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EFFECTS OF PRESCRIBED FALL BURNING ON A WETLAND PLANT COMMUNITY, WITH IMPLICATIONS FOR MANAGEMENT OF PLANTS AND HERBIVORES

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ABSTRACT.—An important contemporary challenge for adaptive resource management is assessing both the direct and indirect effects of management activities by designing appropriate monitoring programs and sound analysis methods. Here we evaluate the effects of prescribed fall burning on a wetland plant community that is managed primarily for spring-migrating geese. During late fall in 2 consecutive years, we burned vegetation in 4 replicate blocks (2.3 ha each) that traversed a natural moisture and associated vegetation gradient. We used ordination, gradient analysis, and contingency table analysis to evaluate how annual changes in relative abundance of plants were affected by burning as well as other important ecological factors. Burning increased species diversity of plants, especially in the 2 wetter vegetation zones, but had no effect on species richness or on the proportion of native plant species. Wetland plant species responded to prescribed burning independently, and their response often differed by vegetation zone and with annual variation in flooding. Burning enhanced the abundance of native foxtail barley (*Hordeum jubatum*) and reduced the abundance of introduced swamp timothy (*Crypsis shoenoides*). Saltgrass (*Distichlis spicata*), a native plant species, was usually less abundant following burning, although the level of response was different for each of the 3 vegetation zones. Two other introduced plant species, quackgrass (*Elytrigia repens*) and reed canarygrass (*Phalaris arundinaceae*), were less abundant after fall burning, especially when spring flooding was more extensive. Wild geese using the experimental blocks for feeding clearly preferred burned sites, suggesting that fall burning can enhance wetland use by geese during spring. Given that simple manipulations such as burning and flooding of a wetland system may often produce complex results, we suggest that on-going management schemes be regularly evaluated with field experiments such as those conducted in this study.

Key words: adaptive management, CANOCO, correspondence analysis, fire, geese, prescribed burning, wetland plant community.

Adaptive management is designed to transform natural resource management from a system based upon uncertainty, derived mostly from descriptive studies, to one based on progressively more accurate scientific knowledge, derived mostly from experimental studies (Holling 1978, Walters 1986, Walters and Holling 1990). The practice of adaptive management requires monitoring and evaluating outcomes of a management activity, and readjusting future management accordingly (Gibbs et al. 1999). Ideally, management and monitoring are designed so that direct effects of management activity can be assessed along with how these effects are influenced by interactions with other important abiotic and biotic factors (Pickett and Ostfeld 1995). Here we assess effects of prescribed fall burning on a wetland plant community and use of the wetlands by migrating arctic-nesting geese during spring. Consistent with our goal of adaptive management, we used an experimental design and analysis that allowed us to determine how the effects of burning on the wetland plant community were contingent on other important ecological factors.

Prescribed burning and livestock grazing have been used to reduce residual plant material in wetlands so that newly emerging plants in the spring are available to herbivorous waterfowl, such as geese (Hanson 1939, Lynch 1941, Goodwin 1979, Smith and Kadlec 1985a, 1985b, Weller 1994). Prescribed burning is often preferred to grazing because it does not involve introduced mammals that require regular attention, and because fire may reduce the relative abundance of introduced and undesirable plant

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species (Uhler 1944, Weller 1994) or it may enhance the abundance of rare indigenous species (Pendergrass et al. 1999). Although fire may be a natural event in some wetlands (e.g., Willard and Wakimoto 1995) and is commonly used to manage wetlands (reviewed by Kozlowski and Ahlgren 1974, Lyon and Stickney 1976, Wright and Bailey 1982, Kantrud 1986, Payne 1992, Weller 1994), few studies have quantified the direct effects of burning on individual plant species in wetlands (e.g., Smith and Kadlec 1985a).

Herein we document the effects of prescribed fall burning on plant species diversity, species richness, and on individual species in a wet meadow plant community in northeastern California that is managed primarily for migrating arctic-nesting geese. Plant communities in the Great Basin floristic region of northern California (Raven 1988) are generally poorly described, and little is known about the effects of disturbances, such as burning, on the dominant plant species. Using a controlled field experiment, we tested the following hypotheses: (1) species diversity and richness of wetland plant communities increase after a disturbance such as fire; (2) the proportion of native versus introduced wetland plant species increases after a natural physical disturbance, such as fire; and (3) burning enhances the use of the wetland plant community by wild geese.

Although our field experiment was designed to determine the effects of prescribed fall burning on the plant community and use of the plants by geese during spring, a statistical comparison of yearly patterns of change in both burned and unburned plots enabled us to investigate how the effects of prescribed burning on plant species are influenced by interactions with other abiotic factors, primarily moisture and flooding regimes, and salinity-alkalinity relationships. We know of no other study that attempts to quantify the relative importance of prescribed burning compared to other important physical factors such as flooding in explaining annual floristic changes in a wetland plant community.

STUDY AREA

This study was conducted in the northern portion of Fall River Valley, Shasta County, California (Fig. 1). The Fall River Valley is 1 of many valleys on the Modoc Plateau in the Intermountain Region of California and lies at the extreme western edge of the Great Basin floristic region (Raven 1988). The northern portion of Fall River Valley is a complexly faulted graben that was occupied by a large Pleistocene lake. Deposits from this lake form much of the light-colored clay, silt, and sandy-silt soil in the valley. Annual precipitation averages about 30 cm, with moderately deep snows in the winter, some spring and fall rains, and relatively dry summers (Raven 1988).

The study area was located on a peninsula at 1009 m between the Tule and Little Tule rivers (Fig. 1). There, Pleistocene lacustrine deposits are overlain by approximately 1 m of more recent basin deposits. Soils on the peninsula are 85% Pastolla muck (0%–1% slope; classified as medial over clayey, mesic, Mollic Andaquepts) and 15% contrasting inclusion of Whipple soils and organic soils in low positions (Ferrari 1994). The Pastolla muck soils have low permeability, are poorly drained, and have a high available water capacity. Runoff is ponded, and the water table is high and maintained by flow from springs. In most years, the peninsula has standing water during late winter and spring, but not during summer and fall.

The seasonally inundated wet meadow on the peninsula is separated from the rivers by earthen levees that border the peninsula. Until October 1988, the low-lying wet meadow was partially flooded each spring and then grazed by cattle during summer and fall. Since 1989, the peninsula has been owned and managed by the California Department of Parks and Recreation principally as a feeding and resting site for migrating geese in the spring. Management by state park personnel has involved partially flooding the study area during early spring and prohibiting livestock grazing. Reduced use of the area by geese following exclosure of livestock led us to initiate this study of prescribed burning and its effect on plant communities and use by migrating geese.

METHODS

Precipitation, Temperature, and Water Level

Monthly precipitation and temperature data were obtained from a weather station that was operated by the California Irrigation Management District (California Department of Water Resources, Sacramento) about 5 km from the

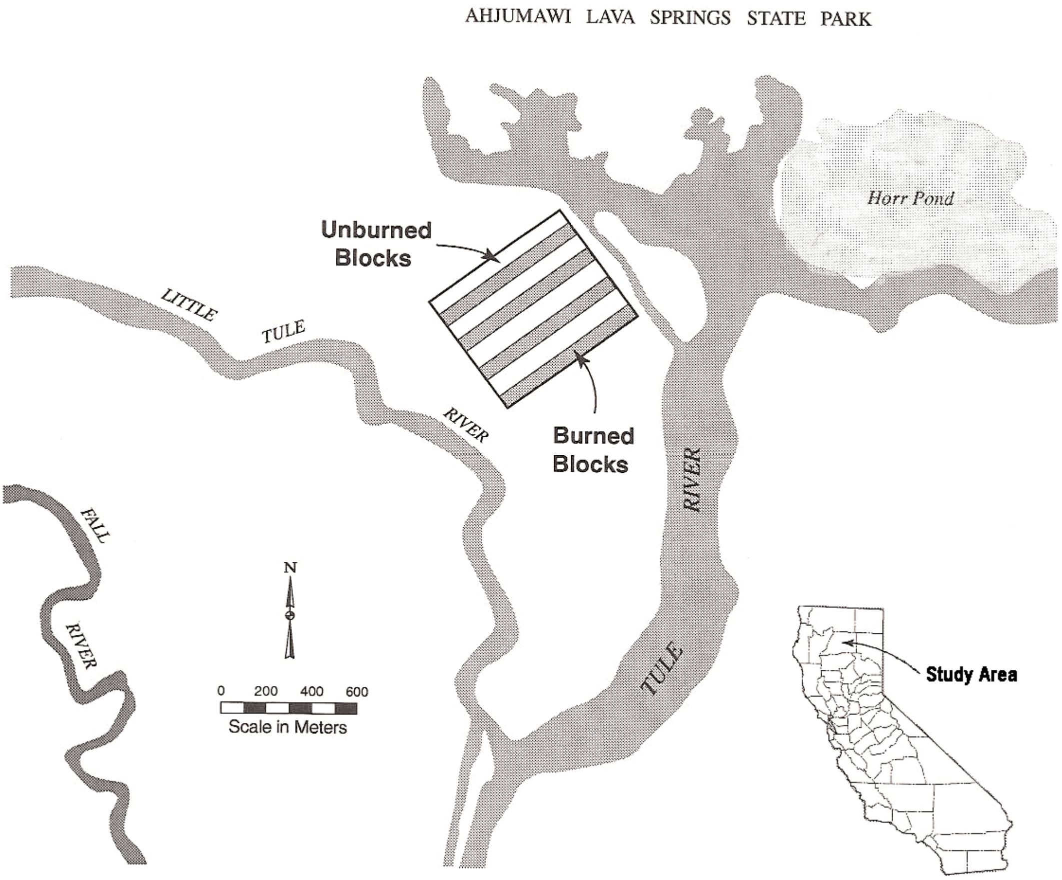

Fig. 1. Map of study area, located on a peninsula in Fall River Valley, Shasta County, California, showing the orientation of the 4 burned and 4 unburned experimental blocks.

study area. During spring 1991 and 1992, as part of the regular management program, California Department of Parks and Recreation personnel flooded portions of the study area to simulate the seasonal flooding that would occur in the absence of levees after spring rains and increased flows caused by snowmelt in the surrounding mountains. To obtain an indicator of yearly differences in flooding extent, we visually estimated the proportion of each vegetation zone on the study area that was covered by standing water in early March and again in early April in both 1991 and 1992.

Field Experiment

VEGETATION MONITORING.—An inventory of plant species on the peninsula was conducted on 15 August 1989 prior to prescribed burning. Native species, such as saltgrass (*Distichlis spicata*) and foxtail barley (*Hordeum jubatum*), and introduced species such as swamp timothy (*Crypsis shoenoides*), quackgrass (*Elytrigia repens*), and canary grass (*Phalaris arundinaceae*) were dominant on the peninsula (Table 1). The survey revealed obvious zonation of the plant community as is commonly observed in seasonally flooded freshwater wetlands with microtopographical elevation changes (Kadlec and Smith 1989, Weller 1994). For purposes of vegetation sampling and analysis, we categorized the vegetation into 3 zones based on the most conspicuous species. (1) *Crypsis* zone: the east side of the peninsula was dominated by *Crypsis shoenoides* with *Distichlis spicata* to a lesser extent (Fig. 1). Plants on the east side of the peninsula must tolerate the longest duration of flooding and the wettest soils. (2) *Distichlis* zone: on slightly higher, drier ground to the west, *D. spicata* formed nearly a monoculture. (3) *Elytrigia* zone: on

TABLE 1. Plant species (scientific and common names) on the peninsula study area in Fall River Valley, Shasta County, California. Surveys were conducted on 15 August 1989 and in early September 1990–1992. Nomenclature follows Hickman (1993). Absence in the *Crypsis* (C), *Distichlis* (D) and *Elytrigia* (E) zones is indicated by a dash. Presence in the *Crypsis, Distichlis,* and *Elytrigia* zones is indicated by an "H" if relative abundance in any block was >5%, by an "M" if relative abundance in any block was at most 2%–5%, and by an "L" if relative abundance in any block was always <2%. Status indicates whether the species is native (N) or introduced (I).

			Zone			
Scientific name	Acronym	Common name	C	D	E	Status
Euphorbiaceae						
Euphorbia spp.	EUSP	spurge	H	M	—	N
Alismataceae						
Sagittaria cuneata E. Sheldon		arrowhead	—	—	—	N
Juncaceae						
Juncus balticus Willd.	JUBA	rush	M	L	L	N
Cyperaceae						
Eleocharis macrostachya Britton	ELPA	spikerush	H	M	M	N
Scirpus pungens Vahl		common three square	—	—	—	N
Scirpus maritimus L. var. *plaudosus* (Nelson) Kük	SCMA	alkali bulrush	M	L	—	N
Poaceae						
Agropyron desertorum (Fischer) Schultes		crested wheatgrass	—	—	—	I
Agrostis gigantea Roth OR *stolonifera* L.		redtop	—	—	—	I
Bromus inermis Leysser		smooth brome	—	—	—	I
Bromus secalinus L.		chess or cheat	—	—	—	I
Bromus tectorum L.		cheatgrass	—	—	—	I
Crypsis shoenoides (L.) Lam.	CRSC	swamp timothy	H	H	H	I
Distichlis spicata (L.) E. Greene var. *stricta* (Torrey) Beetle	DISP	saltgrass	H	H	H	N
Echinochloa crus-galii (L.) P. Beauv.		watergrass	—	—	—	N
Elymus x *macounii* Vassey		Macoun's wildrye	—	—	—	N
Elymus trachycaulus (Link) Shinn.		bearded wheatgrass	—	—	—	N
Elytrigia pontica (Podp.) Holub		tall wheatgrass	—	—	—	I
Elytrigia repens (L.) Nevski	AGRE	quackgrass	—	L	H	I
Hordeum jubatum L.	HOJU	foxtail barley	H	H	H	N
Leymus cinereus (Schribner &Merr.) A. Löve		Great Basin wildrye	—	—	—	N
Panicum capillare L.	PACA	panic grass	H	H	H	N
Phalaris arundinacea L.	PHAR	reed canarygrass	M	M	H	I
Phleum pratense L.		timothy	—	—	—	I
Poa sp.		bluegrass	—	—	—	
Polypogon monspeliensis (L.) Desf.	POMO	rabbitfoot grass	—	L	L	I
Boraginaceae						
Heliotropium curassavicum L.	HECU	heliotrope	L	L	—	N
Chenopodiaceae						
Chenopodium album L.	CHAL	lamb's quarters	H	H	M	I
Asteraceae						
Bidens cernua L.		bur marigold	—	—	—	N
Lactuca serriola L.	LASE	prickly lettuce	—	L	H	I
Convolvulaceae						
Convolvulus sp.		morning glory	—	—	—	
Fabaceae						
Lotus corniculatus L.		birds-foot trefoil	—	—	—	I
Medicago lupulina L.		black medick	—	—	—	I
Trifolium sp.		clover	—	—	—	
Polygonaceae						
Polygonum douglasii E. Greene	PODO	smartweed	H	L	—	I
Rumex crispus L.		curly dock	—	—	—	I
Rosaceae						
Potentilla anserina L. var. *anserina*	POAN	silverweed	H	H	M	N

the higher, drier ground further to the west, *H. jubatum* was interspersed with *E. repens* and with dense low-lying *D. spicata.*

Plant relative abundance was estimated in early September 1990–1992 using a point-intercept method (Mueller-Dombois and Ellenberg 1974). Points were arranged every 2.7 m along 2 randomly selected transects in each of 8 experimental blocks (see below). Transects were parallel and ran the length of each block (approximately 460 m). The same blocks were used across years, but in each year we established a new set of transects; thus, points were independently established within blocks across years. At each point, a sharpened rod (2 mm diameter) was dropped vertically, and species of the plant hit by the rod was recorded. We used a ruler to measure vegetation height every 10.8 m along the same transects. We also measured vegetation height the day after the 2 prescribed burns.

BURNING TREATMENT AND EXPERIMENTAL DESIGN.—We conducted prescribed burning on 3 December 1990 and on 25 November 1991. Burning was timed so that plants were senescent and the residual vegetation was relatively dry. Four burned and 4 unburned blocks were alternately arranged side by side on the peninsula (Fig. 1). Each block was rectangular (50 × 460 m) and averaged 2.3 ha (range 1.9–2.7 ha). The experimental blocks traversed the moisture and vegetation gradients that were correlated with microtopographical elevation changes (generally lower to the east; Fig. 1). We used this experimental design, associated measurements of plant relative abundance, and the statistical analysis described below to determine the relative importance of burning compared to other abiotic factors such as moisture and salinity-alkalinity gradients.

USE OF EXPERIMENTAL BLOCKS BY GEESE.—We monitored use of the experimental blocks by 2 species of herbivorous waterfowl (Cackling Goose, *Branta canadensis minima* Ridgway, and Pacific Greater White-fronted Goose, *Anser albifrons frontalis* Baird) from dawn until dusk on 67 days between 15 February and 28 April 1992. When we observed geese, we used scan sampling (Altmann 1974) conducted every 20 minutes to record the number and behavior (feeding or not feeding) of each individual on burned and unburned blocks. All observations were recorded using a 20X–60X spotting scope from a blind located on the levee just east of the experimental blocks (Fig. 1).

Statistical Analyses

We used repeated measures ANOVA to evaluate annual changes in species diversity, species richness (number of species), and the proportion of native versus introduced plant species in burned and unburned blocks within each vegetation zone. We used Simpson's index of species diversity,

$$D = (\sum P_i^2)^{-1}$$

where P_i is the proportion of total hits along 2 transects for species i and the summation is across all plant species (Simpson 1949). The repeated variable was block (resampled each year), and the crossed variable was vegetation zone.

We used ordination and gradient analysis, specifically correspondence analysis (indirect gradient) and canonical correspondence analysis (direct gradient; CANOCO 1989, Microcomputer Power, Cornell University, Ithaca, NY), and multiway contingency table analysis (Biomedical Computer Programs P series; BMDP 1992) to evaluate annual changes in relative abundance of plant species and how burning interacted with these annual changes. The total number of hits per block for each plant species was used as the dependent variable, which emphasizes proportions (i.e., relative abundance) of each species. The use of correspondence and canonical correspondence analyses is well established in studies such as ours (ter Braak and Prentice 1988, Palmer 1993). To preserve sufficient statistical power, we used only the 8 most common species in the contingency table analysis. For CANOCO analyses, we included only the 16 most common species (Table 1). We verified that all necessary assumptions of correspondence and CANOCO analyses were satisfied (Zar 1999).

Effects of burning were detected in the multiway contingency tables as significant interactions between treatment (T; burned or unburned) and plant species (S), vegetation zone (Z), or year (Y). We present results on the 5 most common species for which we had the most confidence in interpreting the table results. We included vegetation zone (3 categories: *Crypsis, Distichlis, Elytrigia*) as an independent variable in the model because our subjective observations and the ordination analysis clearly identified a moisture-related gradient associated with these zones. Including vegetation zone in the model enabled us to detect interactions between the effects of treatment and vegetation zone on relative density of a plant species.

As per multiway contingency table notation, if there was no interaction between 2 variables (e.g., treatment and vegetation zone) we denoted it by separating their symbols with a comma (T,Z), whereas if there was an interaction we denoted it by a lack of a comma (TZ). In multiway contingency table analysis, data are "fit" to certain models that differ in complexity. The saturated model, by definition, always fits the data best ($P = 1.0$). The goal is to find the simplest model that fits ($P > 0.05$) the data but that is not significantly different from more complex models that also fit the data (Fienberg 1970, Jenkins 1975), following the principle of parsimony. Once the simplest model was determined, we used the methods of Toft (1984a, 1984b) to determine the exact source of a particular significant interaction. In short, this method involves fitting an appropriate null model or models to the data and then examining calculated standardized deviates (i.e., dimensionless, weighted deviations from expected values). The appropriate null model is the same as the simplest model except that the 1 interaction of interest is removed.

We used the goodness-of-fit test with Yates' correction for continuity (Zar 1999) to evaluate use of burned and unburned experimental blocks by foraging geese.

RESULTS

Precipitation, Temperature, and Water Levels

Growing season (March–September) precipitation was less in 1991 than in 1990 and 1992 (Fig. 2A). In 1990, precipitation was greatest during March and especially high in May (Fig. 2A). Mean high and low temperatures for a given month were similar in 1990, 1991, and 1992 (Fig. 2B).

Flooding during spring was more extensive in 1991 than in 1992. In early March 1991, standing water covered 100% of both the *Crypsis* and *Distichlis* zones and 20% of the *Elytrigia* zone, whereas in 1992 standing water covered 100% of only the *Crypsis* zone, 50% of the *Distichlis* zone, and none of the *Elytrigia* zone. By early April 1991, standing water covered 65% of the *Crypsis* zone and none of the *Distichlis* or *Elytrigia* zones, whereas in 1992 there was no standing water on the study area.

Zonation of Vegetation

Vegetation on the study area was dominated by grasses, sedges, and rushes (Table 1). In 1990, prior to any burning, the 3 vegetation zones that were identified *a priori* in the study design were confirmed by the indirect gradient analysis (Fig. 3): (1) *Elytrigia* zone where *E. repens* was associated with *H. jubatum, P. arundinaceae,* and *Lactuca seriola;* (2) *Distichlis* zone where *D. spicata* was the predominant species; and (3) *Crypsis* zone where *C. shoenoides* was associated with *Panicum capillare, Chenopodium album,* and other less abundant species. In addition, each sampling point in an experimental block was assigned to a vegetation zone. This resulted in 8 sites (1 per experimental block) for each vegetation zone that were identified *a priori* in the study design. The 8 sites designated to each vegetation zone were distinctly clustered on the ordination near the plant species associated with that vegetation zone (Fig. 3), demonstrating that the vegetation zones were unambiguous and not arbitrary.

The 1st axis of the unconstrained ordination represented the obvious moisture gradient on the study area, from wet (*Crypsis* zone) with positive values on axis 1, to intermediate (*Distichlis* zone), to dry (*Elytrigia* zone) with negative values on axis 1 (Fig. 3). By definition, axis 1 explains the most variation in occurrence of species in the ordination; in 1990 it explained 41% of the variation (Table 2A). The 2nd axis explained an additional 25% of the variation and, given the position of *D. spicata* (saltgrass) on 1 end of the continuum, this axis appeared to represent a salinity-alkalinity gradient. Axes 3 and 4 represented residual variation.

Efficacy of Burning

Burning in the fall effectively reduced the standing biomass of vegetation as indicated by vegetation height before (measured on 8 September 1990 and 31 August 1991) and just after (measured on 3 December 1990 and 25 November 1991) each burn (repeated measures ANOVA, year effect: $F_{1,\,12} = 0.8$, $P = 0.386$;

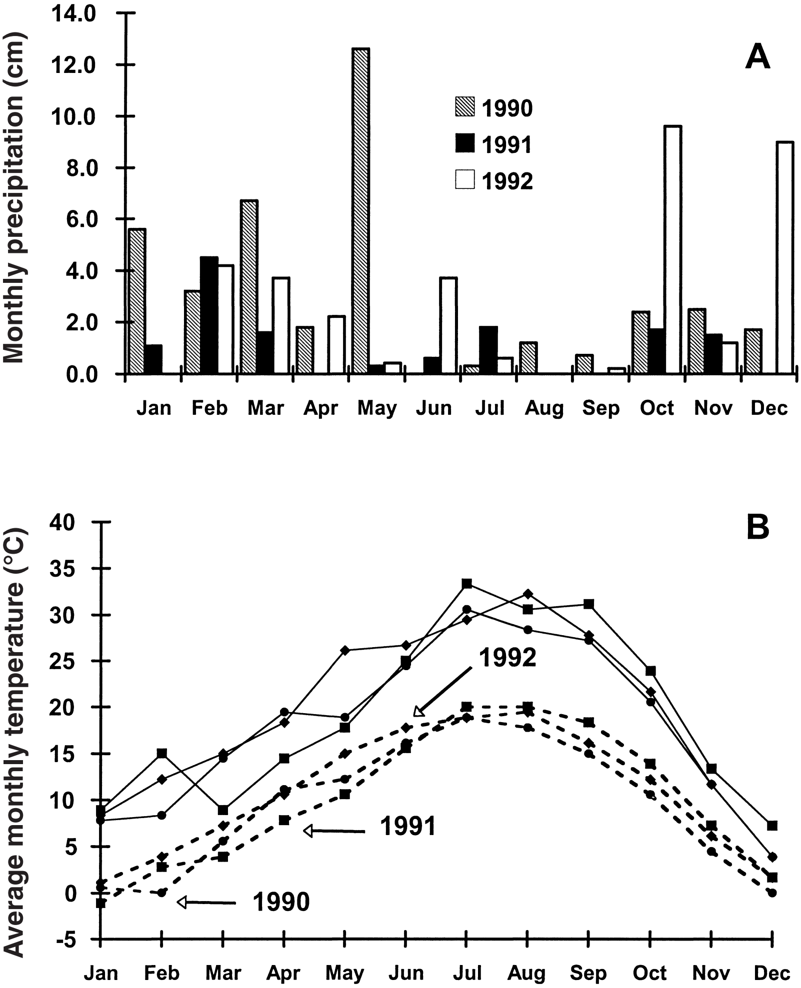

Fig. 2. Total monthly precipitation (cm) and monthly average high (solid line) and low (dashed line) temperature (°C) during 1990, 1991, and 1992 in Fall River Valley, Shasta County, California.

treatment effect: $F_{1, 12} = 24.1$, $P < 0.0001$). Vegetation height in burned plots was reduced from 25.0 ± 1.7 cm to 8.2 ± 0.6 cm in 1990, and from 31.7 ± 1.0 cm to 5.3 ± 0.7 cm in 1991, while vegetation height in unburned plots changed relatively less (24.3 ± 1.4 cm to 19.2 ± 1.4 cm in 1990, and 23.0 ± 1.5 cm to 19.6 ± 0.6 cm in 1991). The prescribed burn in fall 1991 reduced residual vegetation more than the burn in fall 1990 (year × time effect: $F_{1, 12} = 5.4$, $P = 0.04$; treatment × time: $F_{1, 12} = 104.2$, $P < 0.0001$). Burning was uniform across the blocks, as indicated by the relatively small range in vegetation height after burning (7.0–9.8 cm in 1990, 3.6–7.0 cm in 1991).

Effects of Burning on Attributes of the Plant Community

Although more species occurred in the *Distichlis* zone (Fig. 4A; zone effect: $F_{2, 18} = 9.7$, $P = 0.001$), the dominance of 1 species, *D. spicata,* resulted in the *Distichlis* zone having the lowest diversity index for all zones (Fig. 4B). Species diversity was highest in the *Crypsis* zone (Fig. 4B; zone effect: $F_{2, 18} = 16.3$, $P < 0.001$), reflecting more equitable relative abundance of species there. Both richness and diversity of species were highest in 1991 (year effect, richness: $F_{2, 36} = 26.3$, $P < 0.0001$; year effect, diversity: $F_{2, 36} = 29.6$; $P < 0.0001$), although the pattern of annual change in species

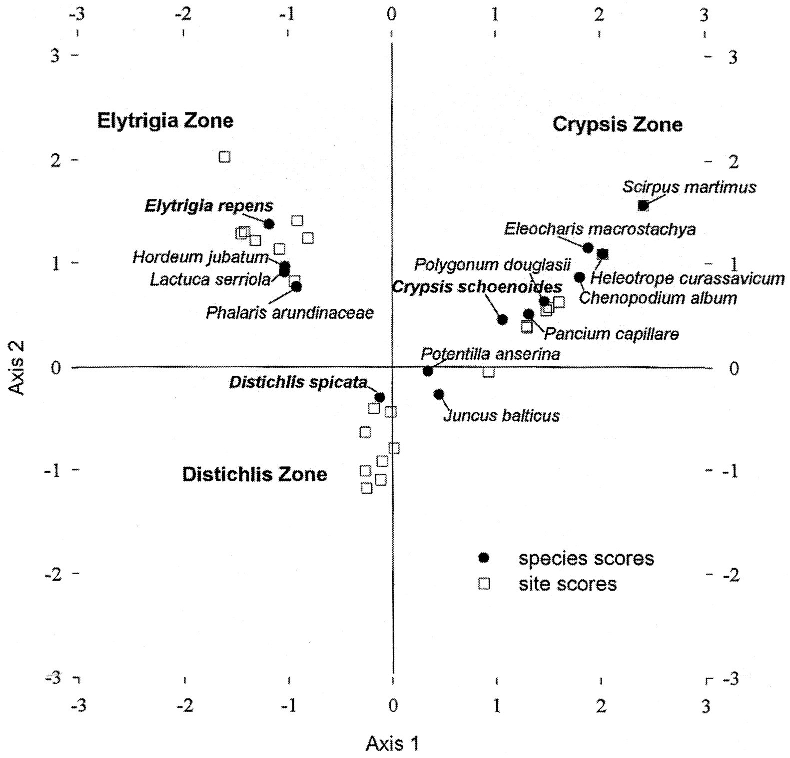

Fig. 3. Ordination of plant species in 1990, prior to prescribed burning, by correspondence analysis. In this analysis species or site positions are unconstrained by data on environmental variables. Scores on the 2 axes for plant species are filled circles and scores for the 8 sites in each zone are open squares. Key species for each of the 3 identifiable vegetation zones are in boldface type.

richness and diversity depended on the vegetation zone (year × zone interaction, richness: $F_{4,36} = 4.2$; $P = 0.007$; year × zone interaction, diversity: $F_{4,36} = 9.5$, $P < 0.0001$). About 50% more species occurred in all 3 vegetation zones in 1991 than in 1990 (Fig. 4A). Higher species richness was maintained in the *Crypsis* and *Distichlis* zones in 1992, but species richness declined in the *Elytrigia* zone in 1992. In 1991, species diversity increased by about 50% in the *Crypsis* and *Distichlis* zones but increased only slightly in the *Elytrigia* zone (Fig. 4B). In 1992, species diversity declined in all 3 vegetation zones.

Burning had no significant effect on species richness (treatment effect: $F_{1,18} = 0.1$, $P = 0.759$; year × treatment interaction: $F_{2,36} = 1.1$, $P = 0.358$; year × treatment × zone interaction: $F_{4,36} = 0.5$; $P = 0.767$; Fig. 4A) or on the proportion of native versus introduced plant species (treatment effect: $F_{1,18} = 0.6$, $P = 0.454$; year × treatment interaction: $F_{2,36} = 0.4$, $P = 0.665$; year × treatment × zone interaction: $F_{4,36} = 1.4$, $P = 0.243$). Burning had a significant effect on species diversity (Fig. 4B), although the increase in species diversity associated with burning was more apparent in 1991 than in 1992 (treatment effect: $F_{1,18} = 0.8$, $P = 0.377$; year × treatment interaction: $F_{2,36} = 4.3$, P = 0.02; year × treatment × zone interaction: $F_{4,36} = 1.5$, $P = 0.237$).

To examine how much variation was explained by the effects of burning, we constrained the ordination with 1 environmental variable, the burn treatment, using canonical correspondence analysis. In this direct gradient analysis, axis 1 discriminated between burned and unburned sites (Fig. 5, Table 2B). As expected, in 1990 prior to the prescribed burning, axis 1 explained little (0.6%) of the variation in plant species (Table 2B), and most species were close to 0 on axis 1 (Fig. 5A). In this direct gradient analysis, only axis 1 was constrained by us to show the effects of the

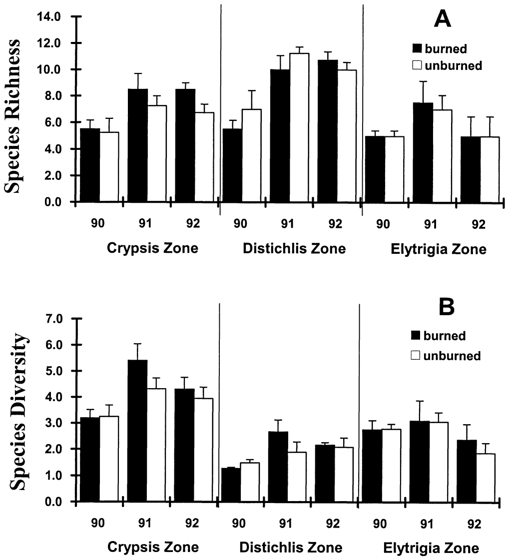

Fig. 4. Plant species richness (A) and diversity (B) in burned and unburned experimental blocks within 3 vegetation zones during 1990–1992 in Fall River Valley, Shasta County, California. Species richness and diversity of plants in 1990 were measured prior to prescribed burning.

burn treatment. Axes 2 to 4 were unconstrained and, as before, were ordered by the degree to which they explained variation in plant species abundance. Thus, axis 2 represented the moisture gradient (compare with axis 1 in Fig. 3); axis 3 represented the proposed salinity-alkalinity gradient (compare with axis 2 in Fig. 3); and axis 4 contained the residual variation (Table 2B).

Plant species increasingly diverged along axis 1 after 1 year (Fig. 5B) and 2 years (Fig. 5C) of burning, suggesting that some species were inhibited (positive values on axis 1) and others were promoted (negative values on axis 1) by burning (compare Figs. 5 and 6). After each year of burning, more variation in plant species

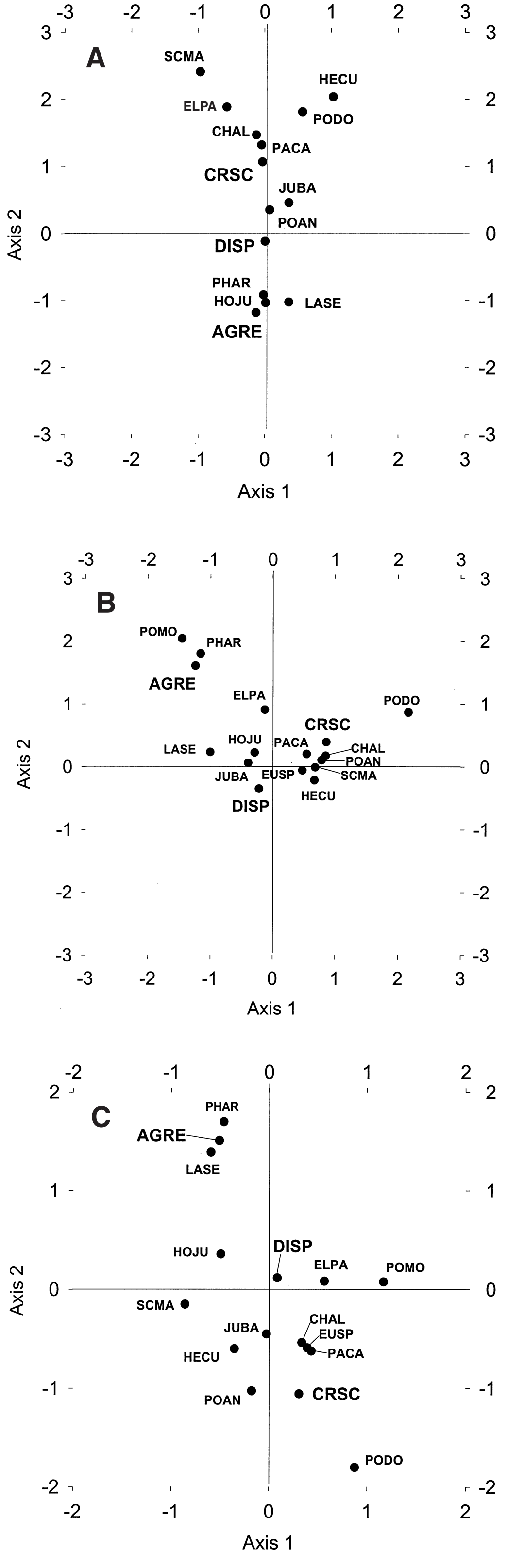

Fig. 5. A, Ordination of plant species in 1990, prior to burning. Axis 1 is constrained by burn treatment; axis 2 is unconstrained and represents the moisture gradient. B, Ordination of plant species in 1991, after 1 burn treatment on 3 December 1990. Axis 1 is constrained by burn treatment; axis 2 is unconstrained and represents the moisture gradient. C, Ordination of plant species in 1992, after a 2nd burn treatment on 25 November 1992. Axis 1 is constrained by burn treatment (see text); axis 2 is unconstrained and represents the moisture gradient. Four-letter acronyms for each plant species are defined in Table 1. Key species for each of the 3 identifiable vegetation zones are in boldface type.

TABLE 2. Summary of indirect (A) and direct (B) gradient analyses. The sum of eigenvalues, the species-burn treatment correlation, and the cumulative percentage of variation in plant species explained by each axis provide different measures of the explanatory power of the ordination. In the indirect gradient analysis, in which all axes are unconstrained, axis 1 represents the moisture gradient and axis 2 represents a salinity-alkalinity gradient; axes 3 and 4 measure residual variation. In the direct gradient analysis, axis 1 is constrained by burn treatment and the remaining axes are unconstrained; axis 2 represents the moisture gradient, axis 3 represents a salinity-alkalinity gradient, and axis 4 measures residual variation.

			Cumulative percent variation			
Year	Sum of eigenvalues	Species–burn correlation	Axis 1	Axis 2	Axis 3	Axis 4
A. Indirect gradient analysis (unconstrained)						
1990	0.912	—	41.4	66.1	77.9	85.3
1991	0.796	—	38.8	68.9	78.3	84.4
1992	0.841	—	39.4	65.9	77.3	83.8
B. Direct gradient analysis (constrained by burn treatment)						
1990	0.912	0.279	0.6	42.0	66.7	78.5
1991	0.794	0.595	4.9	43.9	73.0	79.7
1992	0.830	0.630	9.9	45.8	72.4	79.5

was explained by the effect of burning, increasing to 5% in 1991 and to 10% in 1992; and the species-burn treatment correlation increased notably (Table 2B). However, the moisture gradient represented by axis 2 remained the most important environmental factor even after 1 and 2 years of burning (Fig. 5). This ordination analysis of species-specific responses also suggests that the effect of burning depended on vegetation zone (representing the moisture gradient), in that the species diverged in the 2-dimensional ordination along a diagonal (compare Figs. 5A and 5C).

Effect of Burning on Individual Plant Species

The relative abundance of plant species within each of the 3 vegetation zones changed across years in both burned and unburned blocks (Fig. 6). We assessed the relationship between the species-specific effects of burning and the moisture gradient using multiway contingency table analysis.

The effects of burning on abundance of the 8 most common plant species differed among species, and interacted with vegetation zone (reflecting the moisture gradient) and year (Fig. 6). The 4-dimensional model (dependent variable = number of hits * burn treatment [T] * species [S] * zone [Z] * year [Y]) was the only model that fit the data (χ^2 [likelihood ratio chi-square] = 0.0, $P = 1.0$). However, the χ^2 value for fitting the next-less-complex model of all possible 3-way interactions (model: (YTZ,STZ,SYZ,SYT), $\chi^2 = 74.5$, df = 21, $P < 0.00001$) was relatively small (χ^2 values for models containing only the much simpler 2- and 1-dimensional effects were greater than 4500) suggesting that the additional information provided by the 4th-order interaction was not great.

Given that the 4-way interaction was relatively uninformative, we analyzed key-component 3-way models, decomposing the 4-way model along certain dimensions. We first analyzed years separately while including the species effect [S]. As expected, the [STZ] model was the simplest model that fit the data in all years. Prior to the prescribed burn in 1990, the treatment effect [T] alone was not significant ($\chi^2 = 1.96$, $P = 0.16$), nor was the species-treatment interaction ($\chi^2 = 2.45$, $P = 0.94$). The [SZ] interaction was the strongest effect ($\chi^2 = 804.2$, $P << 0.0000$), which meant that the zones differed in species composition. These results supported the study design (i.e., no treatment effect overall before the treatments began) and the ordination results above (Fig. 3). In 1990, the 3-way [STZ] model was the simplest, best-fit model because of a slight treatment-zone interaction ($\chi^2 = 14.7$, $P = 0.0007$). Thus, there was a pretreatment difference in plant density in the blocks designated for burning versus the control blocks that depended on the zone. This pretreatment bias was also evident in the ordination and will be discussed below under the individual species that contributed to it. Finally, by 1992 the treatment effect was much stronger and statistically significant ($\chi^2 = 98.5$, $P < 0.0000$). Thus, burning had a measurable effect on the plant community in all zones.

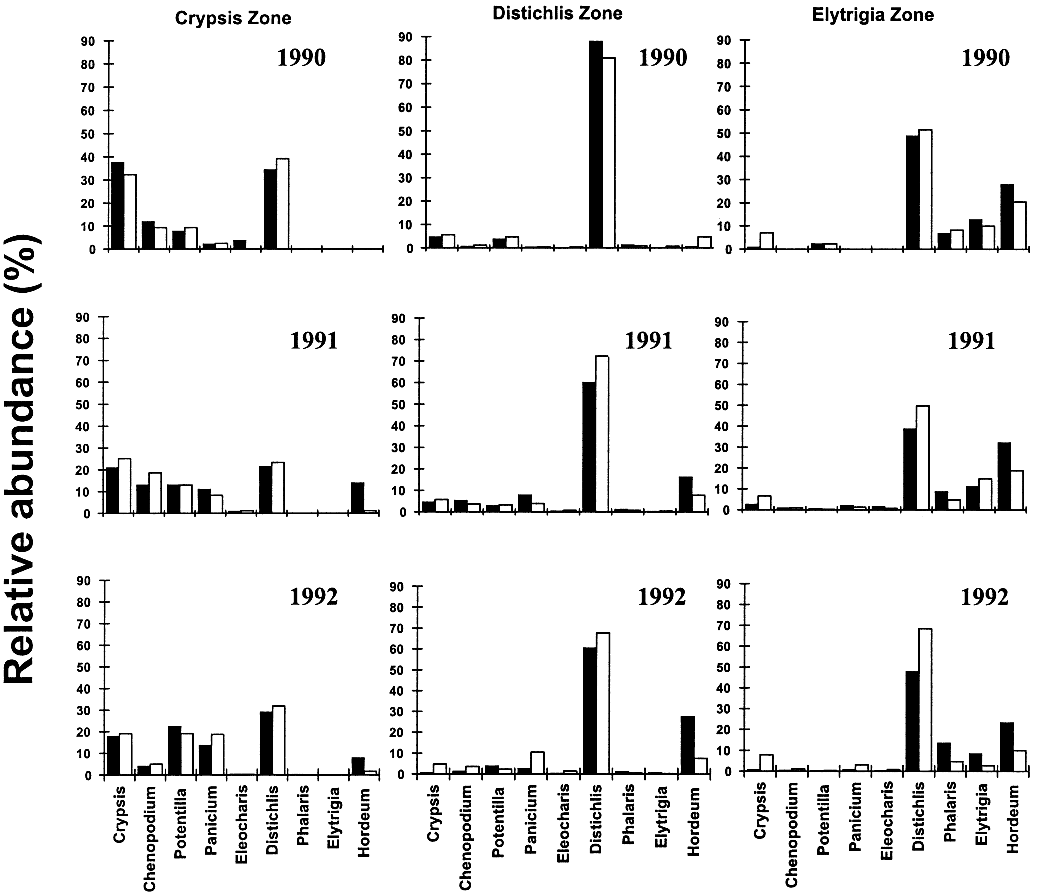

Fig. 6. Relative abundance of all plant species in burned (dark-shaded bars) and unburned (unshaded bars) experimental blocks within 3 vegetation zones during 1990–1992 in Fall River Valley, Shasta County, California. Relative abundance of plants in 1990 was measured prior to prescribed burning.

Next we analyzed the 3-way tables by species (Table 3), interpreting and expanding on patterns evident in Fig. 6. To determine how the effect of burning differed by vegetation zone and year, we examined departures from 2 null models: (1) departures from the null model [TY,ZY] indicate how the effect of burning differed by vegetation zone (i.e, [TZ] effect missing; Table 4), whereas (2) departures from the null model [TZ,ZY] indicate how the effect of burning differed by year (i.e., [TY] effect missing; Table 5). We interpreted these results, by species, as follows:

DISTICHLIS SPICATA.—*D. spicata* was common throughout the study area (Fig. 6), but its relative abundance was greatest in the *Distichlis* zone (by definition), which was intermediate on the moisture gradient (Fig. 5). Before the burn treatment in 1990, *D. spicata* was more abundant than expected in the to-be-burned sites in the *Distichlis* zone (Fig. 6, Table 5). After the initial burn treatment in 1991, *D. spicata* was less abundant than expected in the burned blocks than it was in the unburned blocks (Fig. 6, Table 5) when spring flooding was extensive. The negative effect of burning on *D. spicata* in the *Distichlis* zone in 1991 was not as obvious after the 2nd burning in 1992 (Fig. 6, Table 5). In 1991, the abundance of *D. spicata* showed the strongest differences among zones (Table 4), probably indicating the sensitivity of this species to the joint effects of burning and the flooding regimen that year.

HORDEUM JUBATUM.—At the start of the study in 1990, *H. jubatum* was rare in all but the *Elytrigia* zone, where it was relatively more

TABLE 3. All possible partial associations from fitting the fully saturated 3-factor model separately for each of 5 plant species in unburned and burned plots (n = 4) in Fall River Valley, California. S = plant species (see description in Results); Y = year (1990, 1991, 1992); T = treatment (burned or unburned); Z = vegetation zone (*Crypsis, Distichlis, Elytrigia*).

		Distichlis		*Hordeum*		*Crypsis*		*Phalaris*		*Elytrigia*	
Effect	df	χ^2	*P*-value	χ^2	*P*-value	χ^2	*P*-value	χ^2	*P*-value	χ^2	*P*-value
T	1	1.74	0.1874	340.8	0.0000	0.1	0.7131	34.2	0.0000	5.4	0.0199
Z	2	4511.0	0.0000	631.5	0.0000	0.3	0.5953	39.3	0.0000	153.1	0.0000
Y	2	484.4	0.0000	501.1	0.0000	4.1	0.1279	22.9	0.0000	45.1	0.0000
TZ	2	28.4	0.0000	40.3	0.0000	0.6	0.4556	0.9	0.3444	2.1	0.1503
TY	2	44.6	0.0000	66.8	0.0000	15.9	0.0004	11.1	0.0039	22.3	0.0000
YZ	4	6.2	0.1819	241.0	0.0000	298.9	0.0000	0.01	0.9953	10.1	0.0065
TZY	4	15.3	0.0040	33.8	0.0000	16.5	0.0003	0.6	0.7564	2.1	0.3572

TABLE 4. Environmental variation in the effects of burning on the 5 most common species in the wetland community in Fall River Valley, California. Standardized deviates [(observed – expected) ÷ √expected] from a multiway contingency table analysis that tests for the [TZ] effect (i.e., null model [TY, ZY]) in burned and unburned plots (n = 4). Large standardized deviates indicate strong effects of the 1 interaction that was removed, and the sign (+ or –) of the deviate indicates whether the observed values are greater than or less than the expected values from the null model. Two plant species (*Phalaris arundinacea* and *Elytrigia repens*) were absent from the *Crypsis* vegetation zone.

		Distichlis		*Hordeum*		*Crypsis*		*Phalaris*		*Elytrigia*	
Year	Vegetation zone	unburned	burned	unburned	burned	unburned	burned	unburned	burned	unburned	burned
1990	*Crypsis*	–0.5	+0.5	0	0	–1.4	+1.3	—	—	—	—
	Distichlis	+0.5	–0.5	+3.2	–3.1	+1.0	–1.0	–0.1	+0.1	+1.3	–1.1
	Elytrigia	–0.7	+0.7	–1.8	+1.8	+2.1	–2.0	+0.1	0	–0.4	+0.4
1991	*Crypsis*	–3.4	+3.8	–4.4	+2.9	–2.0	+2.0	—	—	—	—
	Distichlis	+1.8	–2.0	+1.9	–1.3	+1.6	–1.6	+0.8	–0.5	+0.6	–0.6
	Elytrigia	–1.4	+1.6	+0.4	–0.2	+1.5	–1.5	–0.5	+0.3	–0.2	+0.2
1992	*Crypsis*	–1.3	+1.3	–1.0	+0.5	–2.8	+3.3	—	—	—	—
	Distichlis	+0.3	–0.3	–0.1	+0.1	+2.9	–3.4	+0.4	–0.2	–0.1	0
	Elytrigia	+0.4	–0.4	+0.9	–0.4	+1.9	–2.2	–0.2	+0.1	0	0

TABLE 5. Yearly variation in the effects of burning on the 5 most common species in the wetland community in Fall River Valley, California. Standardized deviates [(observed – expected) ÷ √expected] from a multiway contingency table analysis that tests for the [TY] effect (i.e., null model [TZ,ZY]) in unburned and burned plots (n = 4). Large standardized deviates indicate strong effects of the 1 interaction that was removed, and the sign (+ or –) of the deviate indicates whether the observed values are greater than or less than the expected values from the null model. Two plant species (*Phalaris arundinacea* and *Elytrigia repens*) were absent from the *Crypsis* vegetation zone.

		Distichlis		*Hordeum*		*Crypsis*		*Phalaris*		*Elytrigia*	
Year	Vegetation zone	unburned	burned	unburned	burned	unburned	burned	unburned	burned	unburned	burned
1990	*Crypsis*	+0.9	–0.7	0	0	–0.2	+0.2	—	—	—	—
	Distichlis	–1.0	+1.1	+6.6	–4.0	–0.9	+1.2	+0.7	–0.5	+1.1	–1.0
	Elytrigia	–0.7	+0.7	+1.1	–0.7	+0.4	–0.7	+2.0	–1.3	–0.4	+0.4
1991	*Crypsis*	–0.6	+0.5	–0.8	+0.2	+0.2	–0.1	—	—	—	—
	Distichlis	+3.9	–4.1	+3.3	–2.0	–0.8	+1.1	+0.6	–0.4	+0.9	–0.8
	Elytrigia	+0.6	–0.6	+0.5	–0.3	–0.7	+1.2	+0.2	–0.1	+1.7	–1.4
1992	*Crypsis*	–0.1	+0.1	+1.2	–0.3	0	0	—	—	—	—
	Distichlis	–3.2	+3.4	–4.1	+2.5	+1.9	–2.7	–1.1	+0.8	–1.5	+1.4
	Elytrigia	–0.1	+0.1	–1.7	+1.1	+0.6	–1.0	–1.5	+1.0	–2.4	+2.0

abundant in the to-be-burned blocks (Fig. 6, Table 4). After the burn treatments, *H. jubatum* was more abundant than expected in the burned blocks than it was in the unburned blocks in the *Crypsis* zone in 1991 and 1992. Moreover its abundance in the *Elytrigia* zone and especially in the *Distichlis* zone increased notably in the burned blocks in 1992 (Fig. 6, Tables 4, 5). Thus, burning generally enhanced the abundance of *H. jubatum,* although the strong [YZ] interaction (Table 3) indicated that the strength of the burning effect depended on the vegetation zone and year.

CRYPSIS SHOENOIDES.—This species was relatively rare in all but the *Crypsis* zone (Fig. 6), which was wettest on the moisture gradient. Before the burn treatment in 1990, *C. shoenoides* was slightly more abundant than expected in the to-be-burned sites in the *Crypsis* zone, and less abundant in the to-be-burned blocks in the *Distichlis* zone and especially in the *Elytrigia* zone (Fig. 6, Table 4). *Crypsis shoenoides* was suppressed by burning in the drier *Distichlis* and *Elytrigia* zones, especially in 1992, although burning did not suppress *C. shoenoides* as much in the *Crypsis* zone (Fig. 6, Tables 3, 4, 5). Thus, the abundance of *C. shoenoides* was generally suppressed by burning, although the strong [YZ] interaction (Table 3) indicated that the strength of the burning effect depended on the vegetation zone and year.

ELYTRIGIA REPENS AND *PHALARIS ARUNDINACEAE.*—These species were relatively rare overall, and absent from the *Crypsis* zone (Fig. 6). Before the burn treatment in 1990, *P. arundinaceae* was less abundant in the to-be-burned sites in the *Distichlis* and *Elytrigia* zones, while *E. repens* was less abundant in the to-be-burned sites in the *Distichlis* zone, but not the *Elytrigia* zone (Fig. 6, Tables 4, 5). After the 1st burn treatment, *P. arundinaceae* and especially *E. repens* were less abundant than expected in the burned blocks than they were in the unburned blocks in 1991 (Fig. 6, Tables 4 and 5) when spring flooding was more extensive. In 1992, both *E. repens* and *P. arundinaceae* were more abundant than expected in the burned than in the unburned blocks in the *Distichlis* and *Elytrigia* zones (Fig. 6, Table 5). For both *E. repens* and *P. arundinaceae,* the treatment-by-year interactions [TY] were the strongest of the 3 possible 2-way interactions (Table 3).

Effect of Burning on Numbers and Behavior of Geese

Cackling Geese were observed using the peninsula (Fig. 1) on 1 of 67 observation days. On 23 March, 30 Cackling Geese fed for less than 30 minutes in the southern tip of the peninsula and were never close to the experimental blocks. White-fronted Geese were observed using the peninsula on 10 of 67 observation days. On 4 of the 10 days (1 April, 3 April, 10 April, and 17 April), White-fronted Geese were observed using the experimental blocks. On 10 April, 2 geese were present from 1100 hours to 1130 hours, and on 17 April, 6 geese were present from 0740 hours to 1030 hours. On 1 and 3 April, 15–45 geese were present on the experimental blocks from 0730 hours to 1800 hours; most of this time the geese were resting on the flooded portion of the blocks. After 1600 hours on both 1 April and 3 April, the geese began feeding in the experimental blocks. During these evening feeding periods on 1 April and 3 April, more geese were observed in burned blocks (19.8 and 31.5 geese, respectively) than in unburned blocks (1.3 and 1.0 geese, respectively; significant treatment effect on each day, $P < 0.001$), and geese fed only when they were in burned blocks (7.8 feeding geese per scan on 1 April, 11.0 feeding geese per scan on 3 April; no feeding geese on either day in unburned blocks; significant treatment effect on each day, $P < 0.025$).

DISCUSSION

Wetland Plant Communities and the Relative Importance of Fire

We found that burning explained, at most, 10% of the total variation in plant species. The moisture and salinity-alkalinity gradients explained the majority (>60%) of the total variation in plant species. Not surprisingly, management of wetlands typically involves manipulating water levels because it so strongly influences the plant community (Smith et al. 1989, Weller 1994). It does not follow, however, that prescribed burning has an inconsequential effect on wetland plant communities. Instead, our results show that the effects of prescribed burning, like the effects of many other management activities, are often contingent on interactions with other important ecological factors. Below we consider interactions between 3 important ecological factors (burning, moisture, and salinity) as we evaluate the 3 hypotheses initially posed in this study.

Effects of Burning on Attributes of the Plant Community: Does Burning Increase Plant Diversity and Richness, and the Proportion of Native Plant Species?

Species diversity and species richness of plant communities that are infrequently burned typically peak soon after fire and then decline as the community ages (Whelan 1995, Bond and van Wilgren 1996). In one of the few long-term studies that focused on the effects of fire frequency on diversity and richness of wetland plant communities, species diversity declined with fire frequency (from 2.77 in sites burned at 20-year intervals to 1.64 in annually burned sites) in *Spartina* wetlands in northeastern Kansas (Johnson and Knapp 1995). Most studies of the short-term effects of burning on wetland communities show that burning enhances plant diversity and richness (Schmalzer et al. 1991, Cowie et al. 1992, de Szalay and Resh 1997).

In the wet meadow plant community that we studied over 3 years, burning had no effect on species richness, but burning increased plant species diversity especially in the 2 wetter vegetation zones (*Distichlis* and *Crypsis* zones). The increase in plant species diversity was not associated with an increase in the proportion of native versus introduced plant species. Rather, the increase in plant species diversity was caused primarily by a decrease in relative abundance of common native species (e.g., *D. spicata*) and introduced species (e.g., *C. shoenoides*) and an increase in relative abundance of less common native species (e.g., *H. jubatum, Panicum capillare*) and introduced species (e.g., *Chenopodium album*). Thus, natural disturbances such as fire may increase plant species diversity, but not necessarily the diversity of native plant species.

Burning may initially enhance species richness and diversity in wetlands because it produces bare ground, which provides microhabitat for seedling recruitment (Van der Valk 1986), or because the wetlands are dominated by perennial rhizomatious species that resprout readily after fire (Schmalzer et al. 1991). Also, burning may be necessary for the persistence of rare, native, fugitive species in these systems (Kirkman and Sharitz 1994, Pendergrass et al. 1999). Determining which processes are most important in structuring wetland plant communities that are burned requires an understanding of how individual plant species respond to burning.

Effect of Burning on Individual Plant Species

The Clementsian view of an orderly, predictable pattern of succession following disturbance (see Pickett et al. 1987, Luken 1990, Glenn-Lewin et al. 1992) has been applied to post-fire succession (e.g., Phillips 1934, 1935a, 1935b) but has proven generally inadequate, primarily because relative competitive ability often poorly predicts observed changes in plant communities after fire (Bond and van Wilgren 1996). Fire ecologists instead emphasize the interplay between disturbance frequency, species-specific mechanisms of persistence during a disturbance, ability to establish after a disturbance, and the timing of both disturbance events and key life history variables such as time to reproductive maturity and life span (Noble and Slatyer 1980, Bond and van Wilgren 1996, Menges and Hawkes 1998). Thus, an understanding of the patterns of persistence of individual plant species is essential for predicting temporal changes in plant communities after fire.

In this study, the complexity of the plant community's response to prescribed burning was caused by individual species-specific responses to fire that, in turn, depended on site-specific abiotic and biotic conditions. Of the 5 perennial plant species that were most abundant at our study area, 1 native species (*H. jubatum*) was consistently more abundant than expected following burning, and 1 introduced species (*C. shoenoides*) was consistently less abundant than expected following burning. Two introduced species (*E. repens* and *P. arundinaceae*) were less abundant than expected following burning in 1991, when flooding was more extensive, and then more abundant than expected following burning in 1992, when flooding was less extensive. The response of the 5th species (*D. spicata,* native) to burning was different in each of the 3 vegetation zones representing the physical moisture gradient.

Without disturbance such as fire, *H. jubatum* was rare in all but the *Elytrigia* zone, probably because it does not persist in hypersaline soils (Badger and Ungar 1989, 1991). Of the 5 predominant plant species in our study area, *H. jubatum* is the only species that effectively invades disturbance-generated bare space both vegetatively and through seed dispersal (Hadley 1970, Payne 1992). It also emerges early and grows quickly compared to the other 4 common species (Payne 1992), although these traits may negatively affect its abundance if early spring fires coincide with the active growth period (Hadley 1970). Johnson and Knapp (1995) found that wetland plant species, which emerged early in the spring and had rapid shoot growth, increased in relative abundance with frequent fire.

The abundance of *C. shoenoides* was generally suppressed by burning, particularly in the drier *Distichlis* and *Elytrigia* zones, and burning effects were weaker on *C. shoenoides* in the *Crypsis* zone, where this species was most abundant. A common response to burning is suppression of certain plant species (reviewed by Kirby et al. 1988, Pederson et al. 1989, Payne 1992), and this response is often the motivation to burn wetlands that have encroaching woody vegetation, or to burn dense monospecific stands of *Typha, Scirpus, Cladium, Spartina, Phragmites,* and other plants that are considered a nuisance when too common (Sale and Wetzel 1983, Payne 1992, Weller 1994).

Both *E. repens* and *P. arundinaceae,* which were either suppressed or enhanced by burning (depending on flooding regimen), primarily invade disturbance-generated bare space vegetatively (Lyon and Stickney 1976, Payne 1992). Like *H. jubatum,* both *E. repens* and *P. arundinaceae* are intolerant of hypersaline soils (Pederson et al. 1989, Payne 1992), and in our study they were relatively common only in the drier *Elytrigia* zone. Our results suggest that the abundance of both *E. repens* and *P. arundinaceae* may be reduced by burning combined with spring flooding.

D. spicata is a native perennial that rapidly invades disturbance-generated bare space vegetatively (Bertness 1991). It is also quite tolerant of stressful physical conditions, such as hypersaline soils (Hansen et al. 1976, Skougard and Brotherson 1979, Bertness and Ellison 1987, Brotherson 1987) or burial by floating plant debris (Bertness 1991). However, if flooding occurs soon after burning in the fall, standing crop of *Distichlis spicata* during the next growing season is dramatically decreased (Smith and Kadlec 1985a). If flooding is delayed 2–7 weeks after burning in the fall, the depression of *D. spicata* is much less extensive (de Szalay and Resh 1997). We found that fall burning reduced *D. spicata* abundance during the next growing season, especially when spring flooding was extensive, although the level of response was different for each of the 3 vegetation zones.

Does Fall Burning Enhance the Use of Wetlands by Migrating Geese during Spring?

Prescribed burning of wetlands is used to inhibit invasion of shrubs into graminoid wetlands (Kushland 1990), to enhance the abundance of rare indigenous species (Pendergrass et al. 1999), to improve the quality and quantity of available forage for grazing (McAtee et al. 1979a, 1979b, Smith et al. 1984, Schmalzer and Hinkle 1993), and to encourage growth of preferred wildlife food for migratory and wintering waterfowl and shorebirds (Givens 1962, Goodwin 1979, Kadlec and Smith 1989). In such systems, burning in the fall or early spring followed by flooding generally improves habitat conditions during the next growing season, whereas burning in summer reduces wetland plant cover during the summer nesting season and reduces habitat quality for waterfowl in fall and winter (Martz 1967, Fredrickson and Taylor 1982, Laubhan 1995, Fredrickson and Laubhan 1996).

At our study area, the seasonally flooded wetland is managed primarily for spring migrating waterfowl, especially grazing geese, on the assumption that burning in the fall followed by flooding in the spring enhances the availability of newly growing forage because this regime reduces residual litter and provides adjacent flooded sites for birds while they rest. We found that when geese used the experimental blocks for feeding there was a clear preference for burned compared to unburned blocks. Thus, fall burning on a larger scale may provide suitable habitat for grazing geese during their spring migration. Because herbivores directly influence wetland plant communities (Bakker 1985, Fuller et al. 1985, Bazely and Jefferies 1986, Foote et al. 1988), burning may affect the interaction between the herbivore and its food supply, although evidence for such an interaction between fire and herbivory is currently lacking for wetlands (Taylor et al. 1994, Miller et al. 1997) but not for other systems (e.g., grasslands [Hobbs et al. 1991]). If more geese had fed in the experimental blocks during our study, then preferential grazing by geese may have affected the wetland plant community along with burning.

Management Implications

Prescribed burning is an important management tool, especially for ecosystems such as prairies, scrublands, and wetlands that have fire as part of their natural history. Determining the effect of prescribed burning on such plant communities is complicated because its effect is often not simply positive or negative, but is contingent on other important ecological factors (Packard and Mutel 1997, Menges and Hawkes 1998). Using an experimental approach, we show that prescribed burning has direct, positive effects on some wetland plant species (e.g., *H. jubatum*) and direct negative effects on others (e.g., *C. shoenoides*). However, the response of other wetland plant species to prescribed burning depended upon the coincident effects of moisture and salinity-alkalinity gradients. Given this interactive dependency, the use of fire to promote certain plant species has, not surprisingly, produced mixed results (Pendergrass et al. 1999). We suggest that effective management of complex ecological systems like wetlands requires the use of experimental studies such as ours to determine the direct and indirect effects of certain management activities.

Like the management of many other ecosystems, wetland management typically involves implementation of multiple activities. The objectives of wetland management at our study site are typical of many managed wetlands and include (1) enhancement of native plant species, (2) control of invasive introduced plant species (e.g., *P. arundinacea*), and (3) provision of appropriate habitat for native fauna. Prescribed burning in fall combined with flooding in spring achieves the latter goal because burning removes residual cover and makes new spring growth of plants available to geese, and flooding provides safe roost sites adjacent to feeding areas. Prescribed burning combined with flooding does not increase the proportion of native versus introduced plant species, although some native species (e.g., *H. jubatum*) were enhanced by burning. Control of *P. arundinacea* in these wetland plant communities may be possible if prescribed fall burning is followed by flooding in spring, although further study of the interaction between burning and flooding on the abundance of this invasive introduced species is needed.

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LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

BADGER, K.S., AND I.A. UNGAR. 1989. The effects of salinity and temperature on the germination of the inland halophyte *Hordeum jubatum.* Canadian Journal of Botany 67:1420–1425.

______. 1991. Life history and population dynamics of *Hordeum jubatum* along a soil salinity gradient. Canadian Journal of Botany 69:384–393.

BAKKER, J.P. 1985. The impact of grazing on plant communities, plant populations, and soil conditions on saltmarshes. Vegetatio 63:391–398.

BAZELY, D.R., AND R.L. JEFFERIES. 1986. Changes in the composition and standing crop of salt-marsh communities in response to removal of a grazer. Journal of Ecology 74:693–706.

BERTNESS, M.D. 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology 72:125–137.

BERTNESS, M.D., AND A.M. ELLISON. 1987. Determinants of pattern in a New England salt marsh plant community. Ecological Monographs 57:129–147.

BMDP. 1992. Bio-medical programs, release 7.0. Statistical Solutions, Inc., Saugus, MA.

BOND, W.J., AND R.W. VAN WILGREN. 1996. Fire and plants. Chapman and Hall, New York.

BROTHERSON, J.D. 1987. Plant community zonation in response to soil gradients in a saline meadow near Utah Lake, Utah County, Utah. Great Basin Naturalist 47: 322–333.

CANOCO™. 1989. CANOCO software. Microcomputer Power, Cornell University, Ithaca, NY.

COWIE, N.R., W.J. SUTHERLAND, M.K.M. DITLHOGO, AND R. JAMES. 1992. The effects of conservation management of reed beds. II. The flora and litter disappearance. Journal of Applied Ecology 29:277–284.

DE SZALAY, F.A., AND V.H. RESH. 1997. Responses of wetland invertebrates and plants important in waterfowl diets to burning and mowing of emergent vegetation. Wetlands 17:149–156.

FERRARI, C.A. 1994. Soil survey of Intermountain Area, California. USDA National Resources Conservation Service, Washington, DC.

FIENBERG, S.E. 1970. The analysis of multidimensional contingency tables. Ecology 51:419–433.

FOOTE, A.L., J.A. KADLEC, AND B.K. CAMPBELL. 1988. Insect herbivory on an inland brackish wetland. Wetlands 8:67–74.

FREDRICKSON, L.H., AND M.K. LAUBHAN. 1996. Managing wetlands for wildlife. Pages 623–647 *in* T.A. Bookhout, editor, Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, MD.

FREDRICKSON, L.H., AND T.S. TAYLOR. 1982. Management of seasonally flooded impoundments for wildlife. U.S. Fish and Wildlife Service, Resource Publication 148.

FULLER, D.A., C.E. SASSER, W.B. JOHNSON, AND J.G. GOSSELINK. 1985. The effects of herbivory on vegetation on islands in Atchafalaya Bay, Louisiana. Wetlands 4: 105–114.

GIBBS, J.P., H.L. SNELL, AND C.E. CAUSTON. 1999. Effective monitoring for adaptive wildlife management: lessons from the Galapagos Islands. Journal of Wildlife Management 63:1055–1065.

GIVENS, L.S. 1962. Use of fire on southeastern wildlife refuges. Proceedings of the Tall Timbers Fire Ecology Conference 1:121–126.

GLENN-LEWIN, D.C., R.K. PEET, AND T.T. VEBLEN. 1992. Plant succession: theory and prediction. Chapman and Hall, New York.

GOODWIN, T.M. 1979. Waterfowl management practices employed in Florida and their effectiveness on native and migratory waterfowl populations. Florida Scientist 42:123–129.

HADLEY, E.B. 1970. Net productivity and burning response of native eastern North Dakota prairie communities. American Midland Naturalist 84:121–135.

HANSEN, D.J., P. DAYANANDAN, P.B. KAUFMAN, AND J.D. BROTHERSON. 1976. Ecological adaptations of salt marsh grass, *Distichlis spicata* (Gramineae), and environmental factors affecting its growth and distribution. American Journal of Botany 63:635–650.

HANSON, H.C. 1939. Fire in land use management. American Midland Naturalist 21:415–434.

HICKMAN, J.C., EDITOR. 1993. The Jepson manual. Higher plants of California. University of California Press, Berkeley.

HOBBS, N.T., D.S. SCHIMEL, C.E. OWENSBY, AND D.S. OJIMA. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. Ecology 72: 1374–1382.

HOLLING, C.S., EDITOR. 1978. Adaptive environmental assessment and management. John Wiley & Sons, New York.

JENKINS, S.H. 1975. Food selection by beavers: a multidimensional contingency table analysis. Oecologia 21: 157–173.

JOHNSON, S.R., AND A.K. KNAPP. 1995. The influence of fire on *Spartina pectinata* wetland communities in a northeastern Kansas tallgrass prairie. Canadian Journal of Botany 73:84–90.

KADLEC, J.A., AND L.M. SMITH. 1989. The Great Basin marshes. Pages 451–474 *in* L.M. Smith, R.L. Pederson, R.M. Kaminski, editors, Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock.

KANTRUD, H.A. 1986. Effects of vegetation manipulation on breeding waterfowl in prairie wetlands—a literature review. U.S. Department of the Interior, Fish and Wildlife Technical Report No. 3.

KIRBY, R.E., S.J. LEWIS, AND T.N. SEXSON. 1988. Fire in North American wetland ecosystems and fire-wildlife relations: an annotated bibliography. U.S. Fish and Wildlife Service, Biological Report 88.

KIRKMAN, L.K., AND R.R. SHARITZ. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina Bays in South Carolina. Ecological Applications 4:177–188.

KOZLOWSKI, T.T., AND C.E. AHLGREN, EDITORS. 1974. Fire and ecosystems. Academic Press, New York.

KUSHLAND, J.A. 1990. Freshwater marshes. Pages 324–363 *in* R.L. Myers and J.J. Ewel, editors, Ecosystems of Florida, University of Central Florida Press, Orlando.

LAUBHAN, M.K. 1995. Effects of prescribed fire on moist-soil vegetation and soil macronutrients. Wetlands 15: 159–166.

LUKEN, J.O. 1990. Directing ecological succession. Chapman and Hall, New York.

LYNCH, J.J. 1941. The place of burning in management of the Gulf Coast wildlife refuges. Journal of Wildlife Management 5:454–457.

LYON, L.J., AND P.F. STICKNEY. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. Proceedings of the Tall Timbers Fire Ecology Conference 14:355–373.

MARTZ, G.F. 1967. Effects of nesting cover removal on breeding ducks. Journal of Wildlife Management 31:236–247.

MCATEE, J.W., C.J. SCIFRES, AND D.L. DRAWE. 1979a. Improvement of Gulf cordgrass range with burning or shredding. Journal of Range Management 32: 372–375.

______. 1979b. Digestible energy and protein content of Gulf cordgrass following burning or shredding. Journal of Range Management 32:376–378.

MENGES, E.S., AND C.V. HAWKES. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. Ecological Applications 8:935–946.

MILLER, D.L., F.E. SMEINS, J.W. WEBB, AND M.T. LONGNECKER. 1997. Regeneration of *Scirpus americanus* in a Texas coastal marsh following Lesser Snow Goose herbivory. Wetlands 17:31–42.

MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, Inc., New York.

NOBLE, I.R., AND R.O. SLATYER. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5–21.

PACKARD, S., AND C.F. MUTEL. 1997. Perspective. Pages 9–18 *in* S. Packard and C.F. Mutel, editors, The tallgrass restoration handbook. Island Press, Washington, DC.

PALMER, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74:2215–2230.

PAYNE, N.F. 1992. Techniques for wildlife habitat management of wetlands. McGraw-Hill, Inc., New York.

PEDERSON, R.L., D.G. JORDE, AND S.G. SIMPSON. 1989. Northern Great Plains. Pages 181–202 *in* L.M. Smith, R.L. Pederson, and R.M. Kaminski, editors, Habitat management for migrating and wintering waterfowl in North America, Texas Tech University Press, Lubbock.

PENDERGRASS, K.L., P.M. MILLER, J.B. KAUFFMAN, AND T.N. KAYE. 1999. The role of prescribed burning in maintenance of an endangered plant species, *Lomatium bradshawii.* Ecological Applications 9:1420–1429.

PHILLIPS, J.R.V. 1934. Succession, development, the climax and the complex organism: an analysis of concepts. Part I. Journal of Ecology 22:88–105.

______. 1935a. Succession, development, the climax and the complex organism: an analysis of concepts. Part II. Journal of Ecology 23:210–223.

______. 1935b. Succession, development, the climax and the complex organism: an analysis of concepts. Part III. Journal of Ecology 23:554–571.

PICKETT, S.T.A., S.L. COLLINS, AND J.J. ARMESTO. 1987. Models, mechanisms and pathways of succession. Botanical Review 53:335–371.

PICKETT, S.T.A., AND R.S. OSTFELD. 1995. The shifting paradigm in ecology. Pages 261–278 *in* R.L. Knight and S.F. Bates, editors, A new century for natural resources management. Island Press, Washington, DC.

RAVEN, P.H. 1988. The California flora. Pages 109–137 *in* M.G. Barbour and J. Major, editors, Terrestrial vegetation of California. California Native Plant Society, Special Publication Number 9, Sacramento.

SALE, P.J.M., AND R.G. WETZEL. 1983. Growth and metabolism of *Typha* species in relation to cutting treatments. Aquatic Botany 15:321–334.

SCHMALZER, P.A., AND C.R. HINKLE. 1993. Effects of fire on nutrient concentrations and standing crops in biomass of *Juncus roemerianus* and *Spartina bakeri* marshes. Castanea 58:90–114.

SCHMALZER, P.A., C.R. HINKLE, AND J.L. MAILANDER. 1991. Changes in community composition and biomass in *Juncus roemerianus* Scheele and *Spartina bakeri* Merr. marshes one year after a fire. Wetlands 11:67–86.

SIMPSON, E.H. 1949. Measurement of diversity. Nature 163:688.

SKOUGARD, M.G., AND J.D. BROTHERSON. 1979. Vegetational response to three environmental gradients in the salt playa near Goshen, Utah County, Utah. Great Basin Naturalist 39:44–58.

SMITH, L.M., AND J.A. KADLEC. 1985a. Fire and herbivory in a Great Salt Lake marsh. Ecology 66:259–265.

______. 1985b. Comparisons of prescribed burning and cutting of Utah marsh plants. Great Basin Naturalist 45:462–466.

SMITH, L.M., J.A. KADLEC, AND P.V. FONNESBECK. 1984. Effects of prescribed burning on nutritive quality of marsh plants in Utah. Journal of Wildlife Management 48:285–288.

SMITH, L.M., R.L. PEDERSON, AND R.M. KAMINSKI, EDITORS. 1989. Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock.

TAYLOR, K.L., J.B. GRACE, G.R. GUNTENSPERGEN, AND A.L. FOOTE. 1994. The interactive effects of herbivory and fire on an oligohaline marsh, Little Lake, Louisiana, USA. Wetlands 14:82–87.

TER BRAAK, C.J.F., AND I.C. PRENTICE. 1988. A theory of gradient analysis. Advances in Ecological Research 18:271–317.

TOFT, C.A. 1984a. Activity budgets in two species of bee flies (*Lordotus:* Bombyliidae, Diptera): a comparison of species and sexes. Behavioral Ecology and Sociobiology 14:287–296.

______. 1984b. Resource shifts in bee flies (Bombyliidae): interactions among species determine choice of resources. Oikos 43:104–112.

UHLER, F.M. 1944. Control of undesirable plants in waterfowl habitats. Transactions of the North American Wildlife Conference 9:295–303.

VAN DER VALK, A.G. 1986. The impact of litter and annual plants on recruitment from the seed bank of a lacustrine wetland. Aquatic Botany 24:13–26.

WALTERS, C.J. 1986. Adaptive management of renewable resources. Macmillan Publishing Company, New York. 374 pp.

WALTERS, C.J., AND C.S. HOLLING. 1990. Large-scale management experiments and learning by doing. Ecology 71:2060–2068.

WELLER, M.W. 1994. Freshwater marshes: ecology and wildlife management. 3rd edition. University of Minnesota Press, Minneapolis.

WHELAN, R.J. 1995. The ecology of fire. Cambridge University Press, New York.

WILLARD, E.E., AND R.H. WAKIMOTO. 1995. Vegetation recovery in sedge meadow communities within the Red Bench Fire, Glacier National Park. Pages 102–110 *in* S.I. Cerulean and R.T. Engstrom, editors, Fire in wetlands: a management perspective. Proceedings of the Tall Timbers Fire Ecology Conference, No. 19., Tall Timbers Research Station, Tallahassee, FL.

WRIGHT, H.A., AND A.W. BAILEY. 1982. Fire ecology: United States and southern Canada. John Wiley & Sons, Inc., New York.

ZAR, J.H. 1999. Biostatistical analysis. 4th edition. Prentice Hall, Upper Saddle River, NJ.

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