RESEARCH ARTICLE

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Effects of Drainage, Fire Exclusion, and Time-Since-Fire on Endemic Cutthroat Grass Communities in Central Florida

Rebecca Yahr'

Eric S. Menges

Dawn Berry'

Archbold Biological Station
P.O. Box 2057
Lake Placid, FL 33852 USA
ry2 @ duke.edu

Current address: Duke University, Department of Botany, Box 90338, Durham, NC 27708 USA
2 Current address: Florida Game and Fresh Water Fish Commission, 505 Lakeside Drive, Lake Placid, FL 33852 USA

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ABSTRACT: In sites historically dominated by the central Florida endemic cutthroat grass *(Panicum abscissum* Swallen), we compared the effects of two management regimes in place for 55 years: natural (undrained, with periodic fire) versus altered (drained and fire excluded). In 1995 we sampled a total of 55 sites dominated by cutthroat grass in 1940 at Archbold Biological Station in south-central Florida. We assessed cutthroat grass abundance, flowering, and associated community composition and structure. Cutthroat grass vigor was markedly reduced where management combined fire exclusion and altered drainage. Nearly 75% of sites managed to mimic natural conditions remained in cutthroat grass, while nearly 66% of sites with altered management shifted to other vegetation types. The most common results of fire exclusion and drainage were the invasion of former cutthroat grass sites by bayhead species, xeric oaks, or pines. Cutthroat grass flowers only within a few months after fire, but no other effects of time-since-fire were found in a chronosequence of 0—28 years. Without hydrological alteration, cutthroat grass may persist under a fairly wide range of fire-return intervals. Restoration of drained areas may be hampered by poor recolonization by cutthroat grass. Historically, highly flammable cutthroat grass communities may have been important in increasing fire frequency in local landscapes.

Index terms: cutthroat grass, endemic species, fire, grasslands, management

INTRODUCTION

Plant communities dominated by herbaceous species and maintained by periodic disturbances are particularly sensitive to changes in land management practices because they are susceptible to being over-grown by woody vegetation. Woody species are quick to invade meadows, savannas, and other grasslands where the fires that historically maintained herbaceous vegetation have been excluded by human intervention (e.g., San Jose and Farinas 1991, Magee and Antos 1992). Mesic temperate grasslands are especially prone to invasion by woody species without periodic disturbances from fire or large herbivores (e.g., Bowles and McBride 1998).

Frequent fires also influence community structure in part by limiting or exhausting carbohydrate reserves of resprouting woody species (Axelrod and Irving 1978, White 1983). In addition, changes in disturbance regimes can alter plant species composition if reproduction is inhibited by either the absence of fire (Petersen 1983, Abrahamson and Hartnett 1990) or inappropriate season of burn (Robbins and Myers 1992). The flowering response of many grass species is strongly dependent upon season of burn (Henderson et al. 1983, Abrahamson 1984), although responses vary by species and by year (Glenn-Lewin et al. 1990). Season of fire is also implicated in the replacement of some species over time under specified regimes (Howe 1994).

Because natural fire regimes are not intact in fragmented landscapes, land managers recognize the need for active and deliberate prescribed fire management (e.g. Main and Menges 1997). Stewards of conservation lands in and around Florida's Lake Wales Ridge are faced with making land management decisions on the basis of only a small body of data. We know that fire exclusion can cause flatwoods, dry prairies, and seasonal ponds to be replaced by bayheads-seasonally flooded broadleaved evergreen hardwood stands (Peroni and Abrahamson 1986 and references therein, Abrahamson and Hartnett 1990, Landman and Menges 1999). Grasslands in coastal sites also can be replaced (Duncan et al. 1996). However no study has yet focused on management of central Florida's endemic cutthroat grass communities.

Cutthroat grass communities are seasonal wetlands, typically dominated by cutthroat grass *(Panicum abscissum).* These communities can vary from dense monospecific swards in seasonal depressional marshes or seasonal ponds. to gently sloping lawns with patchy shrub cover of gall-berry *(Ilex glabra),* saw palmetto *(Serenoa repens),* orfetterbush *(Lyonia lucida),* or highly diverse and mixed herbaceous seepage slopes (Bridges and Orzell 1998). Along the slopes of the Lake Wales Ridge and the geologically similar but much younger Bombing Range Ridge, cutthroat grass occurs in seeps on an elevation gradient along which a series of distinct community types is distributed (Bridges and Orzell 1998). Nomenclature follows Wunderlin (1998).

In areas away from the ridge slopes, how-ever, only a subset of these types occurs. On the southern end of the Lake Wales Ridge, cutthroat grass frequently occurs as a dominant in depressional seasonal ponds, or as a dominant in a distinct zone about the border of wetter zones of seasonally flooded ponds dominated by Edison's St. John's-wort *(Hypericum edisonianum)* or maidencane *(Panicum hemitomum).* These seasonal wetlands are interspersed in a mosaic of scrub and flat-woods. We follow a scheme modified slightly from the Archbold Biological Station vegetation classification (Abraham-son et al. 1984), which distinguishes nine separate vegetation types in which cut-throat can be found on the southern Lake Wales Ridge: cutthroat grass-dominated seasonal ponds, cutthroat grass edges (around another pond type), cutthroat grass flatwoods, palmetto flatwoods, gallberry flatwoods, wiregrass *(Aristida beyrichiana)* flatwoods, seasonal ponds dominated by other species, scrubby flatwoods, and bay-heads.

Cutthroat grass communities can sustain frequent fires due to rapid regeneration of fine, flashy fuels. Cutthroat grass communities are also suspected to be sensitive to changes in fire history (Bridges and Orzell 1998) and to play a strong role in maintaining fire frequencies in the larger up-land landscape (Menges 1998). Even in fire-managed areas, insufficiently frequent fires (Bridges and Orzell 1998) may threat-en the long-term persistence and diversity of some cutthroat grass community types.

As a plant of seasonal ponds and seeps, cutthroat grass is probably also susceptible to alterations in drainage. With both fire exclusion and drainage, cutthroat grass vegetation can be invaded by bay trees (a guild of evergreen hardwoods) or xeric shrubs (Peroni and Abrahamson 1986, Bridges and Orzell 1998). Flowering of cutthroat grass is cued by growing-season fires (Abrahamson 1984, Rob-bins and Myers 1992). Growth is generally vegetative from rhizomes at or just below the soil surface, with individual plants probably persisting for several decades. Cutthroat grass recovers slowly (if at all) from mechanical disturbances such as disking or pig rooting. Flowering is not only cued by fire but also by treatments mimicking some effects of fire, such as clipping (Robbins and Myers 1992); and plants flower sporadically along road-sides and following other mechanical disturbance (Bridges and Orzell 1998).

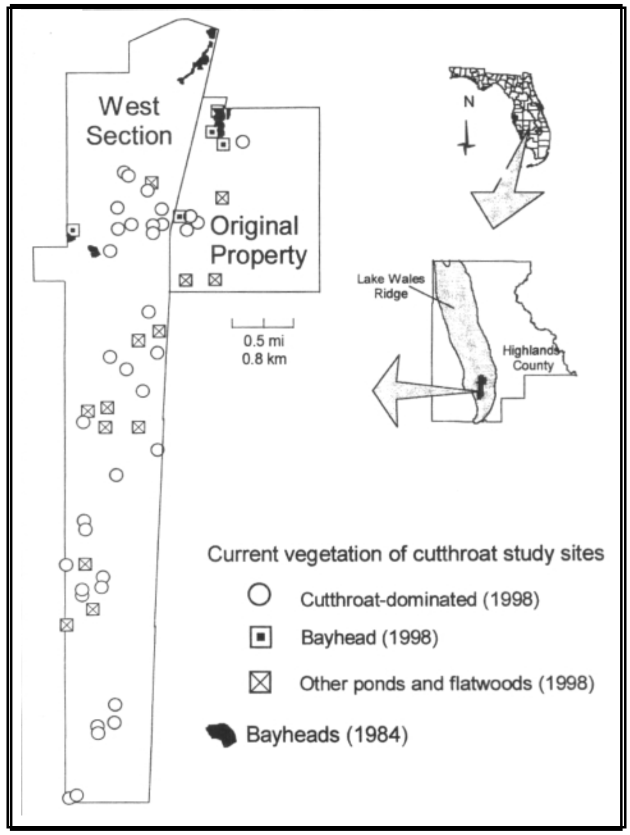

Figure 1. Distribution of study sites and current vegetation of former cutthroat-grass-dominated areas at Archbold Biological Station, Highlands County, Florida. The original property has been altered (drained and without fire) since 1932, and the west section has received periodic fire without alteration of hydrology ("natural" management regime).

The specific objectives of this study were to determine the role of fire-return interval (time-since-last-fire), fire history (long-term fire exclusion versus periodic burning), and drainage on structural and compositional characteristics of this endemic community and its dominant and defining species.

Since the term "cutthroat" historically has been used to refer both to a grass species and the communities it dominates, we de-fine the term in this paper as referring to only the species *Panicum abscissum* Swallen (Poaceae), unless it is used as an epithet describing cutthroat-grass-dominated communities, as in "cutthroat grass flatwoods."

MATERIALS AND METHODS

Species

Cutthroat grass is found scattered in 11 counties in south and central peninsular Florida, but occurs as a dominant only in Highlands and Polk Counties (Bridges and Orzell 1998). Most extant occurrences are found in association with the Lake Wales and Bombing Range Ridges. Cutthroat grass was long listed as a Federal Candidate 2 species (Wood 1994), reflecting the need for more research before potential listing as a threatened or endangered species.

Study Sites

Study sites were distributed throughout Archbold Biological Station (ABS) (Figure 1), a privately owned natural area of 1,948 ha located at the southern end of the biogeographically unique and endemic-rich Lake Wales Ridge (27°11'N, 81°21 ' W, Highlands County, Florida). Cutthroat grass at ABS exists largely in dense mono-specific stands in seasonal ponds within a matrix of more mesic flatwoods and up-land vegetation such as xeric scrubby flat-woods and rosemary scrub. Most of the sampling sites represent historic, and often extant, seasonal ponds.

Management history is well documented for discrete areas of ABS, and there is a complete fire history since 1968 as well as records of drainage ditch installation. Two "treatment blocks" corresponding to sepa-rate land parcels on the station property have been subjected to two distinct man-agement regimes (Figure 1). The original oroperty was historically, and for the most part remains, fire excluded (experiencing no burns since at least 1927) and has been drained by numerous ditches installed in 1932. Prescribed fire has since been reintroduced in some areas but did not affect cutthroat grass until 1990. The west section has been neither drained nor fire excluded, and has experienced periodic wild burns throughout this century and pre-scribed fires since 1977. Under the current ABS fire plan, cutthroat-grass-dominated vegetation types (seasonal ponds and flatwoods) will most often be burned at 2- to 5-year or 6- to 9-year fire-return intervals (Main and Menges 1997), but in 1995 parcels existed in all time-since-fire classes.

This study has the disadvantage of not being experimental. Instead, we took ad-vantage of two distinct treatment combinations that have been in place since 1932. No replication of sites was possible in the available area. However, within-site repli-cation across different local hydrological and vegetative conditions probably increas-es the robustness of the results. In addition, because the management regimes presented here are typical of many cutthroat-dominated sites, we hope that these findings can be used as a frame of refer-ence for cutthroat-dominated areas off the Lake Wales Ridge.

Methods

Our basic approach involved (1) identify-ing cutthroat-grass-dominated areas on 1940-vintage aerial photographs; (2) sam-pling cutthroat grass vigor, vegetation type, and dominant vegetation in 1995 (55 years later) in a subsample of the 1940 sites; and (3) assessing the effects of the two con-trasting management regimes.

Mapping and Selecting Former Cutthroat Grass Areas

We used 1940-vintage aerial photographs to photo-interpret cutthroat-grass-dominat-ed vegetation in sections 5, 7, 8, 18, 19, 30, and 31 of Archbold Biological Station. The outlines of cutthroat-grass-dominated vegetation were then transferred to 1989 aerials with topographic lines (Southwest Florida Water Management District, scale 1 inch == 200 feet).

During the mapping process, we checked our ability to photo-interpret cutthroat grass swards by applying our methods to recent aerials. We then ground-truthed areas of seasonal ponds and flatwoods identified as cutthroat grass dominated. We correctly mapped the community and its boundaries in 53 out of 57 (93%) of these test sites.

We documented the fire and drainage histo-ries of each of the sites determined to have been cutthroat grass dominated in 1940. In the west section, we checked the burn histo-ries for each site based on ABS fire records (unpublished data beginning in 1967). For each site, we determined year, intensity (light, moderate, severe), and coverage (par-tial or complete) of the last burn. We exclud-ed all sites only lightly or partially burned. In the Original Property, we excluded sites where drainage conditions were uncertain. We also excluded undrained areas that were within 50 m of a drainage ditch. In some areas of I.he original property, fire was rein-troduced beginning in 1990, and we includ-ed only those sites that had completely burned once between 1990 and 1995.

After we excluded only lightly or partially burned sites and sites where fire was recently reintroduced in the fire-excluded parcel, a total of 125 sites remained. We assigned each of the remaining sites to one of two treatment combinations (Figure 1): altered (drained and fire-excluded [Original Property]) or natural (neither drained nor fire-excluded [West Sec-tion]). Of 29 Original Property sites mapped as cutthroat grass in 1940, we randomly se-lected 12. In the West Section, we stratified sampling randomly by year of last burn to investigate effects of time-since-fire over a total of 43 (of 96) sites.

Transect Location and Cutthroat Grass Sampling

In each study site, we located a transect along the long axis of the patch on the map of 1940 cutthroat grass vegetation. The transects varied in length depending on the size of the former cutthroat grass patch. The aerial photos on which the map was made provided enough resolution (1 inch = 200 feet) to accurately locate these transects in the field using visible land-marks such as trees or roads.

Along each transect, we located ten 30-cm by 30-cm quadrats in stratified random fashion. In each quadrat, we measured flowering (number of flowering culms) and recorded four estimates of above-ground vegetative cutthroat grass vigor: percent cover (ocular estimate of total cut-throat grass canopy coverage), number of green clumps or tillers, aboveground green biomass (clipped 2 cm above ground lev-el, dried and weighed in the lab), and height of the sward (measured by height of pro-jected continuous canopy). All four mea-sures of cutthroat grass vigor were closely correlated (all r values > 0.7, $n=61$, $p < 0.001$). Therefore, we used cutthroat grass dry weight as our best estimate of cut-throat grass vigor and present no further results on the other three measures.

Our initial observations corroborated Rob-bins and Myers' (1992) finding that cut-throat grass flowering in native vegetation was cued almost exclusively by growing-season fire. Consequently, we added an-other 16 randomly chosen sites in the West Section with postfire intervals of 2–65 months in order to resolve postfire flower-ing response.

Current Vegetation Type and Dominant Species

We classified the current vegetation type for each transect, using a scheme modified slightly from the ABS vegetation classifi-cation (Abrahamson et al. 1984). We identified nine vegetation types: cutthroat-grass-dominated seasonal ponds, cutthroat grass edges (around another pond type), cutthroat grass flatwoods, palmetto flat-woods, gallberry flatwoods, wiregrass flatwoods, seasonal ponds dominated by other species, scrubby flatwoods, and bay-heads. To increase sample sizes for most analyses, we collapsed these nine vegetation types into five types (cutthroat-grassdominated, ponds dominated by other species, flatwoods, scrubby flatwoods, and bayheads). The effects of treatments on the current vegetation type were analyzed using contingency tables and chi-square tests.

In each quadrat we also recorded one or a few dominant species in each of three strata (herbs, lacking aboveground woody tissue; shrubs, with aboveground woody tissue and height less than 3 m; and trees, greater than 3 m tall). We visually estimated percent canopy coverage for each shrub and tree species and recorded a species as dominant if it covered at least one-third of the quadrat. Dominant species need not have been rooted in the quadrat. We re-corded dominance as frequency over each site. All fieldwork was carried out in late winter and early spring before the year's new tillers appeared.

Dominance in each stratum for each species was represented by different variables. To increase sample sizes and decrease the number of tests, we combined dominant bayhead species (loblolly bay *[Gordonia lasianthus],* sweet bay *[Magnolia virginiana],* swamp bay *[Persea palustris],* and dahoon holly *[Ilex cassine])* for shrub and tree dominance. We also summed the two scrub oaks, myrtle oak *(Quercus myrtifolia)* and sand live oak *(Q. geminata).* We analyzed 11 dominance variables, one for the tree layer (south Florida slash pine *[Pinus elliottii* var. *densa* Little and Dorman]), one combined tree and shrub layer (bayhead species), seven shrub layer dominants (Edison's St. John's-wort, saw palmetto, gallberry, Atlantic St. John's-wort *[Hypericum reductum],* fetterbush, oaks *[Quercus* spp.], and swamp bay), and two herb layer dominants (cutthroat grass, shortspike bluestem *[Andropogon brachystachyus]).* We analyzed the effects of management regime on the percent of quadrats with each species or species group dominant at the site (former cutthroat-grass-dominated patch) level.

The distributions of dominance variables included many zeroes and therefore could not be transformed to satisfy the assumptions of parametric statistics. Instead, we used nonparametric Mann-Whitney U tests to compare the "altered" management regime to the "natural" regime. We report both unadjusted p values and those adjusted for the 12 independent analyses (dominance values for 11 species plus cutthroat grass dry weight, 1 set of U tests each; criticalp value for study-wide significance at the 0.05 level is 0.0042).

Time-Since-Fire

In the West Section, we investigated the role of time-since-fire on both cutthroat grass and community dominants (using the same species and species groups above). We performed regressions on the number of years since the last fire on cut-throat grass dry weight and dominance variables. For sites in the West Section with no record of the year of the last fire, we assigned a fire year of 1966—the year preceding station fire records. Since this area was actively fire managed before ABS acquired it, and stand structure was not characteristic of overgrown habitats at that time (K. Main, ABS Land Manager, pers. com.), this estimate is probably reason-able. We analyzed all data using SPSS software (1997).

RESULTS

Effects of Management Regime on Cutthroat Grass

Cutthroat grass vigor was markedly reduced under the historically "altered" management regime of fire exclusion and drainage. Compared to "natural" management, the 12 sites that were both fire excluded and drained had less than one-third the cutthroat grass dry weight (2.86 g vs. 10.27 g per quadrat, U=118, unadjusted p=0.004; Table 1, Figure 2a). In addition, cutthroat grass declined by more than half as a dominant herb in the altered management regime (30% vs. 68%, U=102, p=0.001; Table 1, Figure 2b).

Table 1. Mean values for dominance and cutthroat grass dry weight per quadrat for the two management regimes (sample sizes for number of ponds) andp values for Mann-Whitney U tests. See text for species included in Bayhead and Scrub Oak categories.

Variable[a]	Natural Management (n=43)	Fire Excluded, Drained (n=12)	Unadjusted p
Cutthroat grass dry weight (g)	10.27	2.86	0.004'
Panicum abscissum (H)	68.37	30.00	0.001"
Pinus elliottii var. *densa* (T)	41.16	75.00	0.006
Hypericum edisonianum (S)	34.88	10.00	0.078
Serenoa repens (S)	22.09	23.33	0.171
Ilex glabra (S)	10.23	18.33	0.042
Andropogon brachystachyus (H)	4.88	9.16	0.386
Hypericum reductum (S)	8.84	0.00	0.139
Bayhead species (TS)	3.48	21.67	0.007
Lyonia lucida (S)	5.81	5.83	0.145
Scrub oaks (S)	0.05	19.17	0.000*
Persea palustris (S)	0.01	0.14	0.009

[a] Except for cutthroat grass dry weight, all are dominance variables, and are listed in order of study-wide means. Dominance was calculated for each site as frequency of species that covered more than 30% of each quadrat in each of three strata: (T) tree layer dominance, (S) shrub layer dominance, or (H) herbaceous layer dominance; TS is tree or shrub layer dominance.

[b] Significant at $p < 0.05$ when adjusted studywide for 12 U tests.

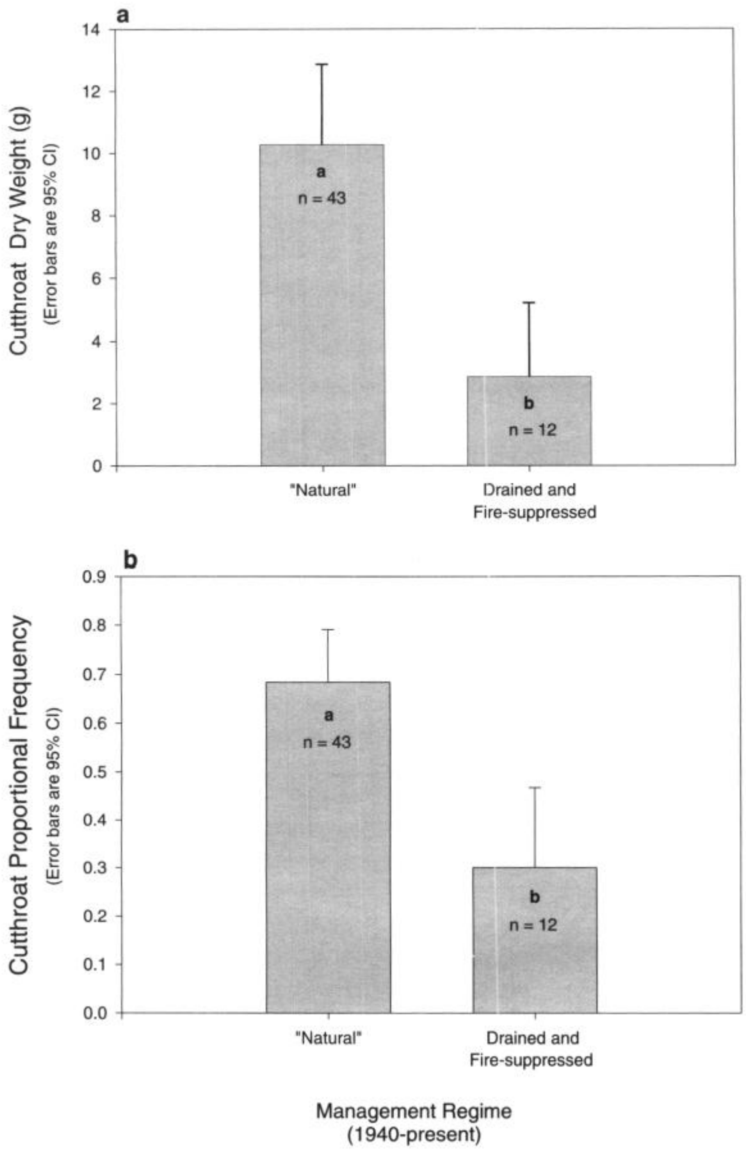

Figure 2. Effects of management regime on (a) cutthroat grass vegetative vigor as measured by aboveground biomass, and (b) dominance in the herbaceous layer, measured as proportional (percent-age of quadrats occupied by site) frequency. For each, different letters indicate significant pairwise differences (adjusted p-values) detected using Mann-Whitney U tests.

Cutthroat grass only flowers within a few months of fire, after which the plants are vegetative. Of the 16 sites that were 2–65 months postfire, all 6 of the sites burned within the prior growing season exhibited a strong flowering response (Figure 3). None of the sites we sampled was burned during the dormant season. Flowering was also observed in 6 of the original 61 sites that were 0–28 years postfire (9.8%); 5 of these were burned the previous growing season. Plants in one of five two-year-old burns also flowered. Otherwise, we found no effects of time-since-fire on any measure of cutthroat grass vigor.

Effects of Management Regime on Vegetation Type

Cutthroat-grass-dominated vegetation has generally persisted in areas managed with periodic fires and intact hydrology. In the West Section, the area where land management mimicks natural conditions, 32 of 43 sites (74.4%) remained cutthroat grass dominated (Figure 4, Table 2). In sharp contrast, regimes with drainage and fire exclusion were associated with the loss of cutthroat grass as a dominant (Fisher's exact 2-sided test, p = 0.015). Of these 12 sites, 8 (66.7 %) were converted to non-cutthroat-grass-dominated vegetation types, and only 4 sites remained cutthroat grass dominated (Figure 4). Overall, of those sites that were converted to non-cutthroat grass dominated vegetation, half were still recognizably flatwoods or seasonal ponds in structure and composition.

Dramatic conversion of cutthroat-grass-dominated vegetation to woody vegetation types occurred in some areas of the drained and fire-excluded Original Property. Most notably, bayhead species were able to invade where seed sources were nearby (Figure 1). Nine sites were invaded by typical bay shrubs or trees (at least one quadrat was dominated by either trees or shrubs), and of those, five sites were converted to bayheads. Four of the conversions were in the drained and fire excluded areas. Scrub oaks invaded a total of twelve sites (at least one quadrat was dominated by myrtle oak or sand live oak), and two of these were converted to scrubby flatwoods, both of them in the drained and fire-excluded area.

Effects of Management Regime on Species Dominance

The combination of fire exclusion and drainage significantly altered the vegetation of former cutthroat grass sites relative to sites managed to mimic natural conditions (Table 1). Fire exclusion and drain-age also encouraged increases in tree dominance by south Florida slash pine (75% vs. 41%, U=126, p=0.006; Figure 5b). In addition to the effects on cutthroat grass, fire exclusion and drainage were associated with large increases in woody plant cover, particularly bayhead species (22% vs. 3%, U=172, p=0.007; Figure 5c), including *Persea* shrubs (14% vs. 1%, U=184, p=0.009) and scrub oaks (19% vs. 0%, U=72, p < 0.001; Figure 5d). After adjusting for multiple independent tests, we found significant effects on cutthroat grass abundance and dominance, scrub oak dominance, and near-significant results (adjusted p < 0.10) for south Florida slash pine, bayhead species, and *Persea* spp. dominance.

Shrub species that dominate flat-woods (saw palmetto, gallberry, Atlantic St. John's-wort, fetter-bush) appeared insensitive to management regime. The endemic shrub Edison's St. John's-wort, more characteristic of seasonal ponds than flatwoods, was less abundant with both drainage and fire exclusion than it was at nat-urally managed sites. However, this trend was not significant.

In the West Section, where we sampled from a range of times (0–28 years) since fire, we found no effects of time-since-fire on community dominants.

DISCUSSION

Effects of Fire Exclusion and Drainage on Cutthroat Grass Vegetation

Fire exclusion together with site drainage dramatically decrease cutthroat grass vigor and dominance in the seasonal wetlands studied here. In the most extreme cases, cutthroat grass was completely eliminated from sites by 45 years of fire exclusion (Figure 2). At other sites, a few scattered tufts of cutthroat grass remained under canopies of woody plants or between tufts of broomsedge (*Andropogon brachystachyus*). In contrast, most former cutthroat grass areas in the "natural" West Section had complete and healthy appearing swards of this grass. The loss of cutthroat grass in altered areas was accompanied by shifts in vegetation, including increases in xeric oaks, bayhead shrubs, and south Florida slash pine trees in various sites (Figure 5).

Dramatic shifts in species dominance are associated with cutthroat grass decline. With both fire exclusion and site drainage, dominance of woody plants increases. This

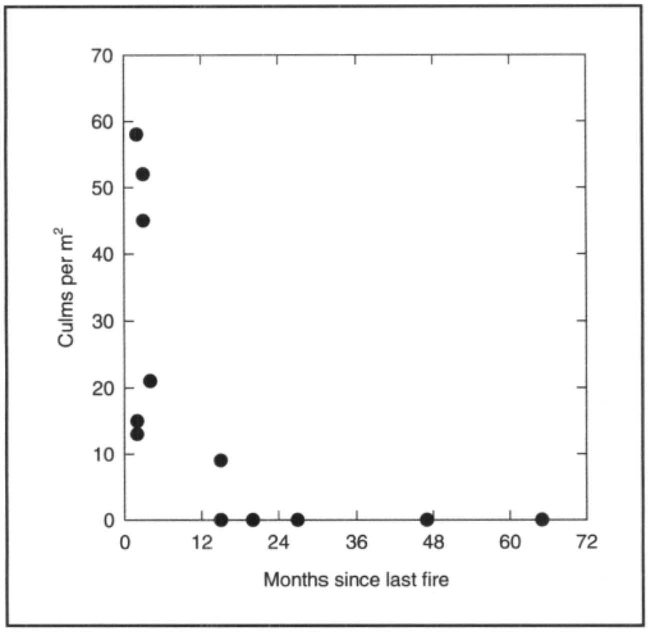

Figure 3. Flowering of cutthroat grass (culms per m²) under natural management, as a function of the number of months since the most recent fire. Each point represents one site.

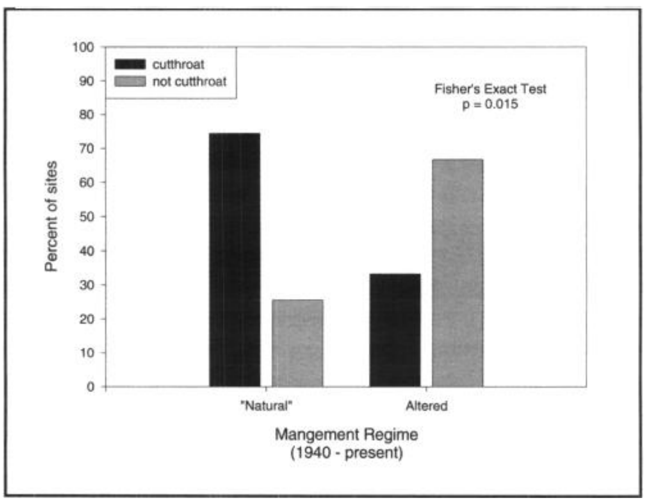

Figure 4. Percent of 1940 cutthroat grass-dominated sites remaining cutthroat grass-dominated in 1995 or becoming dominated by other vegetation, as a function of management regime (natural = with periodic fire and without drainage; altered = drainage and fire exclusion).

is a common result of fire exclusion in many grassland ecosystems and comes as no surprise in cutthroat grass communities, where woody plant seed and other dispersal sources are abundant and near-by. Encroaching rhizomes of oak and eri-caceous species need only advance a short distance from adjacent vegetation, and seeds from bayhead species can fall from plants only a few meters distant from some cutthroat grass swards.

Some of the differences within the "altered" management sites may reflect limited sample sizes and the geographic restriction of other ecosystem components. Most of the sites we sampled rep-resent former or extant seasonal ponds, allowing this study to replicate sampling in this habitat type. However, the management treatments, applied over several decades, were not distributed randomly in the landscape. Factors other than the treatment difference may be responsible for some of the changes we observed in community dominance and structure. These could include pre-1940 differences in vegetation, differences in past grazing regimes (although grazers usually do not eat cutthroat grass), differences in drainage patterns due to hydrologic alteration from roads or railroad rights-of-way, or idio-syncratic vegetation dynamics be-tween 1940 and 1995.

Local effects may exert substantial influences over individual sites or sets of sites. In a third tract adjacent to both the west section and the original property, ditches present along the railroad beds may have served to drain nearby ponds. In that tract, which also had experienced fire exclusion since 1927, five of six former cutthroat grass ponds were converted to short-spike-bluestem-dominated ponds (R. Yahr, E. Menges, and D. Berry, unpubl. data). All five converted sites are immediately adjacent to the boundary fire lane, which runs parallel to the railroad ditch. No sites in this study were invaded by exotic species, but such invasion can occur with severe distur-bances near seed sources.

Similarly, the proximity of the various tracts to bayhead vegetation may have influenced invasion by bayhead species of cutthroat-grass-dominated vegetation patches. In the current study, five sites were converted to bayhead vegetation over the interval examined. Of the four sites that were drained and fire excluded, three were adjacent to the large "North Bayhead" in the ABS Original Property (Figure 1, top right). The single "natural" site that converted to bayhead vegetation is adjacent to the ABS "West Fence-line Bayhead" (Figure 1, west side). In contrast, sites uninvaded by bayhead vegetation in the southern part of the West Section are distant from major bay seed sources (Figure 1). These results are consistent with a more extensive study of bayhead invasion of seasonal ponds (Landman and Menges 1999), which

Table 2. **Current vegetation type and historic** management regime of sampled sites. All sites **were cutthroat-grass-dominated** areas in 1940.

	Management Regime (1940–1995)		
Current Vegetation Type	**"Natural"**	**Drained, Fire Excluded**	**Totals**
Cutthroat grass dominated	32	4	36
Non-cutthroat grass ponds	5	1	6
Flatwoods	5	1	6
Scrubby flatwoods	0	2	2
Bayheads	1	4	5
Totals	43	12	55

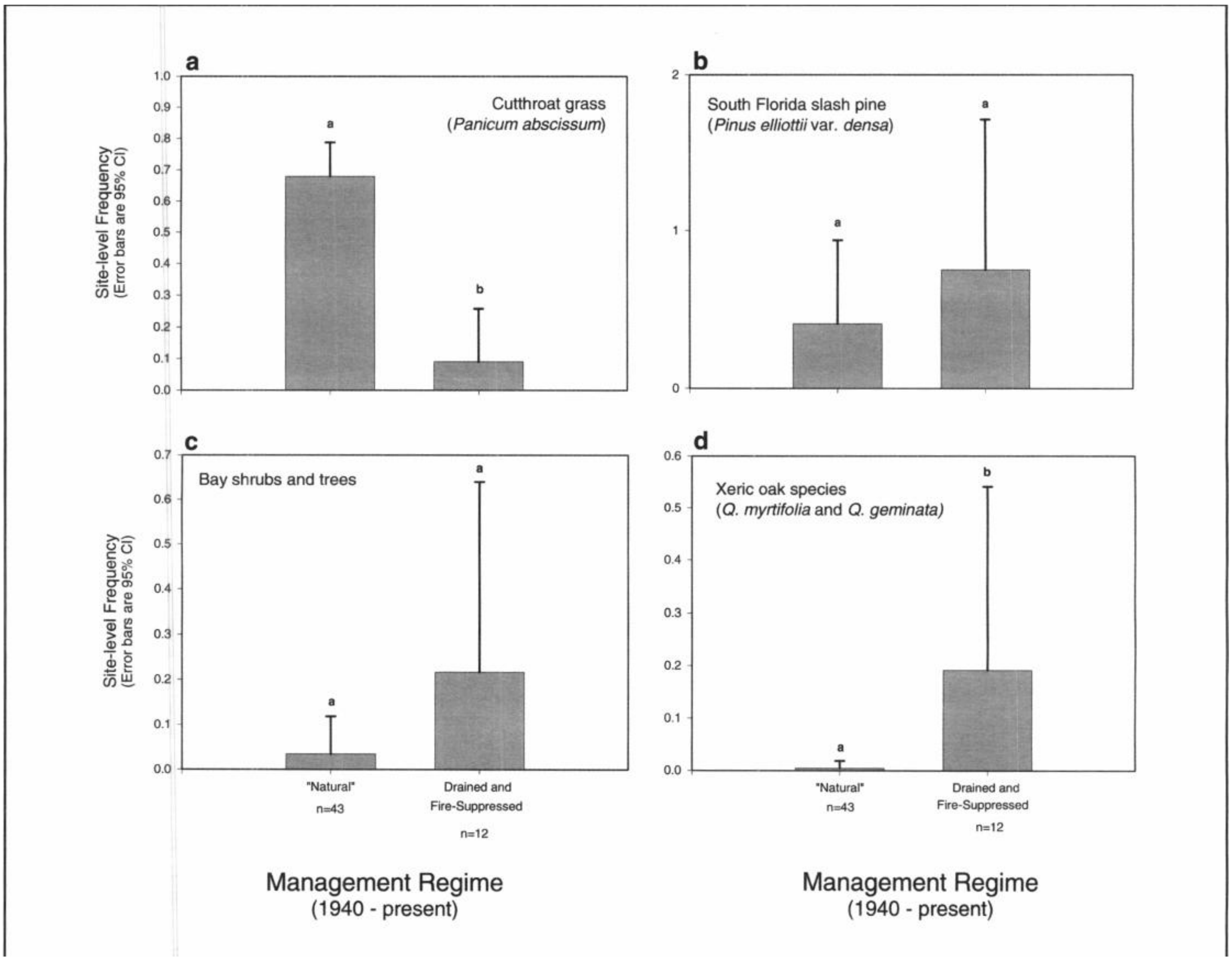

Figure 5. **Effects of management regimes on dominance measured by proportional frequency of (a) cutthroat grass** *(Panicum abscissum)*, **(b) south Florida slash pine** ***(Pinus elliotii*** **var.** ***densa)*****, (c) bayhead shrubs and trees, and (d) xeric oaks** ***(Quercus*** *myrtifolia* **and** ***Q.*** *geminata)*. **For each, different letters indicate significant pairwise differences (adjusted p-values) detected using Mann-Whitney U tests.**

showed that ponds nearer to bayheads were more likely to be invaded, and that the cutthroat grass vegetation zone of current seasonal ponds supported the greatest densities and largest trees of invading bayhead species (Landman and Menges 1999).

In addition, a mosaic of times-since-fire across the "natural" landscape of the West Section may play a role in the eventual fates of particular areas. We found no over-all effect of time-since-fire on species dominance or vegetation type, yet the extreme cases of fire exclusion may still be informative. Although both wild and prescribed fires influenced the "natural" treatment block, not all sites experienced recent fires, a characteristic of the typically patchy fires in the scrub landscape. Fire shadows can be created and maintained by a combination of less flammable habitats and fire breaks. The one site in the west section that converted to a bayhead is an example of a site with almost no opportunity to burn since it is in a small burn unit, dominated by a bayhead, that is neither very flammable nor slated for burning by ABS land managers. This site has not been burned within the period of recorded fire history at ABS. The four sites in the Original Property have not experienced fire since at least 1927.

Bayhead invasion of seasonal ponds is therefore a process that can occur with "natural" fire regimes, but seems accel-erated in seasonal ponds that are near ex-tant bayhead vegetation and that have been drained and protected from fire (this study, Peroni and Abrahamson 1986, Abraham-son and Hartnett 1990, Landman and Menges 1999). The effects of site drainage on individual bayhead species are not well known, but it may prevent mortality of invading individuals during periods of high water level. Shifts in the species composition within bayheads at ABS (toward swamp bay in particular) may also reflect drainage in part (Menges et al. 1993). The effect of fires on bayhead vegetation can include the topkill of plants at bayhead edges, consumption of organic soils, and movement of the bayhead/pond margin into the bayhead (E. Menges, pers. ohs.). The long-term effects of multiple fires on bayhead/pond dynamics are not known from direct studies, but this study can be used to infer that periodic fires can serve to exclude or limit bayhead invasion into seasonal ponds.

Alterations in hydrology may influence other plants that are restricted to poorly drained situations. In fire-excluded sites, the additional factor of drainage resulted in (nonsignificantly) lower dominance of Edison's St. John's-wort (Table 1). This narrow endemic exhibits frequent dieback and may be sensitive to drainage conditions.

Another shift in response to management regime is the increase of south Florida slash pine with drainage and fire exclu-sion. This pine is moderately resistant to postfire mortality, and has generally lower size-specific mortality in seasonal ponds than in other vegetation (Menges and Dey-nip 2000). Although fire has some poten-tial to kill pines and reduce their impor-tance in seasonal ponds, there is evidence that drainage may be more important. Mor-tality in two cohorts of south Florida slash pine in ABS seasonal ponds occurred mainly in response to high water table and not to fire (Abrahamson 1991). However, mortality has occurred mainly in deeper pond zones and has been relatively low in the marginal zones often dominated by cutthroat grass (E. Menges and R. Yahr, unpubl. data).

Management Implications

Although this study was not experimental and has its limitations, it provides clear evidence that active management is neces-sary to maintain cutthroat grass vegetation. Combined fire exclusion and site drainage create conditions favorable for replacement of cutthroat-grass-dominated vegetation by bayhead shrubs and trees, xeric oak shrubs, other grasses, and pine trees. These changes may vary by site; certain sites, for example those distant from bayheads, may be at less risk. Some of these changes (e.g., invasion of bayhead trees) may occur even under "natural" conditions of periodic fire and unaltered drain-age. However, as evidenced by this fifty-five-year study period, fire exclusion and drainage certainly accelerate the changes.

Avoiding drainage may be feasible for nat-ural area managers, especially those respon-sible for large tracts. Restoration of drained areas represents another challenge. Even if the act of plugging drainage ditches restores the original hydrology, recolonization by cutthroat grass may be extremely slow.

In undrained areas, management for vig-orous cutthroat grass communities should involve fire management. This study con-trasted areas burned periodically with those with long periods of fire exclusion, and that comparison does not in itself provide much help in recommending a specific fire regime. Although cutthroat grass may persist under a fairly wide regime of fire-return intervals, this has not received direct study. Many areas at ABS with apparently healthy cutthroat grass swards have been burned less frequently than the 3- to 9-year intervals identified as modal for cutthroat grass vegetation in the ABS fire management plan (Main and Menges 1997). Furthermore, we found no signifi-cant changes in cutthroat grass vigor or community dominance when we compared undrained sites over the first three decades after fire. However, Bridges and Orzell (1998) maintain that cutthroat grass com-munities are "strongly dependent on fre-quent fire" and suggest that in seepage slope communities, bay species can invade within a decade after fire. Frequent burning during the growing season will also promote cutthroat grass flowering, which may encourage recolonization.

Cutthroat grass-dominated flatwoods and ponds may have importance beyond the fact that they are endemic communities. Because they are extremely flammable and can burn at very short intervals (at ABS, spot fires have occurred in cutthroat-grass-dominated ponds only two months after a prior burn), their presence probably in-creases the fire frequency of the central Florida landscape (Menges 1998). This may be important to vegetation types such as Florida scrub that require fire but are not flammable under some conditions. Fires ignited in grassy vegetation of sea-sonal ponds and flatwoods may spread into patches of Florida scrub, increasing the latter's fire frequency. Many endemics of Florida scrub prosper with frequent fires (see review in Menges 1998), so that cut-throat grass's flammable nature may benefit endangered species beyond its own community. Because fire is also needed to conserve cutthroat grass vegetation, fire management creates a positive feedback loop that may restore and maintain structure and function across a broad and di-verse landscape. Likewise, the long-term absence of fire may be implicated in a similar negative feedback loop, leading to dense, fire-resistant bayheads and scrub-derived xeric hammocks. Such communities become increasingly resistant to fire and may not revert to cutthroat grass or scrub with the reintroduction of normal prescribed fire regimes.

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Rebecca Yahr is currently a graduate student in the Botany Department at Duke University and is focusing on ecology, conservation, and population genetics of lichen forming fungi. As a Research Assistant at Archbold Biological Station. she worked on ecology and conservation of rare species, including lichens.

Eric Menges is a Senior Research Biologist at Archbold Biological Station in Lake Placid, Florida. His research interests include population dynamics, population viability, rare plant conservation and management, and fire ecology.

Dawn Berry is the Assistant Crew Supervisor on the Entiat Initial Attack Crew, Wenatchee National Forest out of Entiat, Washington. She has been studying Lake Wales Ridge fire ecology at Archbold Biological Station since 1991, and her cur-rent research compares the effects of mechanical treatments to those of fire. Her applied interests in prescribed fire management have led her to work on fire crews throughout the country.

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