitney test).

Sampling area	Year	Seed count (previous fall)	Seedling count (early spring)
		seeds m^{-2}	seedlings m^{-2}
Unburned	1996	10,116 ± 2,752	1,328 ± 222
	1997	5,687 ± 194	499 ± 44
	1998	3,438 ± 1,418	910 ± 216
	1999	12,605 ± 3,751	1,237 ± 666
	2000		418 ± 70
Burned	1996	52 ± 91*	5 ± 5*
	1997	1,655 ± 1,989*	255 ± 133*
	1998	1,061 ± 848*	485 ± 385
	1999	10,101 ± 8,090	165 ± 196*
	2000		233 ± 188

site during 1996 and 1997, were not different in 1998, and were lower in the burned site in 1999 (not significant for diversity).

Results for species richness were similar to those for vegetative cover. Total plant species richness in the burned site declined over the course of the study. It was slightly higher than that in the unburned site for all quadrat sizes in 1996 ($P = 0.08$), was approximately even in 1997 and 1998, and was lower than that in the unburned site in 1999 ($P = 0.02$) (Figure 4). Forb species richness was greater in the burned than in the unburned site in 1996 ($P = 0.03$) but decreased and was lower by 1999 ($P = 0.04$) (Figure 5). Grass species richness did not show a trend but was lower in the burned than in the unburned site in 1997 and 1999 (Figure 6).

Overall Trends

In 1996, after three successive burn years, burned areas in the Sugarloaf Ridge grassland had lower yellow starthistle populations, increased cover of both native and total forbs, increased total plant cover, increased Shannon diversity, and increased species richness (DiTomaso et al. 1999a). Burning apparently shifted the competitive advantage to fire-adapted native forbs, particularly legumes, and away from poorly adapted introduced species. Increased emergence and survival of the fire-adapted forbs from a long-lived seedbank enhanced species richness and biodiversity. Populations of poorly adapted forb species were reduced to 10% of the vegetative cover in the year after the final burn, compared with 36 to 41% in the unburned site, but the total cover of annual grasses was not affected.

After burn cessation, the grassland degraded rapidly as the competitive advantage shifted away from the fire-adapted forbs, resulting in a gradual decline in populations of these species and a decline in species richness. By most indices, the previously burned grassland was not significantly different from unburned grassland by 1998, with the exception that the yellow starthistle population levels remained significantly lower.

Interestingly, the "trajectory of degradation" continued past 1998, with 1999 values for grass and forb species richness, total plant cover, and Shannon diversity in the burned

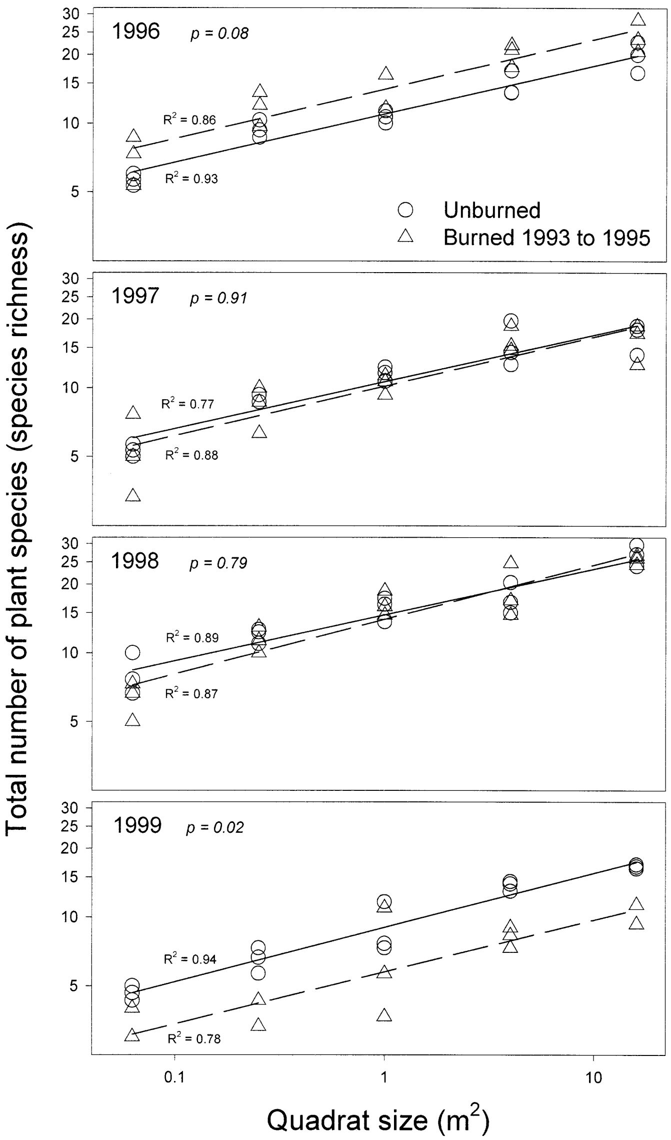

FIGURE 4. Total number of plant species vs. quadrat size for each year (log–log plots). Probability values (likelihood of difference between burned and unburned sites occurring by chance) are indicated for each year (multiresponse permutation procedures analysis).

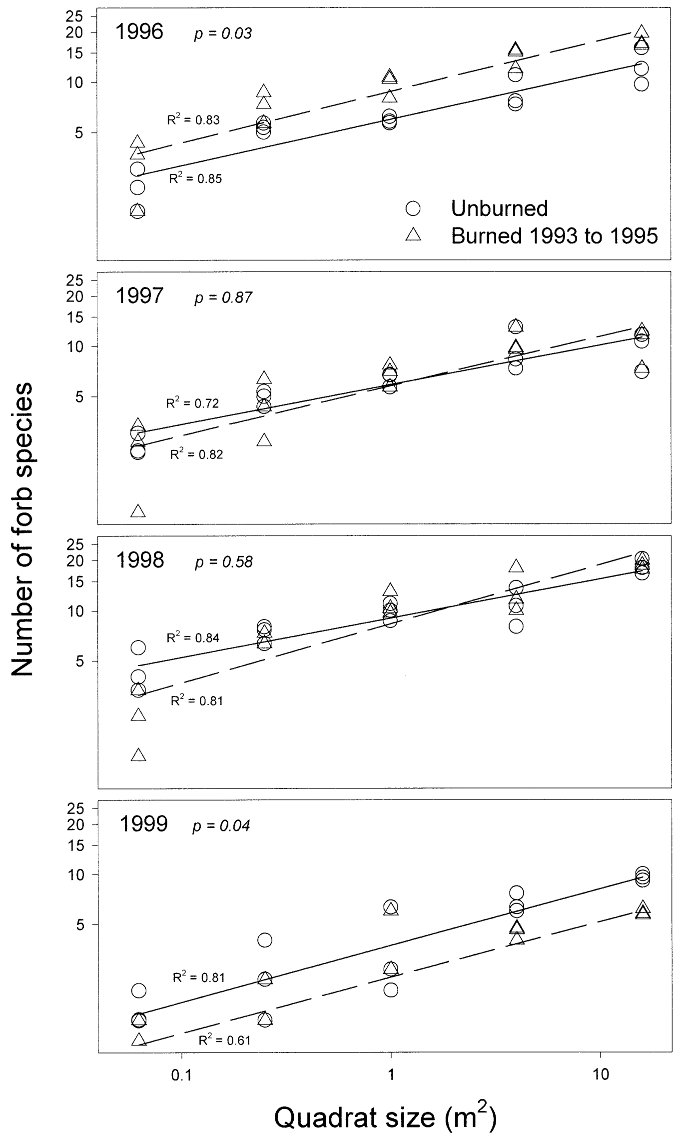

FIGURE 5. Total number of forb species vs. quadrat size for each year (log–log plots). Probability values (likelihood of difference between burned and unburned sites occurring by chance) are indicated for each year (multiresponse permutation procedures analysis).

site dropping below values for the unburned site. One reason may be that whereas populations of fire-adapted forbs continued to decline, populations of poorly adapted species—including yellow starthistle—recovered slowly in the burned site.

These results indicate that the reduction in yellow starthistle by means of burning at Sugarloaf Ridge did not result in a stable community but rather a community in transition back to yellow starthistle–dominated grassland. To refer to the ball-and-cup analogy (George et al. 1992), the system (ball) has not been given sufficient impetus to push it out of the present stable state (cup) and into a new stable state.

One factor for the inability to establish a new stable state was the failure to eradicate yellow starthistle. Burning prevented the production of new yellow starthistle seeds but did not directly affect the soil seedbank. Instead, the seedbank was depleted through germination and seed mortality. Although yellow starthistle seed is relatively short-lived under California field conditions (Joley et al. 1992), a small percentage of the original seedbank remained viable after 3 yr. In addition, abundant seeds were produced on the adjacent unburned land and may have helped to reinfest the burned site.

A second problem is that under a regime of fire suppression, the system may be perpetually off-balance even at reduced yellow starthistle population levels. In addition to interfering with yellow starthistle seed production, burning appears to promote the establishment of native plants, possibly by removing thatch and scarifying seeds. After burn cessation, the system gradually shifts back toward conditions that favor the growth of yellow starthistle over that of the native forbs. This is indicated by rapid declines in vegetative cover, species richness, and diversity after burn cessation. Without periodic fire or intensive management (e.g., herbicides or controlled grazing), and in the absence of many of the original dominant grassland species (Heady 1977), the community may be at a constant risk of invasion.

What are the implications for management? First, yellow

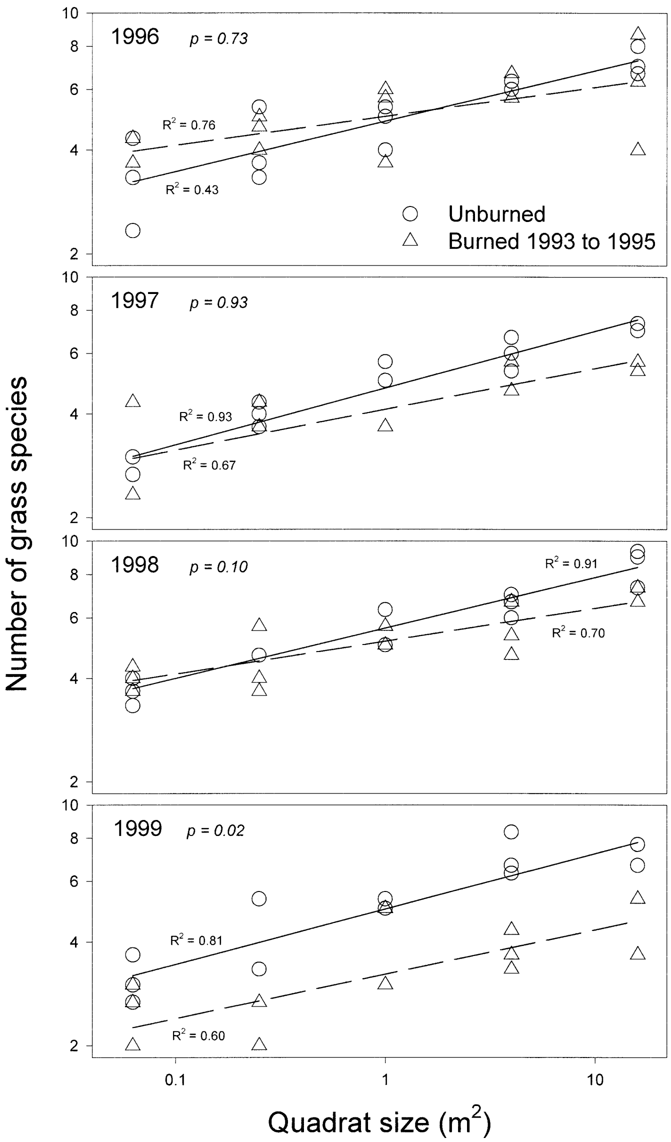

FIGURE 6. Total number of grass species vs. quadrat size for each year (log–log plots). Probability values (likelihood of difference between burned and unburned sites occurring by chance) are indicated for each year (multiresponse permutation procedures analysis).

starthistle reestablishment will be greatly delayed if local eradication can be achieved. Prevention of seed production for 3 yr may not eradicate a yellow starthistle infestation but may reduce the population to the point that survivors can be controlled individually. Follow-up management is essential. In addition, it would be advantageous to control yellow starthistle on a regional basis so that unmanaged patches do not remain to reinfest clean areas.

Second, prescribed burning in California grassland may have other benefits besides yellow starthistle control. For example, many of the native plants at Sugarloaf Ridge appear to be adapted to periodic disturbance by fire. In deciding whether to use prescribed burning in management, it may be helpful to refer to the historic burn regime, e.g., every 2 to 10 yr at Sugarloaf Ridge (Finney and Martin 1992). By the same token, burning for several consecutive years may constitute excessive disturbance. A 3-yr yellow starthistle control program probably should alternate burning with other control techniques such as herbicides or intensive grazing.

Sources of Materials

[1] PC-ORD, MjM Software Design, Gleneden Beach, OR 97388.

[2] StatView, SAS Institute Inc., Cary, NC 27513.

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