

FACTORS INFLUENCING DYNAMICS OF TWO INVASIVE C₄ GRASSES IN SEASONALLY DRY HAWAIIAN WOODLANDS

CARLA M. D'ANTONIO,^{1,4} R. FLINT HUGHES,² AND PETER M. VITOUSEK³

¹Department of Integrative Biology, University of California, Berkeley, California 94720-3140 USA

²Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, Colorado 80309 USA

³Department of Biological Sciences, Stanford University, Stanford, California 94305 USA

Abstract. The introduced C₄ bunchgrass, *Schizachyrium condensatum*, is abundant in unburned, seasonally dry woodlands on the island of Hawaii, where it promotes the spread of fire. After fire, it is partially replaced by *Melinis minutiflora*, another invasive C₄ grass. Seed bank surveys in unburned woodland showed that *Melinis* seed is present in locations without adult plants. Using a combination of germination tests and seedling outplant experiments, we tested the hypothesis that *Melinis* was unable to invade the unburned woodland because of nutrient and/or light limitation. We found that *Melinis* germination and seedling growth are depressed by the low light levels common under *Schizachyrium* in unburned woodland. Outplanted *Melinis* seedlings grew rapidly to flowering and persisted for several years in unburned woodland without nutrient additions, but only if *Schizachyrium* individuals were removed. Nutrients alone did not facilitate *Melinis* establishment.

Competition between *Melinis* and *Schizachyrium* naturally occurs when individuals of both species emerge from the seed bank simultaneously, or when seedlings of one species emerge in sites already dominated by individuals of the other species. When both species are grown from seed, we found that *Melinis* consistently outcompetes *Schizachyrium*, regardless of light or nutrient treatments. When seeds of *Melinis* were added to pots with well-established *Schizachyrium* (and vice versa), *Melinis* eventually invaded and overgrew adult *Schizachyrium* under high, but not low, nutrients. By contrast, *Schizachyrium* could not invade established *Melinis* pots regardless of nutrient level. A field experiment demonstrated that *Schizachyrium* individuals are suppressed by *Melinis* in burned sites through competition for both light and nutrients.

Overall, *Melinis* is a dominant competitor over *Schizachyrium* once it becomes established, whether in a pot or in the field. We believe that the dominance of *Schizachyrium*, rather than *Melinis*, in the unburned woodland is the result of asymmetric competition due to the prior establishment of *Schizachyrium* in these sites. If *Schizachyrium* were not present, the unburned woodland could support dense stands of *Melinis*. Fire disrupts the priority effect of *Schizachyrium* and allows the dominant competitor (*Melinis*) to enter the system where it eventually replaces *Schizachyrium* through resource competition.

Key words: biological invasion; C₄ grasses; competition; exotic grasses; fire; Hawaiian woodlands; invasion; *Melinis minutiflora*; nitrogen; resource limitation; *Schizachyrium condensatum*; seasonally dry woodland.

INTRODUCTION

Dominance patterns of species over space and time have been a major subject of investigation since ecology began developing as a field early this century. For plants, the role of physiological tolerances as well as allocation and competition for nutrients and light have been major foci of research. Several authors have argued that, since plant species face a trade-off between investment in roots vs. shoots, species that are good at dominating nutrient-limited environments cannot dominate light-limited environments and vice versa (e.g., Mooney 1972, Tilman 1982, 1988). However, the order

of arrival of species also can control which species dominate particular sites (Connell and Slatyer 1977). In marine hard substrate communities, many investigators have shown that preemption of space by the existing assemblage is important in inhibiting establishment of other species. The species that gets there first determines patterns of space occupation for many years (e.g., Turner 1985, Dungan 1986, Hughes 1989, Berlow 1997). In terrestrial systems, the role of initial conditions and preemption may vary according to the limiting resource or the type of species being studied (see Grace 1987, Wilson 1988, Wedin and Tilman 1993). Several investigators have documented “inertia effects,” whereby long-lived individuals slow down succession because they may take years to die, even if conditions favoring their dominance and establishment of their progeny have long since become unfavorable.

Manuscript received 18 March 1999; revised 12 November 1999; accepted 11 December 1999; final version received 18 January 2000.

⁴ E-mail: dantonio@socrates.berkeley.edu



PLATE 1. (Left) Unburned woodland with *Schizachyrium condensatum* and native shrubs and trees. (Right) Old burn site 22 years after fire. This site was formerly a *Metrosideros* woodland.

These adults can inhibit the establishment of later arrivals, regardless of resource conditions (e.g., Davis 1986, Milchunas and Lauenroth 1995). The time lags created by such historical effects contribute to a lack of predictability in plant communities (Fowler 1990). The widespread movement of plant species around the globe provides numerous opportunities to see how early arrivals can influence later ones, as well as to examine the potential role of historical factors in determining field pattern.

The role of disturbance in disrupting dominance patterns and promoting species change is broadly recognized in natural communities (Sousa 1984, Pickett and White 1985). In many systems where fire is the dominant form of disturbance, patterns of species change are predictable, and postdisturbance succession eventually results in establishment of the prefire community. Recently, however, the human-caused movement of species has resulted in sometimes-unpredictable responses of communities to disturbances, including fire. Fire can promote invasive, nonnative species at the expense of natives (reviewed in D'Antonio 2000). Because fire is often used as a management tool, it is important to accurately predict its potential impact on long-term species composition. Yet, models of succession developed in systems where fire has been a historic force may not be applicable if propagules of invaders with unique life history traits are present.

In the Hawaiian Islands, introduced C_4 grasses have invaded many seasonally dry habitats, where they promote the spread of fire (Smith and Tunison 1992). Fire, in turn, is damaging to many native species (Hughes et al. 1991, Tunison et al. 1995). Within Hawaii Volcanoes National Park (hereafter HAVO), grass-fueled fires occur from sea level to 2500 m, but have their most devastating impact in the seasonal submontane zone (D'Antonio et al. 2000). Here, perennial C_4 bunchgrasses, *Andropogon virginicus* and *Schizachyrium condensatum* from continental Americas, have become abundant in native woodland. These are partially or wholly replaced after fire by an African C_4 grass,

Melinis minutiflora (Hughes et al. 1991). *Melinis* has a sprawling growth form and can climb over shrubs much like a vine. It forms dense mats up to 1.5 m deep and maintains a large amount of dead biomass (D'Antonio et al., *unpublished manuscript*). Fires in areas dominated by *Melinis* are particularly devastating to native species (Tunison et al. 1995). *Melinis* is also an important invader in Central and South America and Australia (Parsons 1972, D'Antonio and Vitousek 1992).

The objectives of this study were twofold. First, we determined what limits invasion of *Melinis minutiflora* into unburned woodland sites and whether its absence there is a function of its resource use and allocation patterns (in contrast to those of *Schizachyrium*), or whether its scarcity is due to seed limitation or historical factors. Second, we elucidated factors promoting the shift in grass species dominance from *Schizachyrium* to *Melinis* after fire, particularly since the former regenerates from root crowns immediately after fire and thus has an initial growth advantage. We evaluate these questions using a combination of field and greenhouse studies. This also allowed us to contrast competitive interactions in potted-plant experiments with behavior and dominance patterns in the field, as well as to examine how the establishment of one introduced species (*Schizachyrium condensatum*), influences invasion by another potent invader (*Melinis minutiflora*).

STUDY SITES AND SPECIES

Our study sites are within the seasonal submontane zone of Hawaii Volcanoes National Park on Kilauea volcano on the island of Hawaii. They lie within a broad band of what was once a continuous open-canopy forest dominated by *Metrosideros polymorpha* (19°6' N, 155°33' W). Since grass invasions began in the 1960s, fires intruding from campgrounds and roads have extended into the forest. The sites are ~870 m elevation on 500–1000-yr-old pahoehoe lava flows (Holcomb 1987). Soils are predominantly entisols developed from

volcanic ash deposited over the past 500 yr. Soil depth ranges from <10 cm to >1 m; including rocky outcroppings, mean depth is 30–35 cm (D'Antonio, *unpublished manuscript*). The area receives a mean of 1500 mm rain/yr, with a pronounced drought during April–September.

Unburned woodland is dominated by the evergreen tree *Metrosideros polymorpha*. The understory is dominated by native evergreen shrubs, including *Styphelia tameiameia*, *Dodonaea viscosa*, *Osteomeles anthyldifolia*, and *Wikstroemia phylliraeifolia*. Three species of native sedges are also common. *Schizachyrium condensatum*, which invaded the area in the 1960s, comprises 30% of the aboveground understory biomass and >60% cover in the study area (Hughes et al. 1991). Two other introduced C_4 grasses, *Andropogon virginicus* and *Melinis minutiflora*, make up <8% cover. Native grasses are rare. Burned sites are dominated primarily by *Melinis* and *Schizachyrium*, and, with the exception of *Dodonaea viscosa*, native shrubs are largely lacking. Hughes et al. (1991) describe differences in cover of grasses across our unburned and burned sites: *Melinis* cover increases from 7.2% in unburned woodland up to 79.3% in twice-burned sites, and biomass increases from <10 g/m² to >700 g/m² (D'Antonio et al., *unpublished manuscript*).

Schizachyrium condensatum (formerly *Andropogon glomeratus*), an erect bunchgrass native to tropical America, sends up new tillers from a small root crown each year. Individual stems grow vertically until they begin to flower; at our sites they reach a mean height of 1.1 m, with a maximum height of 1.8 m. After flowering, entire shoots die and new ones are produced from the root crown. Flowering occurs midsummer–December. By contrast, *Melinis minutiflora*, a native to Africa, is a mat-forming, vine-like grass that grows upward and outward, using other species for support. Individual stems live many years and layer on top of one another. Flowering occurs in a synchronous burst in late November. Live leaves die back during seedset in January and February, and new ones begin to appear along the same stems in March and April. *Melinis* mats can reach 1.5 m deep and can carpet large areas of ground completely.

METHODS

Species composition and grass density in burned vs. unburned sites

To survey species composition and change in the unburned and adjacent burned habitat in 1991 and 1998, we resurveyed transects established by Hughes et al. (1991) in 1987. Sites included unburned woodland, woodland that had burned once in 1970 (hereafter “old burn”), sites that had burned once in 1987 (hereafter “young burn”), and sites that had burned both in 1970 and 1987 (hereafter “twice burned”). Aerial photographs from 1965 show that these sites were all part

of the same *Metrosideros* woodland prior to fire. Five sites were used in each burn condition. A “site” is a densely vegetated swale, usually 140–200 m long and ≥20 m wide. Sites were isolated from each other by ≥50 m (generally ≥150 m) by rocky ridges.

In our resurvey, we used a different sampling methodology from Hughes et al. (1991), one that we believe is more appropriate for this vegetation type. We used a modified point intercept method, where each species touching a 1 cm (3/8 inch) diameter vertical tent pole was recorded at 50-cm intervals along two 100-m transects lines through each site. “Cover” refers to frequency and was estimated as the number of points where the pole hit a given species, divided by the total number of sampled points along each line (200). Means were evaluated from data from the two transects per swale, yielding a single value per site before statistical analyses (ANOVA) were conducted ($n = 5$ sites/burn condition). All transects were monitored in 1991, whereas in 1998 we monitored only the unburned and twice-burned transects, since these represent the extremes of habitat condition relative to fire. Within a time point, data were analyzed with a one-way ANOVA. Cover values were compared between 1991 and 1998 for the unburned and twice-burned sites using a repeated-measures ANOVA.

Because differences in cover by *Schizachyrium* between burned and unburned sites could be due to size differences of individuals, we estimated grass density (by size class) of *Schizachyrium* in unburned and burned plots. We defined three size classes and surveyed all clumps occurring in each of five 1 × 1 m plots randomly located within the belt transect describing each site. The number of individuals in each size class was recorded. We also noted whether individuals were overgrown by *Melinis* or were dead. Size classes were as follows: (1) small (0–3 flowering shoots), (2) medium (4–10 flowering shoots), and (3) large (>10 flowering shoots). Data were analyzed initially with a nested ANOVA, treating plots as subsamples within sites. However, since this nesting factor was not significant ($P > 0.30$ for all), we pooled the data (Underwood 1996) for ease of presentation.

We estimated *Schizachyrium* seedling survival for one year on a cohort of seedlings in 10 randomly located 1 × 1 m plots in each habitat type (two plots per site). Within these, all *Schizachyrium* seedlings beyond the cotyledon stage were marked and recensused for survival nine months later. We also noted the presence of cotyledon stage *Melinis* and monitored for *Melinis* recruitment beyond the cotyledon stage.

Seed bank sampling and seed germination trials

We sampled germinable seed in the seed bank by collecting 8 cm × 4.5 cm (depth × width) soil cores from within each habitat type. Four cores were taken at random locations along a centerline through each site ($n = 5$), resulting in 20 cores per habitat type.

Cores were collected in October 1990, and February and June 1991. Each was spread evenly over the surface of a 20 cm diameter plastic saucer containing 3 cm of potting soil. Cores were misted daily for three months, and emerging seedlings were identified and removed. Flats were stirred after two months to stimulate further germination. Only densities of emerging *Melinis* and *Schizachyrium* are presented here. Data were analyzed initially with a nested ANOVA. However, before final analysis, samples within a site were treated as individual replicates, because the *P* value for the nesting factor was always >0.30 (Underwood 1996). Data were analyzed with one-way ANOVAs within a sample, with habitat (burn condition) as a fixed effect. The full data set was analyzed with a two-way ANOVA, with time and habitat as fixed effects. We did not use a repeated-measures ANOVA, because sample locations were randomly chosen each time.

To test the effect of photon flux density on germination and early seedling growth, we established six different shade boxes in an outdoor setting at the Hawaii Volcanoes National Park (HAVO) Research Center. Conditions ranged from $<1\%$ of ambient light to full sunlight ($2100 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$). Seeds of both grass species were collected from the vicinity of Kipuka Nene. In February 1991, they were planted into vermiculite trays. Each tray was divided into six subunits, and each subunit received six seeds. We planted six trays of each species for each light level and randomly arranged the trays within the shade boxes. All trays were examined weekly for two months for emerging seedlings. At 2 mo, seedlings were separated from the vermiculite using water and were oven dried to a constant mass, which was later measured on a Kahn Microbalance (Kahn Instruments, Wethersfield, Connecticut).

Seedling outplant experiments in unburned forest

To examine factors limiting establishment of *Melinis* into the unburned woodland, we outplanted small *Melinis* seedlings into unburned sites and followed their survival. Treatments were arranged factorially, with seedlings assigned to one of three nutrient classes (+N, +P, or no nutrients) and two vegetation treatments (*Schizachyrium* removed vs. intact). *Schizachyrium* removal had been conducted and maintained for one year prior to initiating this experiment (see D'Antonio et al. 1998). Outplanted seedlings were 2–4 cm tall and were grown from seed collected in a nearby burned site. The first year, four seedlings were planted 10 cm apart into each of five plots per treatment. The second year, entirely new plots were laid out, and six seedlings were outplanted into each, with six replicates per treatment. The first set of seedlings was outplanted in October 1991 and monitored for two years. The second set, also monitored for two years, was outplanted in November 1992. Fertilizer was applied at a rate of $100 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for both the N- and P-amended plots using granular

ammonium nitrate or P_2O_5 as supertriple phosphate. Half of the annual dose was added one week after outplanting, while the other half was added six months later.

Potted plant competition studies

We set up a pot experiment to examine the importance of interspecific competition relative to intraspecific competition for seedlings under two light and two nutrient levels. Grass seedlings were started in flats and outplanted to 7.6-L (2-gallon) pots at one month of age, with two seedlings per pot. Five monospecific and five mixed-species pots were planted per species and environmental condition. We paired seedlings by height at the time of planting. We filled the bottom 3 cm of each pot with volcanic cinder and then filled the pots to within 3 cm of the top with an cinder/ash mix (1:9, cinder:ash). Ash was collected downslope of our sites from submontane dunes formed by the 1790 eruption of Kilauea. Nutrient treatments were (1) ambient (no amendment added), or (2) 25 kg/ha of N-P-K osmocote fertilizer added every three months for one year. Light treatments were (1) ambient (no shade cloth), or (2) 7–10% of ambient (achieved using two layers of plastic shade cloth). *Melinis* seedlings were kept from shading *Schizachyrium* by diverting their trailing stems with shishkebob skewers for the first six months, so that competitive interactions were largely for belowground resources. At the time of harvest (one year), plants were separated into roots, shoots, and reproductive material, which were dried and measured for mass. Data were analyzed separately for each species using a three-way ANOVA, with light (high vs. low), nutrients (high vs. low), and competitive environment (intra- vs. interspecific) as fixed effects. We also conducted three-way ANOVAs on monospecific pots, using light, nutrients, and species as fixed factors, so that the two species could be compared directly.

Another pot experiment was used to examine whether seedlings of one species could invade pots with established individuals of the other species, and whether this was dependent on soil nutrients. Juvenile plants of both *Melinis* and *Schizachyrium* were collected from Kipuka Nene in April 1991, and again placed into 7.6-L pots, but with one plant per pot. At three-month intervals after planting, half of the pots were amended with osmocote fertilizer. All pots were at ambient light levels and were kept continuously moist. When plants had been in pots for six months, we introduced 10 seeds/pot of either *Melinis* or *Schizachyrium*. Simultaneously, we planted 10 seeds of each species into replicate pots that had no established individuals (hereafter “empty pots”); half of these received the fertilizer amendment. There were four pots per treatment. If more than three seedlings emerged in a pot, their number was thinned to three. After six months, “invaders” were harvested, dried and measured for mass. Final “invading” seedling size data were analyzed with a

TABLE 1. Percentage occurrence of dominant grass (*Schizachyrium condensatum*, *Melinis minutiflora*) and shrub (*Styphelia tameiameia*, *Dodonaea viscosa*) species along 100-m transects in burned and unburned sites near Kipuka Nene, Hawaii Volcanoes National Park.

Site	<i>Schizachyrium</i>		<i>Melinis</i>		<i>Styphelia</i>		<i>Dodonaea</i>	
	1991	1998	1991	1998	1991	1998	1991	1998
Unburned	76.4 ^a (2.5)	68.4 ^a (3.3)	8.5 ^a (3.3)	12.2 ^a (4.7)	34.2 ^a (2.7)	30.0 ^a (1.9)	11.3 ^b (1.8)	9.3 ^a (1.1)
Young burn	54.9 ^b (3.2)	71.2 ^b (6.0)	0.0 ^b	5.5 ^{b,c} (2.2)
Old burn	38.6 ^c (6.4)	75.5 ^b (5.1)	0.8 ^b (0.3)	24.5 ^a (3.4)
Twice burned	37.8 ^c (3.4)	20.8 ^b (3.0)	93.4 ^c (1.8)	78.5 ^b (1.9)	0.0 ^b ...	0.0 ^b ...	3.2 ^c (0.8)	11.8 ^a (1.5)
<i>F</i> (1991) or <i>t</i> (1998)	19.19	10.67	72.35	12.94	158.85	15.11	17.99	1.32
<i>P</i>	0.001	0.001	0.001	0.001	0.0001	0.001	0.001	0.23

Note: Values represent means (1 SE). Where the same lowercase letters follow means within a column, these values are not considered significantly different ($P > 0.05$) using post hoc Bonferroni comparisons; $n = 5$. *F* values are for 1991 within-column comparisons (df = 3, 16); *t* values are for 1998 within-column comparisons (df = 1, 8).

two-way ANOVA, with nutrients (high vs. low) and competitive environment (adult intra-, adult interspecific, or empty pot) as fixed effects.

Both pot experiments were set up in a cleared field at 1000 m elevation within the seasonal submontane zone of HAVO. The site received 2000 mm of rain during the yearlong experimental period. Pots were randomly arrayed outdoors on tables and were rotated among tables at two-month intervals to minimize variation in light environment.

Field competition experiment

To examine the impact of *Melinis* overgrowth on *Schizachyrium* individuals, we removed *Melinis* from around target *Schizachyrium* in eight locations in each of old, young, and twice-burned habitats (total locations = 24). There were not enough unburned patches of *Melinis* with *Schizachyrium* to include the unburned habitat. At a given location, three overgrown individuals of *Schizachyrium* were selected and randomly assigned to one of the following three treatments: (1) complete removal of *Melinis* from a 1 m diameter circle around a target *Schizachyrium* (hereafter "total removal"), (2) *Melinis* stems were bent away from *Schizachyrium* stems without disturbing their roots to eliminate or reduce shading (hereafter "partial removal"), or (3) *Melinis* was left intact around target *Schizachyrium* (hereafter, control). To minimize soil disturbance, *Melinis* roots were clipped just below the root crown. Resprouting individuals were re-clipped. The number of live and reproductive stems on each target plant was recorded initially and at six-month intervals for one year. In addition, live and recently dead leaf tissue was collected for N analysis at the end of the year. Tissues were dried at 65°C to constant mass, chopped finely with scissors, and ground through #20 mesh on a Wiley Mill (Thomas Scientific, Swedesboro, New Jersey, USA). Tissue nitrogen was assayed with a Fisons Instrument CHN analyzer (Fisons Instruments,

Beverly, Massachusetts, USA) at University of California–Berkeley. Data were analyzed initially with a two-way ANOVA, using habitat and treatment as factors; but, because habitat effects were never significant ($P > 0.20$ in all cases), post hoc comparisons among treatments were conducted using Tukey comparisons with all habitats pooled. Growth data were analyzed as the log-transformed net increase in number of shoots over a given time interval.

Responses of seeds and grasses to heating

We subjected seeds to six temperature treatments, in the range ambient 120°C, prior to planting the seeds into vermiculite flats. For each species, six batches of 200 seeds were separated from a large bag of seed collected three months prior to the experiment. The seeds were placed into an envelope and transferred into the appropriate temperature oven for 4 min, after which they were planted into vermiculite flats. These were monitored weekly, and germinating seedlings were counted and discarded. The effect of treatment on germination was assessed using χ^2 analyses, with successive elimination of treatments starting with those apparently contributing least to the original χ^2 value, in order to determine which treatments caused deviation in the distribution of germinating seedlings away from random.

In order to assess the direct impact of fire on survival of individual plants, we tagged *Melinis* and *Schizachyrium* individuals in each of two sites designated for controlled burning/experimental revegetation by HAVO. Thirty individuals of each species were tagged at the first site, and 20 at the second site. Both sites had already burned once in the early 1970s (see old burn sites in Tables 1) and were dominated by *Melinis* and *Schizachyrium*. The first site was burned in a low-intensity fire in January 1993, and grass survivorship was determined by resprouting over the next nine months. The second site was burned in a high-intensity fire in

June 1995, and survivorship was likewise determined. A plant that had no green tissue after nine months was considered to have been killed by fire. In addition to measuring survival of marked plants, we monitored grass seedling establishment by counting grass seedlings in 60 25 × 25 cm plots across each site using a stratified random sampling technique.

RESULTS

Community structure

As with the surveys of Hughes et al. (1991), *Schizachyrium condensatum* cover in the unburned transects was higher than in all other habitats (Table 1). It declined significantly between 1991 and 1998 (Table 1; Time, $F = 38.09$, $df = 1, 8$, $P < 0.0001$). The decline was greater along the twice-burned than along unburned transects (Time × Habitat, $F = 4.47$, $df = 1, 8$, $P < 0.067$). In the unburned sites, *Schizachyrium* was approximately eight times more frequent than *Melinis*. *Melinis* cover in 1991 and 1998 were similar to measurements made by Hughes et al. (1991) in 1987 and was consistently seven times higher along burned than unburned transects (Table 1). Like *Schizachyrium*, *Melinis* cover declined along the twice-burned transects between 1991 and 1998, but remained unchanged in the unburned woodland (Time, $F = 38.09$, $df = 1, 8$, $P < 0.0001$; Time × Habitat, $F = 102.68$, $df = 1, 8$, $P < 0.0001$). This decline may be the result of phenological differences, since 1991 surveys were done in January when *Melinis* plants were at peak biomass and in full fruit, whereas 1998 surveys were done in November of a severe drought year when individual plants were small and not flowering.

Hughes et al. (1991) observed that the dominant shrub in the unburned woodland, *Styphelia tameiameia* was absent from burned sites in 1991, and we found no recovery by 1998 in the twice-burned areas. The few individuals present in the old burn sites in 1991 were on rocky outcroppings that never burned, and, although these sites were not surveyed in 1998, we visit them regularly and have seen no evidence of recruitment by this species. The only significant change in native species cover was an increase by the subdominant shrub, *Dodonaea viscosa*, along the twice-burned transects between 1991 and 1998 (Time, $F = 7.916$, $df = 1, 8$, $P < 0.023$) due to growth of seedlings present in 1991. *Dodonaea* remained unchanged in the unburned transects (Time × Habitat, $F = 19.25$, $df = 1, 8$, $P < 0.002$; Table 1). We do not believe that the increase in *Dodonaea* in the twice-burned sites will eventually lead to a decline in *Melinis*, because the vine-like *Melinis* typically grows all over *Dodonaea* branches, as well as surrounding the base and stem of each shrub. In addition, the canopy of individual *Dodonaea* shrubs is not dense, and the shade cast seems unlikely to restrict *Melinis* growth.

The density of established *Schizachyrium* individuals

TABLE 2. Density of *Schizachyrium* clumps in unburned and burned woodland sites.

Site	Small	Medium	Large	Total
Unburned	8.8 ^a (1.3)	8.7 ^a (0.8)	2.9 ^a (0.4)	20.4 ^a (1.6)
Young burn	3.0 ^b (1.1)	3.7 ^b (1.3)	1.2 ^b (0.4)	7.9 ^b (2.4)
Old burn	2.8 ^b (0.5)	3.3 ^b (0.7)	0.9 ^b (0.3)	6.9 ^b (1.2)
Twice burned	5.5 ^{a,b} (1.3)	1.2 ^b (0.4)	0.05 ^b (0.05)	6.8 ^b (1.5)
<i>F</i>	6.02	20.69	16.15	19.56
<i>P</i>	0.001	0.001	0.001	0.001

Notes: Data from all four transects were pooled, because the nesting factor was always $P > 0.30$ (see Underwood 1996); $n = 20$. Numbers represent means (no. clumps/m²) with 1 SE in parentheses. *F* values are for within-column comparisons; df for all *F* values = 3, 66. Where the same lowercase letter follows two means within a column, these values are not statistically distinguishable at $P > 0.05$ using a post hoc Tukey test.

was lower in all burned sites, compared to unburned habitats (Table 2). The difference between habitats was evident in all size categories and in all burned habitats vs. the unburned (Table 2). There were no significant differences among the burned habitats in numbers in each size class, although the proportion of individuals in each class was strongly skewed towards the small size class in the twice-burned plots (79% vs. mean of 40% in other habitat types).

During the almost one year of observation on permanent plots, we observed a flush of grass seedlings in February and March in many plots, corresponding to late winter rains. These cotyledon-stage grasses were too dense to count, and, with the exception of a few *Schizachyrium*, most of them died. In the unburned woodland, three of our 10 plots contained cotyledon-stage *Melinis* plants at this time, but all were dead within five months. We believe that both light stress and drought stress contributed to this mortality, because most seedlings became severely etiolated prior to disappearing, and the spring of that year was very dry. For analysis of percent survival, *Schizachyrium* seedlings were divided into two size categories, (1) small (3–5 cm tall, or just beyond cotyledon stage), and (2) medium (6–10 cm). Survival was poor in most sites for small-sized individuals (Table 3), and the distribution of mortality among sites was not different from random ($\chi^2 = 4.09$, $P > 0.25$). By contrast, mortality of medium-sized seedlings was lower than expected (based on random) in both unburned and old burn habitats, and higher than expected in twice-burned habitat ($\chi^2 = 13.40$, $P < 0.005$), where *Melinis* cover was consistently the highest.

Seed bank and seed germination

The number of grass seedlings emerging per core showed a seasonal pattern for both species (Table 4), with a germination peak from February cores and a low

TABLE 3. Mortality of marked *Schizachyrium condensatum* seedlings in 1-m² plots at each site.

Site	Class 1		Class 2	
	Mortality	n	Mortality	n
Unburned	63.6	22	5.3	38
Young burn	88.9	36	25.0	44
Old burn	25.0	12	5.9	34
Twice burned	71.1	38	47.1	17

Notes: Mortality is represented as a percentage of the original cohort marked in January 1991 that was still present in September 1991. Class 1 individuals were 3–5 cm tall when marked. Class 2 individuals were 5–8 cm tall when marked.

from October cores. *Schizachyrium* tended to have higher germination in cores from unburned than from burned sites during the peak period. More *Melinis* seeds germinated from burned than unburned sites, but it is important to note that some did germinate from unburned cores. Values were highest in February, when *Melinis* seedlings emerged from 12 out of 20 unburned cores; although absolute values appear low (Table 4), they translate into >2000 seeds/m². The highest number of *Melinis* seedlings were consistently from the old burn cores, suggesting that the *Melinis* seed bank builds up over time since last fire, or that *Melinis* in these sites produces more seed. We do not believe the latter explanation, since *Melinis* biomass is the same in all burned habitats (D'Antonio et al., unpublished manu-

script) and flowering was not obviously different among the areas. Conversely, *Schizachyrium* seedling emergence declines, since the young burn and twice-burned cores tended to have more *Schizachyrium* than the cores from the old burn sites (Table 4).

Both *Melinis* and *Schizachyrium* seeds germinated less in low light (Table 5). At 1% and 3% of ambient sunlight, germination was reduced by 50% for *Melinis* and 33% for *Schizachyrium*. This reduction was also observed at 33% of ambient light for *Melinis*, but not for *Schizachyrium*.

Melinis minutiflora seedlings were larger than those of *Schizachyrium* at all light intensities except <1%. Size was progressively reduced as light intensities were decreased for both species (Table 5). At the lowest light intensity, *Melinis* seedlings were <1% the size of those grown at ambient light, and most were barely alive. These observations suggest that they are ultimately intolerant of these conditions. By contrast, *Schizachyrium* seedlings were >10% of their biomass at ambient light and showed little mortality.

Melinis outplant experiment into unburned woodland

The survival of outplanted *Melinis* seedlings was strongly influenced by presence of *Schizachyrium* during both experimental periods (Fig. 1). Almost no seedlings survived in the presence of *Schizachyrium*, regardless of nutrient treatment. Despite differences in

TABLE 4. Mean number of *Melinis* and *Schizachyrium* seedlings emerging from 5 cm wide × 8 cm deep soil cores, over a three-month period following collection date.

A) Mean number of seedlings emerging						
Species	Habitat	October 1991	February 1992	June 1992		
<i>Melinis</i>	UB	1.15 ^a	5.60 ^a	1.50 ^a		
	YB	2.60 ^b	15.25 ^{a,b}	8.10 ^b		
	OB	10.00 ^b	25.40 ^b	8.10 ^b		
	TB	3.25 ^b	17.90 ^b	5.80 ^{a,b}		
Within-date comparison						
$F_{3,76}$		5.968	7.950	2.933		
P		<0.001	<0.001	0.039		
<i>Schizachyrium</i>	UB	0.75 ^a	7.45 ^a	5.15 ^a		
	YB	0.85 ^a	4.35 ^a	5.05 ^a		
	OB	0.65 ^a	2.45 ^b	1.20 ^{a,b}		
	TB	0.40 ^a	4.50 ^{a,b}	0.25 ^b		
Within-date comparison						
$F_{3,76}$		0.83	4.70	4.38		
P		<0.483	<0.005	<0.007		
B) Two-way ANOVA						
Source	Species					
	<i>Melinis</i>			<i>Schizachrium</i>		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
Habitat	14.34	3, 228	<0.001	7.59	3, 228	<0.001
Time	35.48	2, 228	<0.001	19.82	2, 228	<0.001
Habitat × Time	2.52	6, 228	0.02	2.85	6, 228	0.011

Notes: In panel (A), where the same lowercase letter follows two means within a column (for a given species), those values are not statistically distinguishable using Bonferroni comparisons tests (Systat 6.04). UB = unburned, YB = young burn, OB = old burn, TB = twice burned.

TABLE 5. Germination and seedling growth of *Melinis* and *Schizachyrium* after two months of exposure to six different light levels.

Species	Percentage of full sunlight					
	1	3	18	33	49	100
Percentage germination						
<i>Melinis</i>	10.4 ^a (1.8)	12.7 ^a (2.5)		13.9 ^a (1.8)	27.1 ^b (2.6)	25.5 ^b (3.1)
<i>Schizachyrium</i>	51.4 ^a (4.8)	45.1 ^a (3.3)		75.0 ^b (5.4)	67.4 ^{a,b} (6.7)	75.0 ^b (3.6)
Biomass						
<i>Melinis</i>	0.002 ^a (0.001)	0.029 ^a (0.001)	0.140 ^{a,b} (0.012)	0.283 ^c (0.034)	0.226 ^{b,c} (0.043)	0.394 ^c (0.011)
<i>Schizachyrium</i>	0.012 ^a (0.002)	0.018 ^a (0.002)	0.045 ^b (0.002)	0.070 ^c (0.002)	0.079 ^c (0.006)	0.114 ^d (0.005)

Notes: Numbers are means of six flats per light level per species (with 1 SE in parentheses). Where the same lowercase letter follows two means, these values are not statistically distinguishable ($P > 0.05$) using a Tukey post hoc multiple-comparisons test. Comparisons were only done within a species. Percentage germination data for the 18% treatment are lacking, due to accidental spilling of several seed trays, but biomass is available for those individuals that emerged in this treatment.

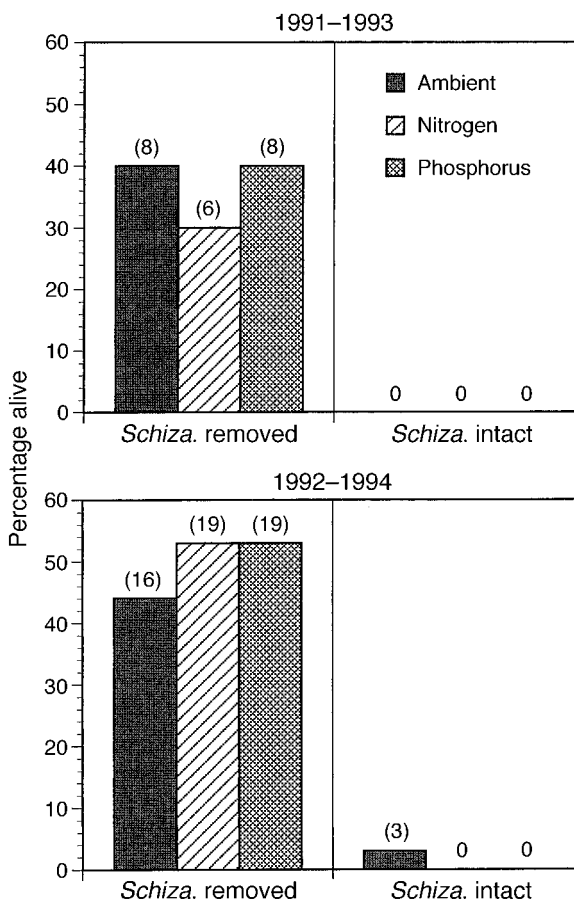


FIG. 1. Percentage of outplanted *Melinis minutiflora* seedlings outplanted to plots with *Schizachyrium* ("Schiza.") removed or intact that were still alive at the end of each of two experimental periods. Numbers in parentheses are actual numbers of seedlings alive. The key indicates nutrient treatments; "Ambient" indicates that no nutrients were added.

rainfall patterns between years when the outplant experiments were initiated, overall survival was similar with ~40% of seedlings surviving in *Schizachyrium*-removal areas. Addition of nutrients did not affect survival or time to reproduction. All surviving seedlings became reproductive and produced 5-8 flowering shoots.

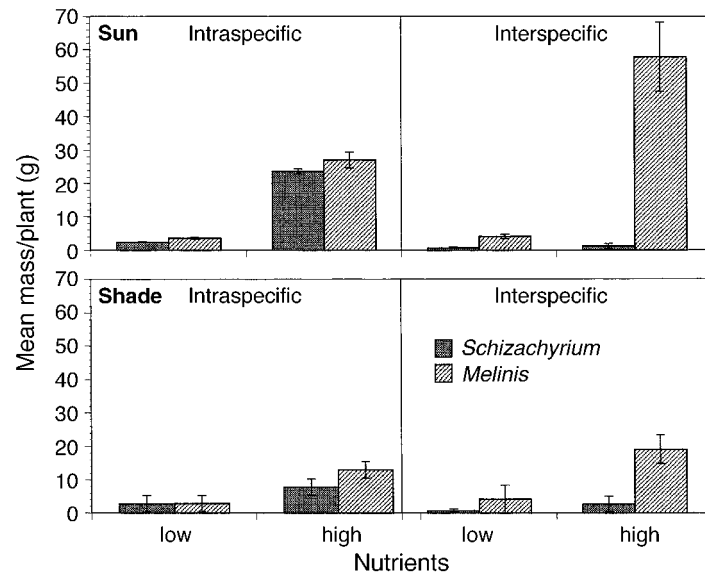
Pot experiments

Growth of both *Melinis* and *Schizachyrium* seedlings was enhanced by nutrient addition and high light (Figs. 2-4, Table 6). Both species achieved their largest total biomass in the full-sun high-nutrient condition (note difference in y-axis scale in Figs. 2 and 3; Light \times Species, $F = 1.469$, $df = 1, 32$, $P < 0.234$; Nutrient \times Species, $F = 1.685$, $df = 1, 32$, $P < 0.20$), and their total biomasses were similar when both were under intraspecific competition. Neither species could respond well to nutrient addition in the shade. There was a trend for *Melinis* to respond more than *Schizachyrium* to nutrient addition in the shade (Species \times Light \times Nutrients, $F = 3.154$, $df = 1, 32$, $P < 0.085$).

In interspecific pots, *Melinis* individuals grew much larger than *Schizachyrium* plants, and even larger than their counterparts in intraspecific pots in full-sun/high-nutrient conditions (Table 6). Indeed, interspecific competition consistently depressed *Schizachyrium*, compared to its performance with conspecifics, while it consistently benefited *Melinis*.

Reproduction was reduced by low light and increased by nutrients in both species (Fig. 3). Shading eliminated flower production in *Schizachyrium* during the time course of this study. However, it is possible that shading simply delayed flowering and that we harvested before it had occurred. Nutrients enhanced flower production only in the sun (Table 6). *Melinis* reduced flower production by *Schizachyrium* (Fig. 3, Table 6), particularly in the high-light high-nutrient environ-

FIG. 2. Total (roots + shoots) dry biomass (g) of *Melinis* and *Schizachyrium* plants at the time of harvest in the potted plant seedling study. Bars represent means \pm 1 SE; $n = 5$.



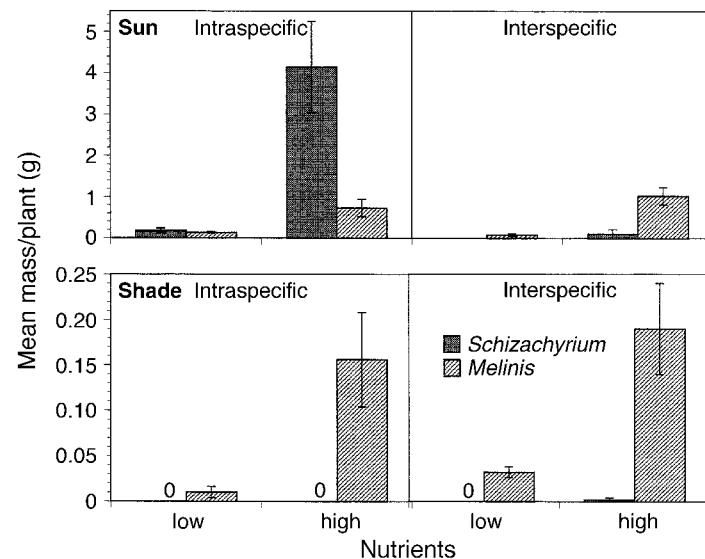
ment. Reproduction in *Melinis* was not influenced by the presence of *Schizachyrium*, but was reduced by low light and low nutrients.

Melinis plants had greater investment in roots (measured as root:mass ratio, hereafter RMR) than did *Schizachyrium* plants in all treatments (Fig. 4). Shading reduced root investment for both species (Table 6). Higher nutrients led to lower RMR in *Schizachyrium*, in both inter- and intraspecific competition. This was only true for *Melinis* under interspecific competition; with intraspecific competition, *Melinis* increased RMR with an increase in added nutrients (Competition \times Nutrients, $F = 24.35$, $df = 1, 32$, $P < 0.0001$).

Nutrients and the identity of the established competitor had a significant effect on the outcome of com-

petition between established plants and colonizing seedlings (Fig. 5; for *Melinis* seedlings, Nutrients, $F = 56.22$, $df = 1, 18$, $P < 0.001$; Competitor identity, $F = 35.62$, $df = 2, 18$, $P < 0.001$; for *Schizachyrium* seedlings, Nutrient, $F = 6.66$, $df = 1, 18$, $P < 0.019$; Competitor identity, $F = 36.75$, $df = 2, 18$, $P < 0.001$). Established *Schizachyrium* suppressed *Melinis* seedling growth at low nutrients, but this advantage was lost at high nutrients. Under high-nutrient conditions, seedlings of *Melinis* achieved the same biomass as they did in "empty" pots (Fig. 5), and established *Schizachyrium* began to discolor as the *Melinis* seedlings grew. Established *Melinis* plants suppressed all seedlings regardless of nutrient level; *Schizachyrium* seedlings only grew well in "empty" pots.

FIG. 3. Reproductive biomass of *Melinis* and *Schizachyrium* plants harvested from the potted plant seedling study. Bars represent means \pm 1 SE; $n = 5$. Note the difference in y-axis scale for sun vs. shade plants, reflecting the much greater size of sun plants.



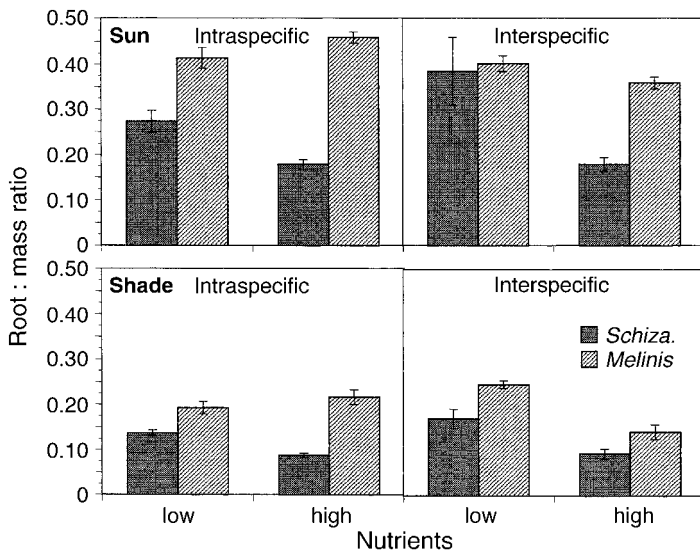


FIG. 4. Root : mass ratio (RMR; dry mass roots/total dry mass) for plants harvested from the potted plant seedling study. Bars represent means \pm 1 SE; $n = 5$.

Field competition

Our surveys of *Schizachyrium* individuals revealed that in unburned sites <0.1% of existing *Schizachyrium* plants were overgrown by *Melinis* stems, whereas in the twice-burned and old burn sites, 80% and 41%, respectively, of *Schizachyrium* plants were overgrown. Removal of *Melinis* biomass from around adult *Schizachyrium* resulted in a significant increase in growth of *Schizachyrium* in all locations. Both partial and total removal of *Melinis* increased shoot production (Table 7), but total removal had the largest effect. Leaf tissue N for both live and dead leaves was enhanced in the total-removal treatment, relative to both partial removal and control plants (Fig. 6), suggesting greater access to soil N.

Grass species responses to fire

Germination of *Melinis* seeds was not affected by the temperatures in our heating experiment (Fig. 7, $\chi^2 = 1.850$, $P < 0.80$). By contrast, germination of *Schizachyrium* seeds decreased with increasing temperatures (Fig. 7, $\chi^2 = 59.91$, $P < 0.001$). The significant χ^2 was due to a decrease in germination at 105°C and 120°C. Germination rates overall were 18.8% for *Melinis* and 81.3% for *Schizachyrium* seeds (excluding the two highest temperatures).

Adult *Melinis* plants clearly lack the ability to withstand fire: *Melinis* survival was 30% and 0% in our low- and high-intensity burns, respectively. By contrast, *Schizachyrium condensatum* tolerated even high-intensity fires. In the low-intensity burn, 93.5% of *Schi-*

TABLE 6. ANOVA results from potted plant seedling study.

Response variable	Total biomass		Reproductive biomass		Root : mass ratio	
	F	P	F	P	F	P
<i>Schizachyrium</i>						
Light	104.90	0.0001	15.90	0.001	31.91	0.001
Nutrients	342.99	0.0001	13.41	0.001	19.00	0.001
Compet. envir.	410.28	0.0001	14.15	0.001	2.88	0.099
Light \times Nutrients	104.58	0.0001	13.41	0.001	2.94	0.096
Light \times Compet. envir.	139.65	0.0001	14.15	0.001	0.78	0.385
Compet. envir. \times Nutrients	247.50	0.0001	11.90	0.002	1.80	0.189
Three-way interaction	143.35	0.0001	11.90	0.002	0.56	0.458
<i>Melinis</i>						
Light	23.88	0.001	7.98	0.008	366.37	0.0001
Nutrients	86.34	0.001	10.38	0.003	3.18	0.084
Compet. envir.	11.42	0.002	0.48	0.499	9.47	0.004
Light \times Nutrients	22.39	0.001	14.10	0.001	3.68	0.064
Light \times Compet. envir.	4.29	0.046	0.73	0.400	4.66	0.039
Nutrients \times Compet. envir.	9.33	0.005	1.08	0.307	24.35	0.001
Three-way interaction	4.95	0.033	0.23	0.634	0.83	0.371

Notes: Treatments were as follows: Light, sun vs. shade; Nutrients, low (unamended) vs. plus NPK; and Compet. envir., monospecific pots vs. interspecific mixed with density held constant. For all F values, $df = 1, 32$.

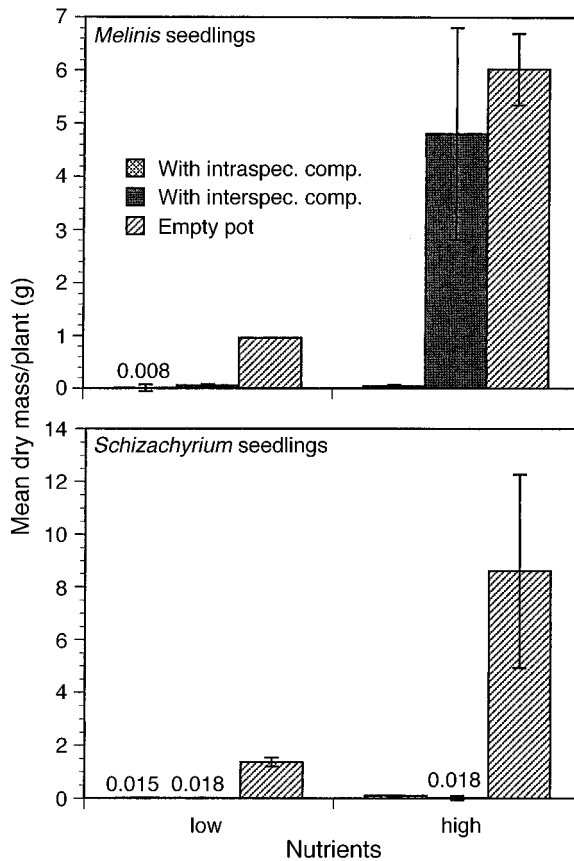


FIG. 5. Dry mass of aboveground plant material of seedlings harvested from the established plant-pot study. Bars represent the mean (± 1 SE) biomass of seedlings harvested from a pot that had an established *Schizachyrium*, *Melinis*, or no previously established plants. Means over seedlings within a pot were taken before those among pots within a treatment; $n = 4$.

TABLE 7. Net change in number of live tillers of *Schizachyrium condensatum* individuals in the *Melinis*-removal experiment.

Treatment	After 5 mo		After 14 mo	
	Change†	n	Change†	n
Total removal	18.3 ^a (2.3)	23	36.0 ^a (5.4)	24
Partial removal	7.0 ^b (1.2)	24	9.4 ^b (1.8)	24
Control	-0.9 ^c (0.7)	24	-3.3 ^c (0.7)	24
$F_{2,62}$	44.25		57.85	
P	<0.0001		<0.0001	

Notes: Because site effects were not significant ($F = 1.75$, $df = 2, 62$, $P = 0.182$, first interval; $F = 1.70$, $df = 2, 62$, $P = 0.191$, 14 mo), values presented here are means for all sites combined. F values are for treatment effects within a time interval (column) using a two-way ANOVA on log-transformed data. Where different lowercase letters follow means within a column, these are statistically different ($P < 0.05$) using a post hoc corrected Bonferroni comparison.

† Values reported are mean changes in number of tillers (with 1 SE in parentheses).

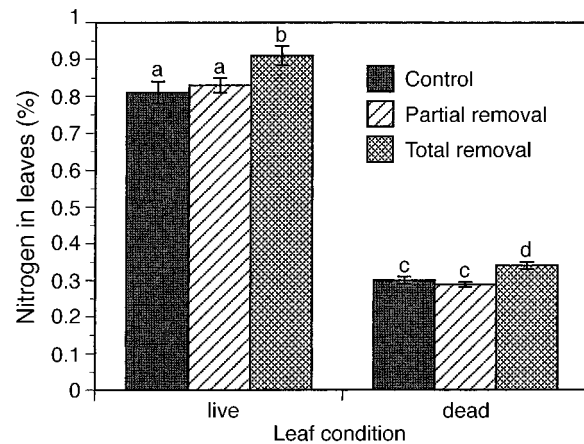


FIG. 6. Percentage N in leaf tissue from live and dead *Schizachyrium* leaves harvested from the *Melinis*-removal experiment. Values from all three habitats are combined, because habitat was not a significant source of variation; $n = 24$. Values represent means ± 1 SE. Where the same lowercase letters appear above two means, these values are not statistically different ($P > 0.05$) using a post hoc Tukey comparison.

zachyrium individuals regenerated within nine months, while in the high-intensity fire, 40% of *Schizachyrium* individuals regenerated. By contrast, after our low-intensity fire, seedling emergence from the seed bank at five months was far higher for *Melinis* than for *Schizachyrium* (mean, 232 vs. 2.4 seedlings/m², $n = 60$). This corresponds to the relative abundance of the species in the seed bank (Table 4). After the high-intensity burn, no seedlings of either grass were found during the first six months, despite adequate rainfall.

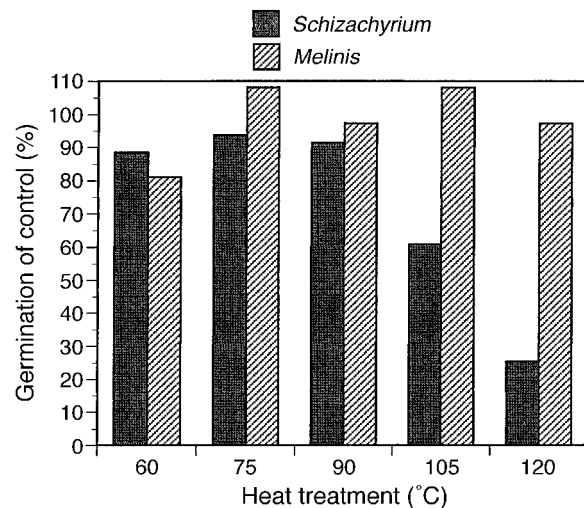


FIG. 7. Response of *Schizachyrium* and *Melinis* seeds to temperature treatments. Values represent total percentage of seeds germinating per tray over the two-month germination trial, divided by the percentage germination in the control (seeds not experiencing an artificial heat treatment).

DISCUSSION

Our data suggest that the patterns of grass domination described by Hughes et al. (1991) in their chronosequence study are relatively stable: *Schizachyrium* domination of the woodland understory and *Melinis* domination of burned sites has continued relatively unchanged. These patterns are surprising, since *Melinis* is in the seed bank in many areas of the unburned woodland, and it was consistently a dominant competitor to *Schizachyrium* in the greenhouse. Our field, laboratory, and greenhouse data suggest that *Schizachyrium*'s continued dominance in the unburned woodland is the result of priority effects (*Schizachyrium* got there first), followed by competitive suppression of *Melinis* seedlings by established *Schizachyrium*. Without *Schizachyrium*, we believe that *Melinis* could dominate the unburned woodland. Indeed, in grass removal plots established in 1991 and maintained until 1997 (D'Antonio et al. 1998), *Melinis* seedlings were constantly invading.

If *Melinis* can be found in the seed bank in the unburned woodland in patches lacking adult *Melinis*, why is it not more abundant there? It is common for species to be present in the seed bank, but lacking in the aboveground community (e.g., Leck et al. 1989). In a nearby Hawaiian site, Drake (1998) found that, while >95% of the aboveground plant cover was native species, 67% of the seed bank was comprised of exotic species. In our sites, we believe that the suppression of *Melinis* colonization is due to low light. At the soil surface in the presence of *Schizachyrium*, light levels in the unburned woodland are <3% ambient (Hughes and Vitousek 1993, D'Antonio et al. 1998), and in the greenhouse *Melinis*' germination and seedling growth were very poor at these low values. In the woodland, we observed numerous cotyledon-stage *Melinis* in permanent plots with dense adult *Schizachyrium*, but they did not survive. The limited survival of *Melinis* in outplant experiments, when *Schizachyrium* was not removed, is likely also to result from light, not nutrient, limitation, since we added abundant fertilizer with no apparent effect. Furthermore, we observed that seedlings outplanted under *Schizachyrium* became very etiolated.

In the *Schizachyrium* removal plots used for our outplant experiments, we demonstrated elsewhere (D'Antonio et al. 1998) that *Schizachyrium* had a negative effect on the growth and recruitment of woody species. It could therefore be argued that *Melinis* was only able to invade these plots because of the competitive stress *Schizachyrium* had exerted on the native community prior to our outplant experiment, making our experimental results and observations of *Melinis* invasion artifactual. However, after four years of native-species recovery in these removal plots, biomass, biomass N pools, and litterfall of native species had completely compensated for the removal of *Schizachyrium*, but irradiance at the soil surface was sub-

stantially higher than in plots with *Schizachyrium* (D'Antonio et al. 1998). We believe that, because of their growth form and climatic conditions in this region, shrubs and trees in this habitat cannot by themselves create the extremely low light conditions characteristic of a typical dense *Schizachyrium* stand. In addition, we have observed *Melinis* invasion into understory habitats elsewhere in Hawaii where *Schizachyrium* was never present (C. M. D'Antonio, *personal observation*; also see Asner and Beatty 1996), so we reject this explanation for our experimental results.

Our density survey data for *Schizachyrium* in the unburned woodland suggests that death of individuals is rare. Most observed mortality is in feral pig (*Sus scrofa*) disturbances, and we believe that pigs create enough heterogeneity in the light regime in the forest understory to account for the occasional patches of *Melinis* that occur there. Spatz and Mueller-Dombois (1975) and Aplet et al. (1990) observed a strong positive association of some introduced plants with feral pig disturbances in Hawaii. Although we noted pig activity while censusing permanent transects in 1991 and 1998, we did not follow the fate of pig-disturbed areas. Nonetheless, we believe that these offer an opportunity for *Melinis* seedlings to grow into adults in the absence of suppression by *Schizachyrium* and that the *Melinis* patches then act as seed sources to the surrounding forest. With continued access to these sites by feral pigs, we anticipate a slow increase in *Melinis* abundance.

In contrast to the patterns observed in the field, pot experiments suggested that *Melinis* should always be the dominant competitor. Possible reasons for this apparent discrepancy include historical factors, herbivory in the field, or differences in resource limitation between pot and field situations. Our data suggest that in the unburned woodland, asymmetric competition for light gives established *Schizachyrium* an advantage, whereas in our potted-plant studies species interacted for soil resources. Even in our second pot experiment, pots with established *Schizachyrium* had relatively high light levels at the soil surface, compared to the field, since there was only one established plant per pot and pots were well spaced on an open bench. In this situation, and in contrast to our field outplant experiment, *Melinis* could invade by seed when nutrients were added. N, P, and K were added together in the pots, which also makes a direct comparison to the outplant experiment difficult.

Although *Melinis minutiflora* was in Hawaii decades before *Schizachyrium* (Wester 1992), our sites and surrounding areas were grazed by feral goats throughout the last century, and goats likely slowed the colonization by *Melinis* (Mueller-Dombois 1981). *Schizachyrium* was first recorded in Hawaii Volcanoes National Park (HAVO) in 1961 and was common by 1966 while goats were still prevalent (Doty and Mueller-Dombois 1966, Wester 1992; T. Tunison, *personal communication*). The first fire carried by *Schizachyrium*

was observed in 1968 (J. T. Tunison, *personal communication*). By contrast, *Melinis* was introduced to the island in the early 1900s (Wester 1992) and was described as localized along roadsides (Doty and Mueller-Dombois 1966; J. T. Tunison, *personal communication*) and within goat exclosures (Mueller-Dombois and Spatz 1975, Loope and Scowcroft 1985); it began to increase after goat removal (Mueller-Dombois 1981). In addition, *Schizachyrium* has greater potential for rapid dispersal to new areas than does *Melinis*. Both species are wind dispersed, but *Schizachyrium*'s seeds are attached to a large fluffy plume, whereas *Melinis*'s have a soft unforked awn. By dropping seeds from a known height in the laboratory, we measured terminal velocity of *Schizachyrium* seeds as 0.6 m/s, while seeds of *Melinis* fell at 1.1 m/s. In addition, the mean height of release of *Schizachyrium* seeds in the field is 20 cm higher than that of *Melinis* (C. M. D'Antonio, *unpublished data*), contributing to greater dispersal for *Schizachyrium*.

The importance of timing of propagule arrival to who dominates a site was suggested by Gleason in his observations of plant communities in the early part of this century (Gleason 1926). It is also well known that recruitment of species into a site for sessile organisms (plants and marine invertebrates) is often influenced by competition with established individuals (e.g., Turner 1985, Grace 1987, Weiner 1990, Wedin and Tilman 1993, Connell et al. 1997, Berlow 1997). For invasive nonnative plants, however, the suppression of a later invader by an earlier arrival has not been well documented.

Community and ecosystem response to fire

In burned sites, the strong dominance of *Melinis* is surprising, because *Schizachyrium* regenerates and therefore has a head start after fire. Fire is not known to occur naturally in these sites, and many native plant species respond poorly to it (Smith 1985, Hughes et al. 1991, Smith and Tunison 1992). By contrast, the exotic grasses respond well to fire. It is surprising that *Melinis*, which establishes from seed after fire, nevertheless can become so abundant as to reduce the growth of surviving individuals of *Schizachyrium*. Hughes and Vitousek (1993) demonstrated that *Melinis* also reduces recruitment of native woody species by severely reducing light at the soil surface. In other parts of the world, fire has also been shown to provide a window of opportunity for persistent exotic species to enter a system (see D'Antonio 2000). For example, in South African fynbos, fire results in an increase in the density of invading pines and various exotic shrub species, to the detriment of native species (Richardson et al. 1990).

The mechanisms through which fire rearranges community dominance are not known for many systems, including this one. Altered herbivory and direct stimulation of seed germination by heating (e.g., Tyler

1995, 1996) are not important for the grasses we studied. It is more likely that fire affects nitrogen availability, light, and soil temperature and that these increased resources promote species change. As with other systems where infrequent fire occurs (e.g., Christensen 1973, Hobbs and Schimel 1984, Seastedt et al. 1991, Ojima et al. 1994), Hughes and Vitousek (1993) found elevated nitrogen in burned areas of the forests studied here within one year after fire. Because canopy and understory species are killed by fire, and standing biomass of *Schizachyrium* is reduced, fire dramatically increases light availability, which simultaneously increases soil temperature (e.g., Hulbert 1969, 1988). Phosphorus in surface soils can also increase dramatically after wildfire (e.g., Adams et al. 1994, Romanya et al. 1994, Overby and Perry 1996). Thus the immediate postburn environment is potentially rich in many resources. Our second pot experiment demonstrated clearly that we could promote *Melinis*' invasion of pots containing mature *Schizachyrium* simply by adding fertilizer, given moderate light availability.

Studies of vegetation regeneration in shrubby or woodland habitats document that fire-following and opportunistic seeding species often coexist with resprouting species in the initial years after fire. In many of these systems, however, the postfire invasion of herbaceous species that were not common beforehand is a temporary phenomenon, and resprouting species and/or woody seeding species regain dominance (e.g., Hanes 1977, Heinselmann 1981, Cowling and Pierce 1988, Abrahamson and Abrahamson 1996). In our sites, the invasion of woodlands by the *Melinis* after fire is not temporary; *Melinis* was abundant >22 yr since fire. Numerous other invasive exotic species that are considered to be among the worst "weeds" in other areas have the ability to respond rapidly to disturbance, compete well in the postdisturbance environment, and then hang on for a long time inhibiting the return of the system to its prior state (see Richardson et al. 1990, D'Antonio and Haubensak 1998). These species are not easily categorized, since they are both opportunistic and competitive dominant species.

The persistence of many species in fire-prone habitats is dependent upon their ability to resprout after fire. If *Schizachyrium* recruited only by seed, it would be rapidly outcompeted by *Melinis* and would become uncommon in burned sites. Instead, *Melinis* reduces *Schizachyrium*'s growth by reducing light availability and competing for soil resources (Fig. 6). It is also possible that it reduces *Schizachyrium*'s growth through allelopathy, but we know nothing about this for these species. As with competition among grasses in nitrogen-limited Venezuelan savannas of similar altitude, species replacements after fire may take years (Inchausti 1995). All of our burned sites had been at least nine years since fire when we surveyed grass densities, and, although we found that <5% of *Schizachyrium* individuals were dead, all of those were over-

grown by *Melinis*, and large *Schizachyrium* individuals were rare in burned *Melinis*-dominated sites (Table 2).

Competition, species traits, and resource levels

Experimental evidence supports the contention that dominant competitors tend to have high root investment and high growth rates under a range of nutrient availabilities (e.g., Gurevitch et al. 1990, Aerts et al. 1991, Witkowski 1991). Witkowski (1991) competed an invasive nonnative shrub against a native one under a range of nutrient conditions and found that the competitively superior nonnative species had high root investment and faster growth under all conditions. Likewise, *Melinis* was the dominant competitor under all conditions of mixed species pots in the present study. It has a high root:mass ratio (RMR) and a greater plasticity in aboveground stem orientation than *Schizachyrium* due to its vine-like growth. Aerts et al. (1991) suggest that plasticity in aboveground stem orientation and a vine-like habit may be a means by which plants with high root investment avoid the assumed trade-off between competition for nitrogen and light. Also, by producing new growth on upper parts of old stems each year, *Melinis* does not push new stems up through a dense layer of stems and foliage as *Schizachyrium* individuals do.

In contrast to its plasticity in stem orientation, *Melinis* appears to have less plasticity in RMR than does *Schizachyrium*. Several other studies on potted plants have found that dominant competitors have less plastic RMRs than subordinate species across different nutrient treatments (see review by Reynolds and D'Antonio [1996]). The difference between the allocation behavior of *Melinis* with itself vs. with *Schizachyrium* is intriguing and suggests that nutrient limitation for *Melinis* may be more severe under high nutrients with intraspecific competition.

Management implications

A review of fire effects in lowland and submontane habitats in HAVO suggests that fires in *Melinis* are worse for native species than fires where *Melinis* is absent (Tunison et al. 1993, 1995). Thus, keeping *Melinis* out of sites should be a management priority. The potential for invasion by *Melinis* after fire should be a warning to managers about possible unforeseen consequences of fire (controlled or otherwise). Understanding the biology of an undesirable species like *Melinis* is important prior to attempts at control, particularly using fire. Our data show that although *Melinis* adults are easily killed by fire, a controlled burn must be intense in order to transmit enough heat into the soil to kill *Melinis* seeds. Raison (1979) concluded that soil temperature increases during grass-fueled fires are usually <50–80°C. If soil temperatures at our sites are normally ~25°C and Raison's estimates are correct, then the soil temperatures that are reached (75–105°C) during most fires will not kill *Melinis* seed. In addition,

fire creates ideal conditions for *Melinis* growth, and, even when the seed bank of *Melinis* appears to be reduced as in our high intensity burn, it can readily re-invade if it is in surrounding areas.

Concluding remarks

Recently, Simberloff and von Holle (*in press*) reviewed studies of interactions among invasive, non-native species. They report that few studies quantify effects of invaders on each other. Of those that do, many show that invaders promote one another. This study provides a clear example of how a well-established colonist (*Schizachyrium*), can reduce the rate of establishment of a slower invading nonnative species through asymmetric competition for light. This mechanism is similar to canopy-understory interactions described for a wide range of other systems (e.g., Dayton et al. 1984, Grace 1987, Miller 1987, Weiner 1990, Wedin and Tilman 1993). Ultimately however, *Schizachyrium*, by promoting the spread of fire, indirectly promotes *Melinis*, which then persists in these sites for decades.

In addition to offering the opportunity to understand factors creating patterns in plant communities, invasions are creating new ecological patterns that may not fit models that are developed for other systems. For example, succession following wildfire in other woody species systems (e.g., Hanes 1977, Heinzelman 1981, Cowling and Pierce 1988) is characterized by postfire herbaceous flora including opportunistic species that disappear within 2–8 yr. In our system, fire promotes *Melinis*, which is an opportunistic but also persistent species, and the system does not return towards its prior state, at least during the >20 yr that we have observed it. These new patterns will help ecologists refine models of secondary succession and need to be understood before creative management strategies can be devised.

ACKNOWLEDGMENTS

We gratefully acknowledge the support of J. T. Tunison, director of Hawaii Volcanoes National Park (HAVO) Resources Management and D. Foote, director of HAVO Research (now U.S. Geological Survey Biological Resources Division) for their unflagging support, and previous directors D. Taylor and C. Stone, respectively, for initial access to sites. The HAVO fire crew assisted with experimental burns, and we would particularly like to thank J. Manassian and J. T. Tunison for their support. Field assistance was provided by T. Elias, R. Elliott, Z. Jacobi, R. Ley, M. Mack, K. Peacock, and A. C. Williams. X. Zeng assisted with tissue N analysis. Financial support was provided by NSF BSR 9119618, the Pew Foundation, and the University of California-Berkeley Committee on Research. We also thank E. Berlow, J. Levine, T. Stohlgren, and R. Callaway for feedback on the manuscript.

LITERATURE CITED

- Abrahamson, W. G., and C. R. Abrahamson. 1996. Effects of fire on long-unburned Florida uplands. *Journal of Vegetation Science* 7:565–574.
- Adams, M. A., J. Iser, A. D. Keleher, and D. C. Cheal. 1994. Nitrogen and phosphorus availability and the role of fire in heathlands at Wilson's promontory. *Australian Journal of Botany* 42:269–281.

- Aerts, R., R. G. A. Boot, and P. J. M. van der Aart. 1991. The relation between above- and belowground biomass allocation patterns and competitive ability. *Oecologia* **87**: 551–559.
- Aplet, G. H., S. J. Anderson, and C. P. Stone. 1991. Association between feral pig disturbance and the composition of some alien plant assemblages in Hawaii Volcanoes National Park. *Vegetatio* **95**:55–62.
- Asner, G. P., and S. W. Beatty. 1996. Effects of an African grass invasion on Hawaiian shrubland nitrogen biogeochemistry. *Plant and Soil* **186**:205–211.
- Berlow, E. L. 1997. From canalization to contingency: historical effects in a successional rocky intertidal community. *Ecological Monographs* **67**:435–460.
- Christensen, N. L. 1973. Fire and the nitrogen cycle in California chaparral. *Science* **181**:66–68.
- Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-yr study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological Monographs* **67**:461–488.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119–1144.
- Cowling, R. M., and S. M. Pierce. 1988. Secondary succession in coastal dune fynbos: variation due to site and disturbance. *Vegetatio* **76**:131–140.
- D'Antonio, C. M. 2000. Fire, plant invasions and global change. Pages 65–93 in H. Mooney and R. Hobbs, editors. *Invasive species in a changing world*. Island Press, Covelo, California, USA.
- D'Antonio, C. M., and K. A. Haubensak. 1998. Community and ecosystem impacts of introduced species. *Fremontia* **26**:13–18.
- D'Antonio, C. M., R. F. Hughes, M. Mack, D. Hitchcock, and P. M. Vitousek. 1998. The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. *Journal of Vegetation Science* **9**:699–712.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by introduced grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics* **23**: 63–87.
- Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. Pages 269–284 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- Dayton, P. K., V. Currie, T. Gerrodette, B. D. Keller, R. Rosenthal, and D. Ven Tresca. 1984. Patch dynamics and stability of some California (USA) kelp communities. *Ecological Monographs* **54**:253–290.
- Doty, M. S., and D. Mueller-Dombois. 1966. Atlas of biocology studies in Hawaii Volcanoes National Park. University of Hawaii, Botanical Science paper no. 2. Manoa, Hawaii, USA.
- Drake, D. 1998. Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. *Journal of Vegetation Science* **9**:103–112.
- Dungan, M. L. 1986. Three-way interactions: barnacles, limpets and algae in a Sonoran desert rocky intertidal zone. *American Naturalist* **127**:292–316.
- Fowler, N. 1990. Disorderliness in plant communities: comparisons, cases, and consequences. Pages 291–307 in J. B. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, New York, New York, USA.
- Gleason, H. M. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**:7–26.
- Grace, J. B. 1987. The impact of preemption on the zonation of two *Typha* species along lakeshores. *Ecological Monographs* **57**:283–303.
- Gurevitch, J., P. Wilson, J. L. Stone, P. Teese, and R. J. Stoutenburgh. 1990. Competition among old-field perennials at different levels of soil fertility and available space. *Journal of Ecology* **78**:727–744.
- Hanes, R. L. 1977. California chaparral. Pages 417–469 in M. G. Barbour and J. Major, editors. *Terrestrial vegetation of California*. John Wiley & Sons, New York, New York, USA.
- Heinselman, M. L. 1981. Fire and succession in the conifer forests of northern North America. Pages 374–405 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest succession: concept and applications*. Springer-Verlag, New York, New York, USA.
- Hobbs, N. T., and D. S. Schimel. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. *Journal of Range Management* **37**: 402–405.
- Holcomb, R. T. 1987. Eruptive history and longterm behaviour of Kilauea Volcano. Pages 261–350 in R. W. Decker, R. L. Wright, and P. H. Stauffer, editors. *Volcanism in Hawaii*. U.S. Geological Survey Professional Paper **1350**.
- Hughes, T. H. 1989. Community structure and diversity of coral reefs: the role of history. *Ecology* **70**:275–279.
- Hughes, R. F., and P. M. Vitousek. 1993. Barriers to shrub re-establishment following fire in the seasonal submontane zone of Hawaii. *Oecologia* **93**:557–563.
- Hughes, R. F., P. M. Vitousek, and T. Tunison. 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawaii. *Ecology* **72**:743–746.
- Hulbert, L. C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology* **50**:874–877.
- Hulbert, L. C. 1988. Causes of fire effects in tallgrass prairie. *Ecology* **69**:46–58.
- Inchausti, P. 1995. Competition between perennial grasses in a neotropical savanna: the effects of fire and of hydric-nutritional stress. *Journal of Ecology* **83**:231–243.
- Leck, M. A., V. T. Parker and R. C. Simpson. 1989. *Ecology of soil seed banks*. Academic Press, San Diego, California, USA.
- Loope, L. L., and P. G. Scowcroft. 1985. Vegetation response within exclosures in Hawaii: a review. Pages 377–402 in C. P. Stone and J. M. Scott, editors. *Hawaii's terrestrial ecosystems: preservation and management*. University of Hawaii Cooperative National Park Resources Study Unit, Manoa, Hawaii, USA.
- Milchunas, D. G., and W. K. Lauenroth. 1995. Inertia in plant community structure: state changes after cessation of nutrient enrichment stress. *Ecological Applications* **5**:452–458.
- Miller, T. E., 1987. Effects of emergence time on survival and growth in an early old-field plant community. *Oecologia* **72**:272–278.
- Mooney, H. A. 1972. The carbon balance of plants. *Annual Reviews of Ecology and Systematics* **3**:315–346.
- Mueller-Dombois, D. 1981. Vegetation dynamics in a coastal grassland of Hawaii. *Vegetatio* **46**:131–140.
- Mueller-Dombois, D., and G. Spatz. 1975. The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. *Phytocoenologia* **3**:1–29.
- Ojima, D. S., D. Schimel, W. Parton, and C. E. Owensby. 1994. Long and short term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* **24**:67–84.
- Overby, S. T., and H. M. Perry. 1996. Direct effects of prescribed fires on available nitrogen and phosphorus in an Arizona chaparral watershed. *Arid Soil Restoration and Rehabilitation* **10**:347–357.
- Parsons, J. 1972. Spread of African pasture grasses to the

- American tropics. *Journal of Range Management* **25**:12–17.
- Pickett, S. T. A., and P. S. White, editors. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, London, UK.
- Raison, R. J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. *Plant and Soil* **51**:73–108.
- Reynolds, H. L., and C. D'Antonio. 1996. The ecological significance of plasticity in root weight ratio in response to nitrogen: opinion. *Plant and Soil* **185**:75–97.
- Richardson, D. M., R. M. Cowling, and D. C. LeMaitre. 1990. Assessing the risk of invasive success in *Pinus* and *Banksia* in South Africa mountain fynbos. *Journal of Vegetation Science* **1**:629–642.
- Romanya, J., P. K. Khanna, and R. J. Raison. 1994. Effects of slash burning on soil phosphorus fractions and sorption and desorption of phosphorus. *Forest Ecology and Management* **65**:89–103.
- Seastedt, R. T., J. M. Briggs and D. J. Gibson. 1991. Controls over nitrogen limitation in tallgrass prairie. *Oecologia* **87**:72–79.
- Smith, C. W. 1985. Impact of alien plants on Hawaii's native biota. Pages 180–240 in C. P. Stone and J. M. Scott, editors. *Hawaii's terrestrial ecosystems: preservation and management*. University of Hawaii Cooperative National Park Studies Unit, Manoa, Hawaii, USA.
- Smith, C. W., and J. T. Tunison. 1992. Fire and alien plants in Hawaii: research and management implications for native ecosystems. Pages 394–408 in C. P. Stone, C. W. Smith, and J. T. Tunison, editors. *Alien plant invasions in native ecosystems of Hawaii. Management and Research*. University of Hawaii Cooperative National Park Studies Unit, Honolulu, Hawaii, USA.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**:353–391.
- Spatz, G., and D. Mueller-Dombois. 1975. Succession patterns after pig digging in grassland communities on Mauna Loa, Hawaii. *Phytocoenologia* **3**:346–373.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey, USA.
- Tunison, J. T., J. A. K. Leialoha, R. L. Loh, L. W. Pratt and P. K. Higashino. 1993. *Fire effects in the coastal lowlands of Hawaii Volcanoes National Park*. University of Hawaii Cooperative National Park Resources Studies Unit, Technical Report 88. University of Hawaii, Manoa, Hawaii, USA.
- Tunison, J. T., R. L. Loh, and J. A. K. Leialoha. 1995. *Fire effects in the submontane seasonal zone of Hawaii Volcanoes National Park*. Cooperative National Park Resources Study Unit Technical Report 97: Cooperative Agreement CA8007-2-9004. University of Hawaii, Manoa, Hawaii, USA.
- Turner, T. 1985. Stability of rocky intertidal surfgrass beds: persistence, preemption, and recovery. *Ecology* **66**:83–92.
- Tyler, C. M. 1995. Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology* **83**:1009–1020.
- Tyler, C. M. 1996. Relative importance of factors contributing to postfire seedling establishment in maritime chaparral. *Ecology* **77**:2182–2195.
- Underwood, A. J. 1996. *Experiments in Ecology*. Cambridge University Press, Cambridge, UK.
- Wedin, D., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs* **63**:199–229.
- Weiner, J. 1990. Asymmetric competition in plant populations. *Trends in Ecology and Evolution* **5**:360–364.
- Wester, L. 1992. Origin and distribution of adventive alien flowering plants in Hawaii. Pages 99–154 in C. P. Stone, C. W. Smith, and J. T. Tunison, editors. *Alien plant invasions in native ecosystems of Hawaii. Management and Research*. University of Hawaii Cooperative National Park Studies Unit, Honolulu, Hawaii, USA.
- Wilson, S. 1988. The effect of initial advantage on the course of plant competition. *Oikos* **51**:19–24.
- Witkowski, E. T. F. 1991. Growth and competition between seedlings of *Protea repens* (L.) L., and the alien invasive, *Acacia saligna* (Labill.) Wendl. in relation to nutrient availability. *Functional Ecology* **5**:101–110.