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Intraspecific and Diffuse Competition: The Response of Nassella pulchra in a California Grassland

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INTRASPECIFIC AND DIFFUSE COMPETITION: THE RESPONSE OF *NASSELLA PULCHRA* IN A CALIFORNIA GRASSLAND

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Abstract. In inland California grasslands, the high densities of alien annual species have altered the growing environment for native perennial grasses. Using variable-density plots, we measured the influence of intraspecific competition (conspecifics only) and diffuse competition (mixed-composition neighborhoods that include conspecifics) on growth and survival of *Nassella pulchra,* purple needlegrass. We assessed the effects of intraspecific and diffuse competition in weeded plots and unweeded plots, respectively, across a density gradient of *N. pulchra* plants (16–356 plants/m^2). We used summer fire and spring sheep grazing to reduce diffuse competition in unweeded plots. The potential effect of rooting volume on competitive interactions was explored by establishing plots on two sites of different soil depth. Diffuse competition had an overriding influence on *N. pulchra* growth in all treatments. Intraspecific competitive effects were apparent only in the absence of diffuse competition. The effects of grazing and soil depth on growth were only short-lived interactions with the burning treatment. Burning was a longer-lived interaction, but only in weeded plots. Plant mortality was significantly increased by diffuse competition. Overall, *N. pulchra* survival was greatest in weeded plots, in grazed plots, and in deeper soil plots. The growth of *N. pulchra* individuals was negatively affected by alien annual species in all treatment combinations. Our data indicate that recruitment of *N. pulchra* within inland California grasslands is reduced by the adverse environment created by high densities of alien annual species. Successful attempts to increase populations of *N. pulchra* through management of the grassland community must involve significant modification of the biotic environment.

Key words: California annual grassland; competitive suppression; diffuse competition; grassland restoration; interspecific competition; intraspecific competition; Nassella pulchra; *perennial bunchgrass; purple needlegrass.*

INTRODUCTION

Although originally dominated by perennial grasses (Clements 1934, Burcham 1957, Heady 1988), the Central Valley and foothill grasslands have been converted over the past two centuries to a predominantly annual system (Burcham 1957, Mack 1989) with native perennial grasses generally displaced from the valley floor (Huenneke 1989). The conversion process was coincident at different times with several landscape-level influences, including intensive grazing by livestock, suppression of wildfire, prolonged periods of below average precipitation, and invasion by alien species (Burcham 1957, Bartolome and Gemmill 1981, Mack 1989). These influences on the grasslands occurred throughout California and, with the exception of heavy grazing and outright agricultural conversion, generally involved little physical disturbance.

Most presettlement grasslands were probably dominated by bunchgrasses with *Nassella pulchra* (Hitchc.)

Barkworth the most widespread and abundant (Clements 1934, Burcham 1957, Heady 1988). Today, however, alien species in grassland habitats occur in such high densities that they now define the system (e.g., the ''California annual system'') (Talbot et al. 1949, McNaughton 1968, Heady 1988). These species are primarily native to Europe and preadapted to the mediterranean-type climate of the California grasslands (Jackson 1985). Consequently, the environment of contemporary grasslands is now potentially very different from that in which native species evolved (Evans and Young 1972).

After the first significant precipitation in fall, thousands of nonnative annuals per square meter germinate and emerge (Major and Pyott 1966). As a consequence, intraspecific competition among native plants may be weak because the neighborhood of a *Nassella* seedling may be composed of hundreds of individuals of many species (Bartolome 1979). An estimate of the presettlement density of mature *N. pulchra* based on soil opal phytolith data was 4.2 plants/m^2 (Bartolome et al. 1986); other studies of *N. pulchra* have reported a range of 1–7 mature plants/m^2 (White 1967, Bartolome and Gemmill 1981, Heady et al.

1992). The competition provided by several large bunchgrasses compared to that of hundreds of annual grasses is unknown. As a result of the changes in composition of inland California grasslands, theoretical models such as those using nearest neighbor distances may not appropriately characterize the competitive environment (Berendse 1983).

We hypothesize that the high densities of nonnative annual species, especially grasses, have fundamentally altered the environment experienced by *N. pulchra* seedlings. Whereas intraspecific interactions may have had a significant influence on *N. pulchra* before the introduction of alien annuals, ''diffuse competition'' (sensu MacArthur 1972:45, Wilson and Keddy 1986, Goldberg 1987) from these alien annuals has now become more important. In this paper, the phrase ''diffuse competition'' will be used to signify a competitive neighborhood composed of high densities of many species, including conspecifics of the target plants. In such a neighborhood, the addition or removal of a single neighbor has an insignificant effect on the competition experienced by a target plant.

The decline of perennial grasses in inland grasslands has been attributed to intense grazing coincident with periods of below average precipitation (Burcham 1957, Heady et al. 1992) and the invasion of many alien annual species. However, with average precipitation and reduced grazing, the return to dominance of perennial grasses has not occurred (White 1967, Bartolome and Gemmill 1981). In addition, attempts to restore perennial grass populations via seeding techniques achieve little success unless populations of alien species are reduced or eliminated (Evans and Young 1972, Dyer et al. 1996, Stromberg and Griffin 1996). These observations suggest a strong interaction between alien species and native perennial species during the early stages of establishment and growth.

Prescribed fire and grazing by livestock have been recommended as tools to reduce the suppression of native vegetation by annual grass biomass (Menke 1992). We attempted to manipulate the intensity of diffuse competition with seasonal sheep grazing and prescribed burning, in combination with differences in soil depth. We measured the relative effects of intraspecific and diffuse competition on the survival and growth of *N. pulchra* across a range of planting densities. Differences in the growth response of *N. pulchra* between the two competition environments provided a measure of the impact of alien species. Our objective was to assess the general effectiveness of burning and grazing as grassland management strategies for increasing *N. pulchra* abundance and reducing competition from annual species.

METHODS

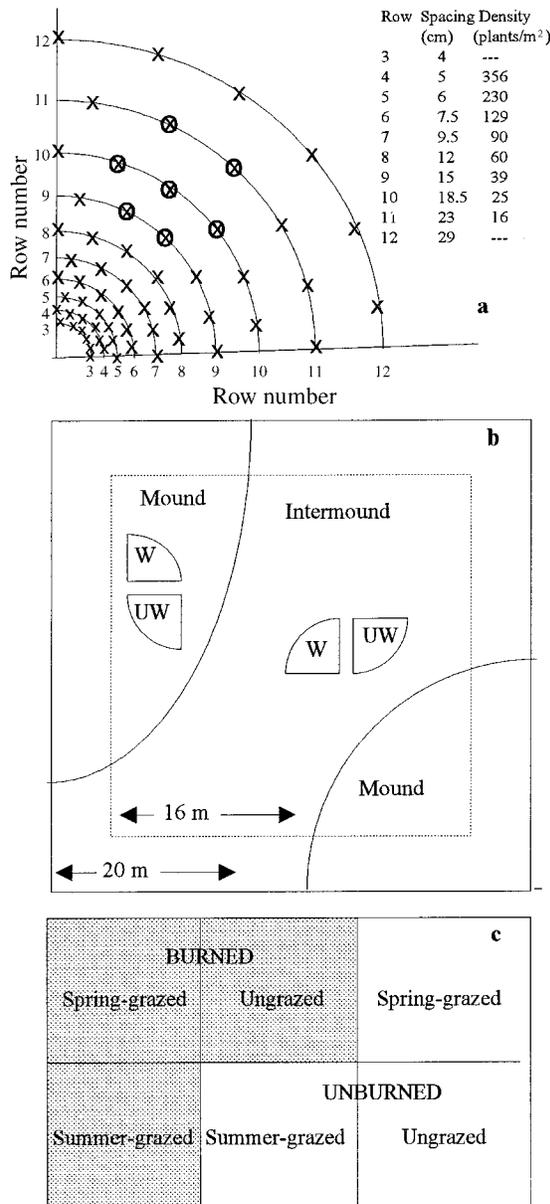This study was conducted at the Jepson Prairie Reserve in Solano County, California. The area is characterized by a ''Mima'' mound topography (Holland and Jain 1988), and is underlain by an impervious clay layer at a depth of ≈20 cm in intermound areas, and ≈65 cm under mounds. The underlying clay creates a perched water table during winter and spring that results in a seasonally wet ''vernal pool'' environment in the lowest intermound areas. The soil at the Reserve is classified as San Ysidro sandy loam (fine, montmorillonitic, thermic, Typic Palexeralfs).

Spatial distribution of *N. pulchra* within the vernal pool habitat at Jepson Prairie reflects the topography of the site. Typically, mature *N. pulchra* plants occur in higher numbers on mounds; fewer occur in the intermound areas, and virtually none in the vernal pools. Changes in floristic composition and edaphic conditions occur along a topographic gradient from mounds to intermounds to vernal pools. Along the gradient, vegetative cover (point frame method) ranges from 100% on mounds to <30% in vernal pools. The percentage of native species ranges from zero on mounds to >70% in vernal pools; and the percentage of alien annual species ranges from 100% on mounds to <7% in vernal pools. The intermound areas are generally intermediate for these characteristics (Holland and Jain 1988).

Eighteen experimental areas (20 × 20 m) (Fig. 1b) were established in 1988, with six treatment combinations of two levels of prescribed burning and three levels of grazing by sheep, in a full-factorial, randomized complete block design with three replications (2 × 3 × 3 = 18) (Fig. 1c). The grazing treatment was applied annually in April (spring) or in August (summer); prescribed burns took place on 1 September 1988 and on 13 September 1991. Ungrazed and unburned controls were included in the design.

N. pulchra seed was collected in 1988 from 18 large individuals from each of the 18 experimental areas. The bulked seed was planted in trays filled with potting soil in November 1990 and germinated in a glasshouse. Seedlings were transferred to 4 cm diameter × 14 cm long plastic tubes when 2–3 wk old, grown in the glasshouse under ambient light for 6 wk, then cold hardened outside the glasshouse until planted.

Individual *Nassella* plants were planted into 24, variable density, ''fan'' plots (Antonovics and Fowler 1985) from 17 February–7 March 1991 in both mound and intermound locations in the unburned experimental areas that were spring grazed or ungrazed. The fan-style plots allowed several planting densities to be analyzed within a single plot (Fig. 1a). Each plot was composed of 12 rows, with six individuals per row within a total area of about 0.75 m². The spacing in Row 3 was 4 cm between plants. The distance to plants in the next row was 5 cm (an increase of 25%), and spacing between plants within that row was also 5 cm. Distances between succeeding rows and between individuals within rows were increased by 25%, so that the distance between plants within Row 12 was 29 cm.

Row	Spacing (cm)	Density (plants/m²)
3	4	---
4	5	356
5	6	230
6	7.5	129
7	9.5	90
8	12	60
9	15	39
10	18.5	25
11	23	16
12	29	---

FIG. 1. Experimental design showing plots, experimental areas, and replicated blocks. (a) Fan plot with eight rows bounded by two buffer rows (Rows 3 and 12) with four target plants per row and two buffer plants (first and last in the row). Plants shown with circles indicate the hexagonal arrangement within the plot. Spacing is in cm; density is in plants/m². (b) Experimental area showing weeded and unweeded plot pairs on two locations of different soil depth (mound and intermound). The outer 2 m of each experimental area was considered a buffer zone. (c) Replicated unit showing six experimental areas in a full factorial of burning and grazing treatment combinations. No fan plots were planted in summer-grazed areas.

Every target plant was surrounded by six neighbors in a hexagonal pattern.

To assess the effect of fire on plant growth, a second set of 24 plots was planted from 23 February–17 March 1992 in spring grazed and ungrazed experimental areas that had been burned the previous fall. Seeds from the same bulk collection were planted directly into plastic tubes, then grown and planted in the same manner as described for the first set of plots. No plots were planted in summer grazed areas.

Pairs of plots were planted in both mound and intermound areas within each experimental area. Within each mound and each intermound, the two plots were placed side by side (Fig. 1b). One was cleared of all living vegetation except the target plants, the other was left unweeded. Removal of vegetation from weeded plots occurred annually in early March with subsequent weeding to remove late-germinating plants. Plots were dropped from the study when overall mortality exceeded 30%, or when mortality of target plants severely compromised the density treatment.

We allowed the plots to establish during the first growing season; we did not take growth measurements until the end of the second growing season. We assessed growth in target plants by measuring changes in basal diameter, because increase in basal diameter in *N. pulchra* was highly correlated with above ground biomass ($r = 0.92$; A. R. Dyer, *unpublished data*). Basal diameter was measured in millimeters using digital calipers in early July of each year. Perpendicular measurements of the long and short axes were taken on plants that were not circular in shape. The values were used to approximate the area of an ellipse using the formula

$$\text{Area} \cong (r_l - 2r_s)r_s + \pi r_s^2 \qquad (1)$$

where r_l is the length of the long axis and r_s is the length of the short axis. The diameter of a circle was calculated with the area value thus generated using the formula

$$\text{Diameter} = 2(\text{Area}/\pi)^{1/2} \qquad (2)$$

and that value was substituted for the original measurements and used in further analysis. All plants were measured in both unburned plots and burned plots after the second and third growing seasons, and in the unburned plots after the fourth season. Censuses were conducted in March and July of each year.

Analysis was performed on data from Rows 4–11 only (5–23 cm spacing), because the highest density Rows 1 and 2 experienced high mortality in the first year (see *Discussion*). Rows 3 and 12 were considered buffer rows, as were the first and last plants in each row. As a result, a total of 32 plants were used for analysis of each plot (n = four plants per density per plot).

The effect of treatments on plant basal diameter (mm) and mortality (arcsine-square root of percent annual loss) were analyzed using the SAS General Linear Model (Littell et al. 1991) with burning and grazing as main effects, soil depth (about 65 cm on mounds and 20 cm on intermounds) as a subplot treatment, and

TABLE 1. Analysis of the increase in basal diameter (mm) of *Nassella pulchra* at Jepson Prairie, California, in response to burning and grazing treatment combinations, soil depth, and planting density. Planting density was used as a covariate in the analysis. No analysis of a grazing effect was possible in the third and fourth years. There was no replication in the fourth year; the data were analyzed as a complete randomized design.

Treatment	Second year			Third year			Fourth year		
	df	MS	F	df	MS	F	df	MS	F
Weeded plots only									
Burn and grazing × soil depth	3	55.40	4.85**	1	0.52	0.01			
Planting density	1	1 248.51	109.41***	1	1 702.55	45.12***			
Burn and grazing × density	3	48.50	4.25**	1	50.71	1.34			
Error	108	11.41		53	37.73				
Total	130			64					
Burned plots only									
Weeded	1	1 822.72	169.13***	1	967.88	30.58***			
Soil depth × weeded	1	63.72	5.91*	1	33.37	1.05			
Planting density	1	724.26	67.21***	1	431.25	13.63***			
Weeded × density	1	357.33	33.16***	1	167.96	5.31*			
Error	104	10.78		56	31.65				
Total	121			65					
Unburned plots only									
Weeded	1	450.03	57.97***	1	342.47	25.17***	1	182.21	3.71†
Grazed × weeded	1	71.91	9.26**	1	...	...	1	...	...
Planting density	1	395.19	50.90***	1	632.72	46.51***	1	1 718.64	34.95***
Weeded × density	1	73.92	9.49**	1	125.12	9.20**	1	27.10	0.55
Error	104	7.76		23	13.60		23	49.17	
Total	119			29			29		

* $P = 0.05$; ** $P = 0.01$; *** $P = 0.001$; † $P = 0.067$.

weeding of all nontarget plants as a sub-subplot treatment. Planting density was included as a covariate. Repeated measures analysis was used to test for changes in treatment response over time. Specific treatments were not included in the GLM model when insufficient replication existed within the treatment for proper analysis (e.g., unweeded and ungrazed plots after the second season). To examine the effect of burning on plant growth, data from unburned plots in their second season (1992) were compared to burned plots in their second season (1993). The same was done for third season data (1993 unburned vs. 1994 burned).

Disturbance of the soil within plots by gophers (*Thomomys bottae*) was a significant cause of *Nassella* mortality throughout the study, and we measured the amount of disturbance in two ways. First, the number of plots damaged by gophers was analyzed using binomial probability tests (Zar 1984) to detect any relationship between treatments and gopher activity. Second, within the burned experimental areas, the amount of soil disturbance along three 18 m line transects within each grazing treatment was recorded in January 1995 when disturbance by gophers was highly visible. Data were collected three months after a burn treatment in experimental areas that had not been burned in the preceding three years. These data were analyzed with the SAS General Linear Model for three levels of grazing (ungrazed, spring grazed, summer grazed) in mound and intermound locations with three subsamples per treatment and three replications.

RESULTS

Plant growth

Unweeded plots.—In unweeded plots, burning, grazing, soil depth, planting density (i.e., main effects), or interactions between factors did not have a detectable effect on basal diameter increase in either the second or third season.

Weeded plots.—Planting density had a strong effect on basal diameter increase in both the second and third seasons ($P < 0.001$, Table 1). In the second growing season, a burning by planting density interaction ($P < 0.01$, Fig. 2) indicated that, at lower densities, increase in basal diameter was greater in burned plots. In addition, a burning and grazing treatment by soil depth interaction ($P < 0.01$, Fig. 3) indicated that increase in basal diameter in the second season was greater on mounds than on intermounds, but only in the burned-ungrazed plots. No interactions were found among treatments in the third season.

The rate of basal diameter increase of *Nassella* in response to weeding was greater in burned than in unburned plots. Basal diameter of plants without apparent diffuse competition (i.e., weeded) in burned plots was 94% greater (second season) and 50% greater (third season) than plants exposed to diffuse competition. The increase in plant size within unweeded plots compared to weeded plots in the unburned treatment was lower (40%, second season; 34%, third season; 18%, fourth season) (Fig. 4). Overall, the mean increase in growth in burned plots was two times greater than growth in unburned plots over the second and third seasons.
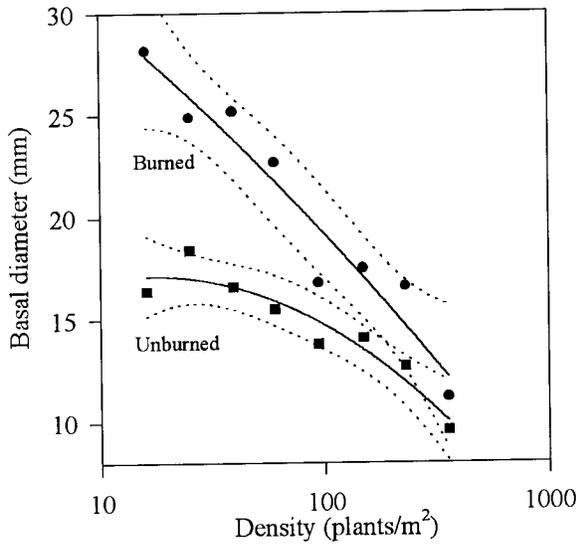
FIG. 2. Relationship between burning treatment and planting density for basal diameter (mm) of *Nassella pulchra* within weeded plots in the second growing season. A negative exponential curve is used to represent the interaction (unburned $r^2 = 0.91$; burned $r^2 = 0.93$). The difference between burned and unburned treatments is significant at $P < 0.01$ ($F_{3, 108} = 4.25$). Dotted lines represent 95% confidence intervals.

Increase in basal diameter was not affected by grazing in any year, and a grazing by weeding interaction was detected only in unburned plots in the second season (Fig. 5, Table 1). Detection of grazing effects after the second season was made less likely because of the loss of plots over time (see data on gopher activity).
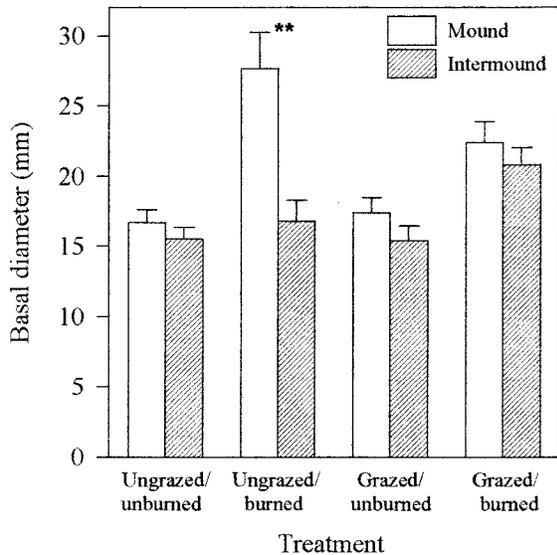

FIG. 3. Basal diameter (mean ± 1 SE) of *Nassella pulchra* in burning and grazing treatments between two soil depths (mound and intermound) in the second growing season. The difference between mound and intermound plots in the ungrazed/burned treatment is significant at $P < 0.01$ (**) ($F_{3, 108} = 4.85$).
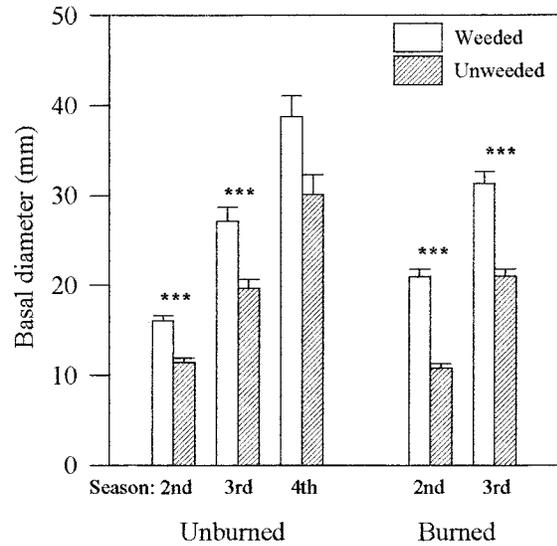

FIG. 4. Increase in basal diameter (mean ± 1 SE) of *Nassella pulchra* due to weeding in burned and unburned plots. Differences between columns within a growing season are significant at $P < 0.001$ (***).

Although soil characteristics and depth to the clay layer differed between mounds and intermounds, the topographic location of the plots did not strongly influence growth. The exceptions to this general trend were ungrazed/burned plots ($P < 0.01$, Fig. 3), and a soil depth by weeding interaction in burned plots ($P < 0.05$, Fig. 6, Table 1). The interactions were found in the second season only.

Diffuse competition negatively affected basal diameter increase of target plants in all plots, regardless of the level of burning, grazing, or soil depth. Plants
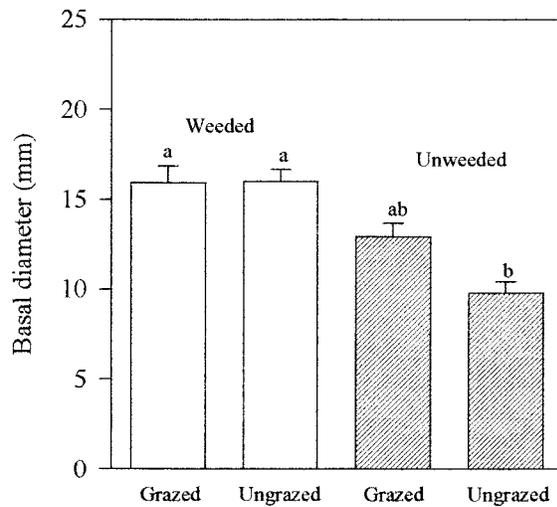

FIG. 5. Grazing by weeding interaction for increase in *Nassella pulchra* basal diameter (mean ± 1 SE) in unburned plots in the second year. The interaction is significant at $P < 0.01$; the overall effect of weeding is significant at $P < 0.001$ ($F_{1, 104} = 57.97$).
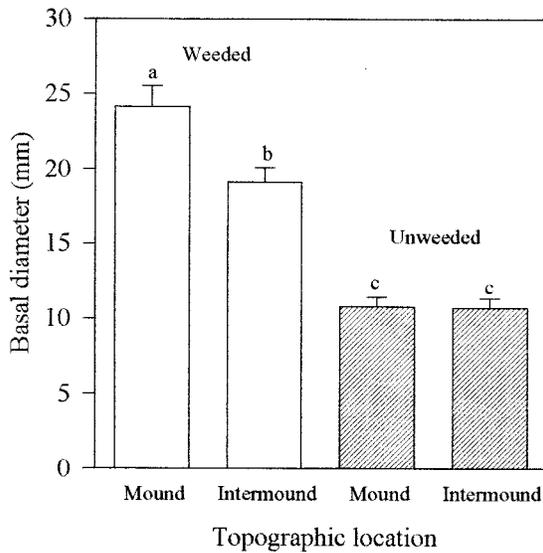
FIG. 6. Soil depth (mound or intermound) × weeding interaction for increase in *Nassella pulchra* basal diameter (mean ± 1 SE) in burned plots in the second year of growth. The interaction is significant at $P < 0.05$; the overall weeding effect is significant at $P < 0.001$ ($F_{1, 104} = 5.91$).

in weeded plots were significantly larger in the second and third seasons regardless of treatment ($P < 0.001$, Fig. 4). In addition, growth increased as density decreased ($P < 0.001$ both years, Fig. 7). The interaction between planting density and type of competitive environment was significant in both years. From the second year graph (Fig. 7a), it appeared that intraspecific competition was as effective as diffuse competition in suppressing growth at the highest planting density. No effects of planting density were detected in weeded or unweeded plots when burning or grazing treatments were considered simply as main effects.

Plant mortality

Individual plant mortality was not strongly affected by any treatment factor (i.e., burning or grazing) when analyzed as a percentage of annual mortality. However, mortality of target plants resulting in the elimination of a plot from analysis was significantly higher in unweeded plots ($P < 0.01$). Of the 14 plots that were eliminated from analysis due to high mortality but not damaged by gophers, 12 were unweeded plots. Of the 12 plots that survived intact, 9 were weeded, 10 were grazed, and 9 were on mounds. The highest density rows in each plot were invariably lost after the first year of growth, suggesting a strong intraspecific effect independent of diffuse competition.

Activity patterns of gophers had a strong effect on *N. pulchra* survival. Gopher disturbance was significantly lower within grazed plots ($P < 0.01$) (Fig. 8). Although grazing did not have a significant direct influence on *N. pulchra* growth or survival, the indirect effect of reducing gopher activity resulted in higher

plant survival in grazed/burned plots ($P < 0.05$). Gopher activity was partly responsible for the loss of all ungrazed mound plots (weeded and unweeded) by the third season.

Plant mortality attributable to gophers occurred in 19 of 46 plots. Based on binomial probability, gophers were more likely to kill plants in weeded plots ($P = 0.05$), in ungrazed areas ($P < 0.05$), and possibly on mounds ($P < 0.1$). Burning had no detectable effect on gopher activity.
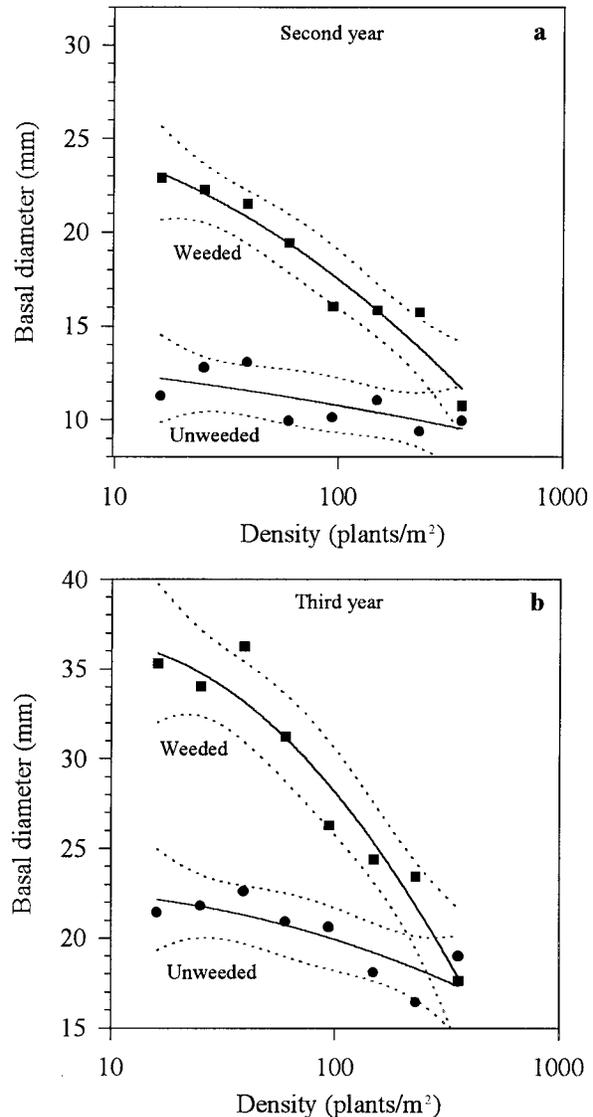

FIG. 7. Relationship between planting density and weeding on increase in basal diameter (mm) of *Nassella pulchra*, showing the difference between the effects of diffuse and intraspecific competition on growth in each of two growing seasons. Interactions are represented by negative exponential curves. (a) Second year: interaction is significantly different at $P < 0.001$, unweeded $r^2 = 0.47$, weeded $r^2 = 0.94$. (b) Third year: interaction is significant at $P < 0.01$, unweeded $r^2 = 0.67$, weeded $r^2 = 0.94$. Dotted lines in both graphs represent 95% confidence intervals.
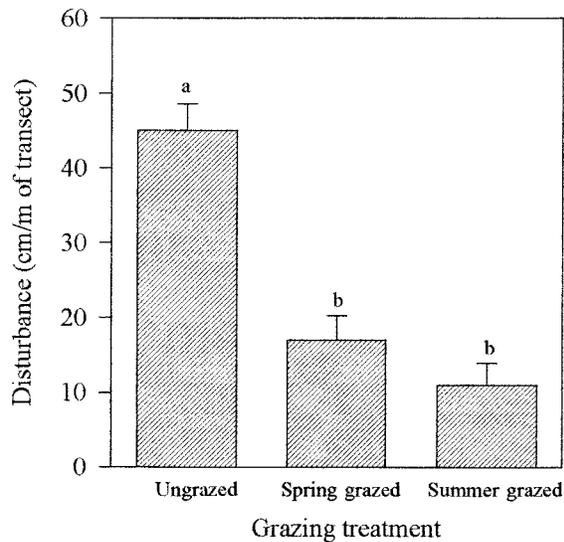
Fig. 8. Amount of gopher activity (cm of disturbance/m of transect) in experimental areas subjected to three grazing treatments. Columns with different letters are significantly different at $P < 0.001$.

DISCUSSION

Using plant removal treatments, we showed a strong influence of diffuse competition on basal diameter and survival of *N. pulchra.* The effect of intraspecific competition on basal diameter increase was also shown, but only in the absence of diffuse competition. The competition provided by a dense multispecies neighborhood of annual plants appears to have an overriding effect on growth and survival of *N. pulchra,* in comparison to both intraspecific competition and to the effects of burning and grazing. Because we did not investigate the effects of other types of neighborhoods (e.g., native annuals) on *N. pulchra,* we cannot reach any conclusions on the competitive environment of the pristine grassland. However, dense neighborhoods of alien annuals appear to be a primary factor in determining the growth and survival of young *N. pulchra* individuals. While nothing is known of the presettlement *N. pulchra* densities and little of recruitment dynamics in natural grasslands today, the inability of *N. pulchra* to re-establish even after being seeded is indicative of the major transformation that has occurred in inland California grasslands. Given the strength of diffuse competition on growth and mortality in this study, our hypothesis that the invasion of alien annual grasses has fundamentally altered the growing conditions for *N. pulchra* would appear to be supported.

The regional distribution of *N. pulchra* in the presettlement grasslands of California was most likely influenced by a combination of edaphic conditions and competition with other native perennials (Bartolome et al. 1980). On a local scale, spacing of mature bunchgrasses suggests that intraspecific competition for one or more limiting resources has influenced long-term

plant density. Soil water is the most important limiting factor in the mediterranean environment, particularly in shallow soils (Roy et al. 1987). Within contemporary inland grasslands, light has become an important limiting factor in spring (Schulz and Biswell 1952, Kay and Owen 1970). Thus, light limitation in spring followed by summer competition for soil moisture may reduce the survival of bunchgrass seedlings. Other grassland studies have underscored the importance of spring conditions on subsequent plant growth (Wright and Van Dyne 1976, Aquiar et al. 1992).

As plants mature, we expect mortality to decrease until a density is reached that reflects the site's carrying capacity. Relictual populations of *N. pulchra* in other California locations have densities of 1–7 mature plants/m^2; basal area represents no more than 10% of the total plant cover (White 1967, Bartolome and Gemmill 1981, Heady et al. 1992). Prior to European settlement of California, the space between mature perennial grasses was probably occupied seasonally by variable densities of native annual grasses, flowering monocots, and annual dicots (Burcham 1961, Wester 1981, Heady 1988).

The rapid conversion of the California prairie to a grassland dominated by alien annual species coincided with decades of heavy, continuous livestock grazing (Burcham 1957, Mack 1989). Intensive year-round grazing in a grassland with no recent history of heavy grazing (Edwards 1992, Painter 1995) represented a massive and prolonged disturbance (Mack and Thompson 1982). Annual European grasses, preadapted to the mediterranean-type climate of inland California and to conditions of seasonal resource availability, clearly found favorable growing conditions. Heavy grazing and European-style agriculture may have created disturbance niches, and some species may have exploited largely unfilled niche space (sensu Grubb 1977).

The rapidity with which nonnative species were able to invade California communities (Burcham 1957, Mack 1989) is indicative of the large-scale disturbance created by the activities of European settlers, as well as the colonizing ability of the many preadapted mediterranean aliens. The overriding negative effect of introduced annual species on the growth and survival of *N. pulchra* is supported in this study by the absence of any effect of burning, grazing, soil depth, or planting density in plots with diffuse competition.

The effect of burning on growth was seen only in plots without diffuse competition, and not after the second season following the burn treatment. The postburn increase in growth may reflect a nutrient flush, a change in soil water availability, or a reduced density of diffuse competitors not seen in unburned plots. Effects of the burning treatment appeared to diminish by the third year, which is consistent with estimates obtained in other California grasslands (Heady 1956, Parsons and Stohlgren 1989, Heady et al. 1992).

We expected differences in soil depth between

mound and intermound areas to have a significant effect on growth and survival of *N. pulchra*. Coexistence between annual and perennial species, especially among grasses, may be based on the ability of perennials to compensate for slower above ground growth rates by gaining access to deeper soil zones (Berendse 1979, 1982). The region from 0–50 cm depth is exploited most intensely by annual grasses (Holmes and Rice, *in press*). Given a soil depth at Jepson Prairie of about 65 cm on mounds, the mound plots may not represent an area of significantly greater resource availability for perennial grasses. Thus, any differences in growth patterns between the mounds and intermounds would likely be subtle and difficult to detect during a 2–3 yr study. However, the intensity of the interspecific competition effect implies a lack of below ground resource partitioning between *N. pulchra* and the annual neighborhood.

Plant mortality patterns in this study are consistent with earlier results within the same experimental areas. Dyer et al. (1996) recorded <1% survival following >20% emergence of precision planted *N. pulchra* seeds. Langstroth (1991) found a 94% decrease in abundance of *N. pulchra* between the one- and two-tillered seedling stage, and a 26% decrease between the two- and three-tillered seedling stage. In contrast, we found mortality of mature *N. pulchra* was 2–6% annually over a 7-yr period (Dyer, *unpublished data*). Therefore, using transplants in the five to ten tiller range, we expected an intermediate mortality rate in our experimental plots.

Throughout most inland California grasslands, native perennial grasses now compete with high densities of aggressive annual species that are potentially better adapted to the contemporary grassland environment. Many annual grasses are adapted to heavy grazing and low nutrient availability (Jackson 1985, Heady et al. 1992). In addition, cool-season annual grasses exhibit rapid growth and rapid resource consumption during periods of slow growth for *N. pulchra* (Jackson 1985, Jackson and Roy 1986). These alien species have invaded all inland California grasslands even in the absence of obvious physical disturbance.

Grazing by livestock has been recommended as a method for controlling alien annual grasses (Menke 1992) and as a management tool to reduce the suppression of native species by alien annual grasses (Heady 1956). We found no effect of grazing on growth even though the grazing treatment was applied annually. However, all analyses after the second growing season were compromised by the high mortality in ungrazed plots. Although a positive effect of grazing on survival is implied by the data, the high mortality in ungrazed plots was probably a result of greater gopher activity in ungrazed experimental areas. The interaction of grazing and gopher activity in addition to the absence of a grazing main effect makes it difficult to predict long-term effects of grazing on *N. pulchra* growth and survival.

A further complication in assessing the importance of the burning and grazing treatments may be related to the interaction between treatments and the timing of application. The burn treatment was applied in late summer when *N. pulchra* was dormant and after all cool-season annuals had died. In contrast, the grazing treatment was applied in early April, the flowering time of many cool-season annual species and a phase of rapid growth for *N. pulchra*. Application of a spring grazing treatment is intended to decrease the above-ground biomass of annual species at a time of high resource availability. However, the grazing treatment also defoliates the perennial grasses and reduces their ability to take advantage of the favorable conditions (Briske and Richards 1994).

We conclude that high densities of invasive alien species have fundamentally altered growing conditions in the California grassland. This alteration probably reflects a reduction of limiting resources such as light in spring and water in early summer (Kay and Owen 1970). We conclude that the application of burning and grazing intended to reduce diffuse competition has had no short-term effect on *N. pulchra* growth. Although potentially favoring native perennials, these treatments did not create unfavorable conditions for alien annuals.

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