

EFFECTS OF DISTURBANCE ON COMMUNITY BOUNDARY DYNAMICS ON CUMBERLAND ISLAND, GEORGIA

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ABSTRACT

Landscape-level boundary dynamics and their underlying causes have received little attention in the United States. Edaphic, climatic, and disturbance factors have been presented as important regulators of landscape heterogeneity. In particular, intense, regularly-occurring wildfires are an important managerial concern in scrub and marsh communities on Cumberland Island, Georgia. Such fires are difficult and expensive to control, and their full impact on plant community structure and boundary dynamics is unknown. The objective of this study was to determine the roles of high-intensity fire and grazing by large ungulates, in controlling scrub/forest and marsh/forest boundaries on Cumberland Island. Methodology included interpreting historical and recent aerial photographs, describing vegetation and soil along community boundaries, and a greenhouse bioassay of soil fertility along boundaries. Results of this study suggest that marsh/forest and scrub/forest boundaries are controlled by fluctuations in water table depth, and succession of scrub to oak-palmetto (*Quercus* spp.-*Serenoa repens*) forest is controlled by soil moisture. Aerial photographs indicated that areal extent of scrub and marsh patches varied independently of disturbance. Scrub/forest boundaries were relatively dynamic compared to marsh/forest boundaries. Marsh and scrub patch sizes were correlated with long-term precipitation patterns. Overstory vegetation change resulted primarily from differences in stature of live oak (*Quercus virginiana*). Vegetation change in the shrub layer reflected differences in grazing pressure from large herbivores. Soil chemical characteristics did not vary along transects perpendicular to community boundaries.

INTRODUCTION

The ecology of natural disturbance and patch dynamics has received considerable attention in recent years. "Patch dynamics" (Thompson 1978) was coined in 1978 and a synthesis of the subject appeared in 1985 (Pickett and White 1985). The influence of disturbance on boundary phenomena between adjacent communities is one of many factors contributing to a system's patch dynamics.

Despite the plea of Wiens et al. (1985) for empirical research of landscape-level boundary dynamics, the subject has received relatively little attention in plant ecology literature. Boundary relationships between heath and bracken in England have been well studied (Watt 1947, 1955, 1964; Miles 1981; Gimingham et al. 1981; Hobbs and Gimingham 1987). Abrupt forest/grassland boundaries in the United States often are maintained by frequent fires or grazing (Wright and Bailey 1982) and factors responsible for maintaining the tallgrass prairie/eastern deciduous forest boundary have been hypothesized (White 1941, Albertson and Weaver 1945, Goss 1960). These exceptions, while suggesting the importance of disturbance as a controlling factor, do little more than underscore the paucity of knowledge concerning boundary dynamics between adjacent communities. Data from physiognomically similar communities are especially sparse.

Wiens et al. (1985) discussed factors which may control boundary dynamics. They listed edaphic factors and climatic variations as the primary agents controlling landscape pattern; the effects of disturbance on boundary dynamics are variable, but are generally secondary in importance. Wiens et al. (1985) hypothesized that frequent, intense disturbances would reduce landscape heterogeneity by dissolving patch boundaries.

Intense wildfires occur every 20-27 years in scrub and marsh communities on Cumberland Island (S. Turner and Bratton 1987). M. Turner and Bratton (1987) expressed concern that intense scrub fires burning into adjacent oak forest could convert forest to scrub. Similar results would be expected as marsh fires burn into oak forest. Although oak forest is relatively resistant to fire and generally burns only when ignited by fires from adjacent communities (scrub or marsh), recovery is slow. Oak forest recovery on barrier islands is additionally hampered by severe grazing by white-tailed deer (*Odocoileus virginianus*) and feral horses (M. Turner and Bratton 1987, Bratton unpublished data).

Boundary dynamics and successional relationships have not been adequately studied on Cumberland Island. Continual conversion of small areas of forest to marsh or scrub eventually could extirpate the forest community. The objective of this study was to determine the role of disturbance in controlling scrub/forest and marsh/forest boundaries.

THEORETICAL CONSTRUCTS

Upon burning into oak-palmetto forests, scrub or marsh fires generally kill large oak trees (Davison and Bratton 1988), creating a gap at the scrub/forest or marsh/forest boundary. Assuming the gap will be colonized by species from adjacent communities, one of two general processes will occur: either oak-palmetto forest will replace itself, or scrub or marsh will replace the forest. A discussion of each is warranted.

Soil differences between communities (even those undetectable by standard

soil analyses) and differences in relative elevation (and therefore drainage) should favor self-replacement of oak-palmetto forest. Replacement may occur in more than one stage; fire-resistant palmetto may quickly assert dominance (out competing other scrub species) and protect oak sprouts from grazing until oak trees are large enough to tolerate grazing and surface fires. In any case, the fire-free interval must be long enough to provide protection for oak establishment.

Scrub and marsh species seem well adapted to burned areas, resistant to grazing, and capable of prolific vegetative reproduction (Davison and Bratton 1988); these characteristics support the hypothesis that scrub or marsh will displace oak forest. A boundary which has been soil-controlled may change if disturbance (e.g., grazing) favors one community over another, if that community is capable of colonizing areas left unoccupied by the other community. Forest displacement may follow one of two pathways: (1) scrub or marsh vegetation will succeed to oak forest at the boundary, or (2) replacement will be permanent. Grazing protection of oak sprouts by scrub or marsh species, adequate drainage in existing forest, and other soil characteristics support the former hypothesis. However, the fire-free interval must be sufficient to allow a fire-resistant oak-palmetto forest to develop. Replacement will be permanent if relatively short fire-free intervals in scrub and marsh vegetation and preferential grazing of oak sprouts retard oak colonization.

STUDY SITE AND METHODS

Study Site

The study was restricted to a 700-ha area of scrub, marsh, and oak-palmetto forest on the northern end of Cumberland Island, the southernmost of Georgia's barrier islands (30° 48' N, 81° 26' W). The study site represented the largest contiguous areas of scrub and marsh communities and the area of highest fire frequency on the island. Most of the study area burned in 1934, 1954, and 1981 (S. Turner and Bratton 1987). Detailed descriptions of freshwater marsh, oak scrub, and oak-palmetto forest can be found in Hillestad et al. (1975) and Davison and Bratton (1988). Scrub vegetation probably is natural on barrier islands, but the historical extent of the community is unknown (Bratton 1983). Hillestad et al. (1975) and Davison and Bratton (1988) considered scrub communities to be fire-maintained seral stages of oak-palmetto forests on Cumberland Island.

Communities sampled in this study were characterized as follows. (1) Marshes were dominated by sand cordgrass (*Spartina bakeri*); woody species were absent. Botanical nomenclature follows Radford et al. (1968) for woody species and Small (1933) for herbs. (2) Scrub vegetation was dominated by dense ericaceous shrubs (e.g., *Lyonia* spp., *Vaccinium* spp.) less than 5 m tall. (3) Oak-palmetto communities were closed-canopy forests 15-20 m tall dominated

by live oak in the overstory with a nearly continuous layer of saw palmetto in the understory. The latter two communities had little herbaceous vegetation and were located on soils of the Madarin series (Sandy, siliceous, thermic Typic Haplohumods). Marsh soils are not classified (Rigdon and Green 1980).

Large herbivores on the island include white-tailed deer, feral horses, and feral hogs. Extirpation of natural predators, including black bear (*Ursus americanus*) and bobcats (*Felis rufus*), combined with inadequate control measures have produced large populations of all herbivores. Recent estimates of white-tailed deer (Nelson et al. 1986) and feral horses (Finley 1985) indicated populations in excess of carrying capacity for both species. Bobcats were reintroduced onto Cumberland Island in October and November, 1988 (Bratton 1989).

Aerial Photograph Interpretation

Aerial photographs were used to map scrub/forest and marsh/forest boundaries. Scrub was defined as dense woody vegetation less than 5 m tall. Scrub/forest and marsh/forest boundaries were delineated onto acetate sheets overlaying aerial photographs taken in 1953, 1962, 1964, 1971, 1980, 1983, and 1988 (photographs described in Table 1). Poor photograph quality prevented delineation of scrub/forest boundaries on the 1964 photographs. A computer algorithm (Hargrove and O'Hop 1988) was used to determine total area occupied by scrub and marsh communities; relative positions of community boundaries were recorded on the acetate sheets.

Descriptive Vegetation and Soil Sampling

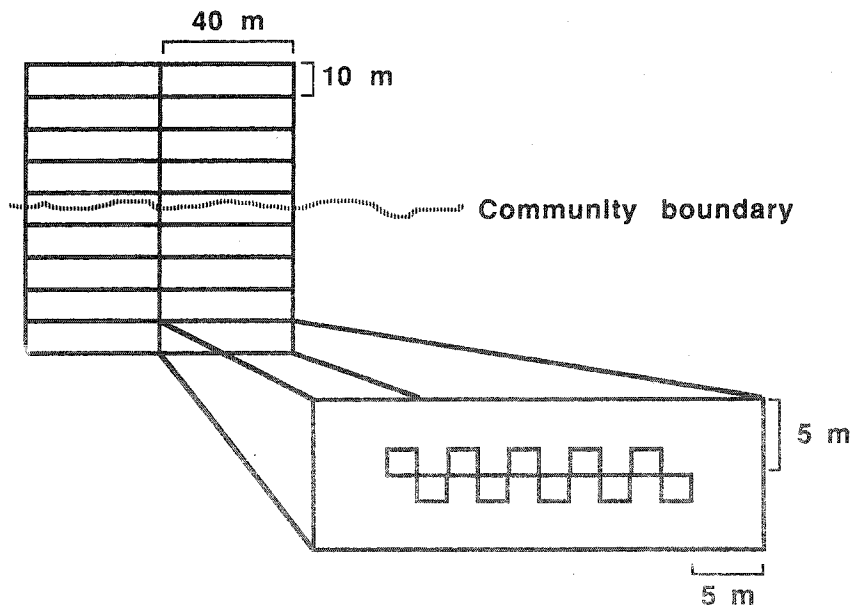
Macroplots were randomly established perpendicular to scrub/forest and marsh/forest boundaries. National Park Service fire records indicated areas which burned as headfires and backfires in the 1981 South Cut fire. Two

Table 1. Characteristics of aerial photographs used to study boundary phenomena at Cumberland Island National Seashore, Georgia.

Year	Film	Scale	Format (cm x cm)
1953	Black & White	1:7,920	61 x 61
1962	Black & White	1:5,000	61 x 61
1964 ¹	Black & White	1:10,000	23 x 23
1971	False-color Infrared	1:20,000	23 x 23
1980	Black & White	1:15,840	61 x 61
1983	False-color Infrared	1:24,000	23 x 23
1988	False-color Infrared	1:8,000	23 x 23

¹Marsh only.

Figure 1. Arrangement of 10x40-m plots within 80x90-m macroplots and 2x2-m subplots in 10x40-m plots.



80x90-m macroplots were established across scrub/forest and marsh/forest boundaries in each fire type. Each macroplot was divided into 18 10x40-m plots such that one pair of plots straddled the boundary, with 4 pairs of plots on either side of the boundary (Fig. 1). Macroplot locations were permanently marked with brass-capped concrete benchmarks (McPherson 1988).

Trees were defined as woody plants with diameter at breast height (dbh) greater than 2.5 cm. All other woody plants were classified as shrubs. Dbh was recorded for each tree, by species, in each 10x40-m plot. Cover of shrubs was estimated ocularly in 10 2x2-m subplots in each plot. Density of all shrubs except saw palmetto was recorded in 2-cm size classes in each subplot (0-2 cm, 2-4 cm, 4-6 cm, 6-8 cm, and 8-10 cm) and basal area was calculated from these data. Subplot data were summed to produce a single estimate of shrub density, cover, and basal area for each plot. Two green-brier species (*Smilax bona-nox* and *S. rotundifolia*) were indistinguishable, and were therefore grouped together. Similarly, live oak and laurel oak (*Q. laurifolia*) seedlings were grouped. Height of the tallest live oak or laurel oak seedling in each 2x2-m plot was recorded. Species which occurred in fewer than 3 10x40-m plots were deleted before analysis (Gauch 1982).

Transects were surveyed with transit, rod, and auto-level along a 90-m line perpendicular to the boundary (the centerline of each macroplot). Relative elevation, depth of O, A1, and A2 horizons, soil pH and macronutrients, and depth and type of litter were sampled every 5 m along the line; soil profiles

were exposed to determine horizon depths. Soil chemical characteristics were sampled at depths of 0-30 cm, 30 cm-top of B horizon, and the upper 15 cm of the B horizon and analyzed by the Cooperative Extension Service Soil Testing Laboratory (Athens, Georgia) after air drying. Soil moisture was determined gravimetrically along one scrub/forest and one marsh/forest transect on or about the first and fifteenth day of each month, February-June 1988. Two samples were collected in early morning every 10 m along transects at depths of 0-15 cm and 15-30 cm. Deep water throughout the sampling period precluded measuring soil physical and chemical characteristics in marshes beyond the marsh/forest boundary.

Soil Fertility Bioassay

The large degree of species overlap between scrub and forest communities (Hillestad et al. 1975) indicates that soil fertility may control productivity, thereby influencing the scrub/forest boundary. A greenhouse bioassay experiment was used to quantify relative productivity of soils on either side of community boundaries.

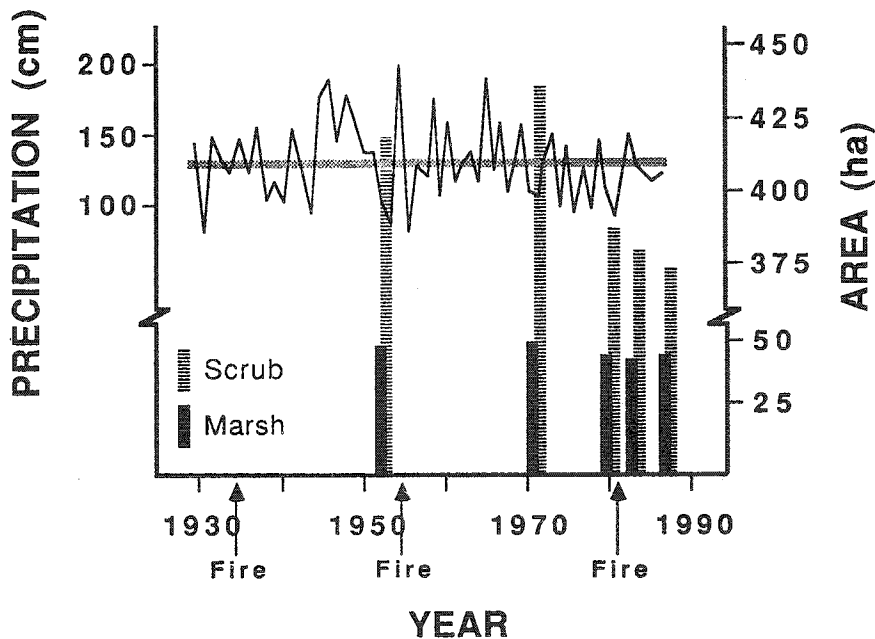
Four soil samples were collected every 10 m along the center line of each macroplot and placed intact into 12.5-cm pots. Fifteen seeds of a non-native warm season (C4) annual grass ("Sugar Graze" sorghum-sudangrass hybrid [*Sorghum vulgare* Pers. x *Sorghum halapense* Stapf.]) were placed in each pot. Pots were randomly arranged in a greenhouse, watered and weeded regularly, and thinned to a density of 10 plants/pot. Percent germination was recorded. Plants were removed from pots 6 weeks after seedling emergence by washing soil from roots. Plants were dried at 60°C for 6 days and weighed. Total oven-dry biomass was expressed on a per-plant basis to account for differences in germination between pots (some pots did not produce 10 plants).

RESULTS

Aerial Photograph Interpretation

Total area occupied by five marshes in the Whitney Lake complex differed only slightly between years. Marsh area varied from 45 ha in 1983 to 50 ha in 1971 (Fig. 2). The minor differences in marsh size appeared to be related to precipitation patterns. "Large"-marsh years (1953, 1962, 1964, 1971) were preceded by relatively wet decades; small-marsh years (1980, 1983, 1988) followed a dry period in the late 1970s and early to mid-1980s. Marshes expanded or contracted more or less uniformly; boundaries did not shift measurably, with respect to fixed points, between years. Scrub boundaries were more dynamic than marsh boundaries over time. Total area varied from 373 ha in 1988 to 456 ha in 1962. Scrub area was greatest following wet decades (1940s, 1960s) and declined steadily during the relatively dry 1980s. Between 1971

Figure 2. Annual precipitation at Brunswick, Georgia and area occupied by scrub and marsh communities in various years on Cumberland Island, Georgia. Horizontal cross-hatched line shows long-term average precipitation. Large fires occurred in the study area in 1934, 1954, and 1981 (climatic data from NOAA 1930-1987; fire history data from S. Turner and Bratton 1987).



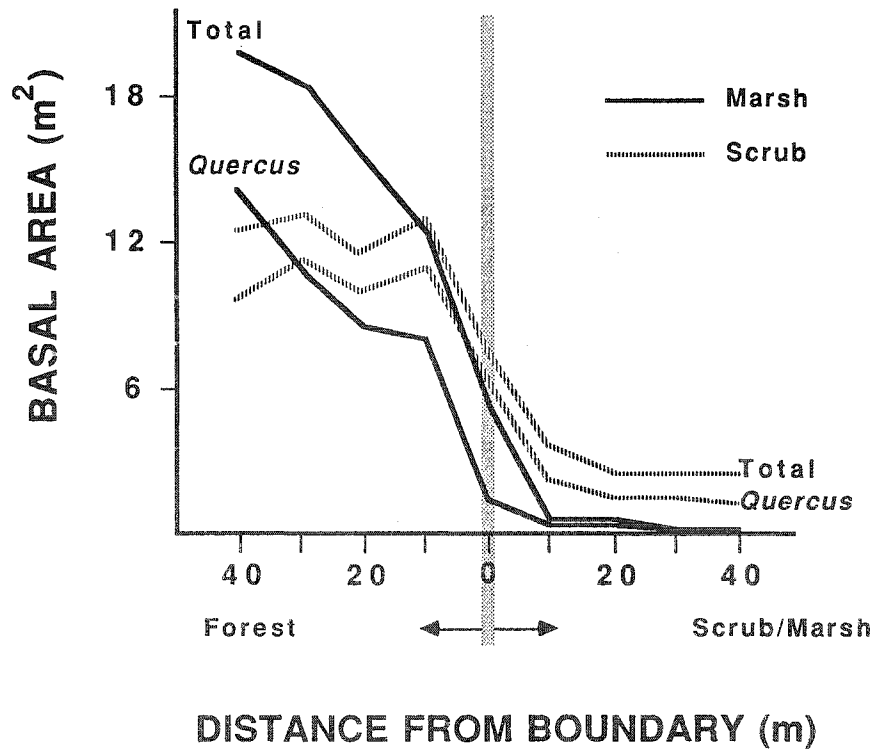
and 1988 (the period of greatest areal change), oak-palmetto forest advanced 11 and 12 m into scrub at the southern and northern scrub/forest boundaries, respectively. The eastern boundary, primarily bordered by marshes and lowland hardwood forest, and western boundary, primarily bordered by mixed pine-oak and oak-palmetto forests, did not shift measurably between years.

Descriptive Vegetation and Soil Sampling

Analysis of variance revealed significant ($P < 0.05$) interactions (community x macroplot position, community x species). Therefore, the response of vegetation to macroplot position was investigated at the level of the individual species within a community type.

Differences in tree (dbh > 2.5 cm) structure along scrub/forest macroplots largely resulted from a change in stature of live oak, which comprised 50-88% of total basal area. Live oak basal area declined from a mean of 10.4 m² in forest plots to less than 2.0 m² in scrub plots (Fig. 3). A similar pattern was evident along marsh/forest macroplots. Live oak basal area did not differ

Figure 3. Mean basal area of *Quercus virginiana* and all species combined along forest/marsh and forest/scrub macroplots on Cumberland Island, Georgia.



between forested plots adjacent to scrub and forested plots adjacent to marsh.

Live oak density did not differ ($P > 0.15$) along scrub/forest macroplots, or among forested plots along marsh/forest macroplots. Live oak density declined from 68 trees/ha in forested plots (10-40 m from boundary) to 13 trees/ha at the marsh/forest boundary, with no trees in marsh plots. Average density along scrub/forest macroplots (all plots) was 514 plants/ha, which was greater than density in any plot adjacent to marshes. Hence, forested plots adjacent to marshes were characterized by relatively few trees of large diameter compared to forested plots adjacent to scrub.

Basal area and density of nearly all woody species decreased ($P < 0.05$) along marsh/forest macroplots. Exceptions were species which occurred patchily or infrequently (e.g., sparkleberry [*Vaccinium arboreum*], muscadine [*Vitis rotundifolia*], summer grape [*V. aestivalis*]). By contrast, macroplot position did not affect basal area or density of any species except live oak and wild olive (*Osmanthus americanus*) along scrub/forest macroplots. Basal area of wild olive, a characteristic forest species, declined ($P < 0.05$) from 1.2 m², 40 m from the scrub/forest boundary in the forest, to 0.4 m² at the

boundary. Mean density was 369 and 63 plants/ha, respectively, in the same locations. Wild olive was absent from scrub plots.

Structure of shrub (dbh < 2.5 cm) vegetation was similar to that of the overstory. Cover, basal area, and density of stagger-bush (*Lyonia ferruginea*), red bay (*Persea borbonia*), saw palmetto, dwarf blueberry (*Vaccinium myrsinites*), green-brier, and live oak were affected ($P < 0.05$) by position along marsh/forest macroplots, primarily a result of the absence of woody plants in marsh plots. Measured attributes did not differ ($P > 0.05$) along marsh/forest macroplots for infrequently-occurring species (wax myrtle [*Myrica cerifera*], fetter-bush [*Lyonia lucida*], sparkleberry, and muscadine).

Basal area and density were not affected ($P > 0.05$) by macroplot position for any shrubs along scrub/forest macroplots. Cover of only one species varied with macroplot location: live oak cover increased ($P < 0.01$) along the gradient from forest plots (mean \pm S.E. = $6.2 \pm 1.2\%$) to scrub plots (mean \pm S.E. = 1.2%) to scrub plots (mean \pm S.E. = $18.1 \pm 2.6\%$), from a minimum of 3.7% ($\pm 1.0\%$) 40 m from the boundary in the forest to a maximum of 21.7% ($\pm 6.6\%$) 20 m from the boundary in the scrub. Live oak cover was greater ($P < 0.01$) on headfire macroplots (mean \pm S.E. = $17.7 \pm 2.3\%$) than backfire macroplots (mean \pm S.E. = $7.5 \pm 1.7\%$). Basal area and density of live oak similarly differed ($P < 0.05$) between fire types.

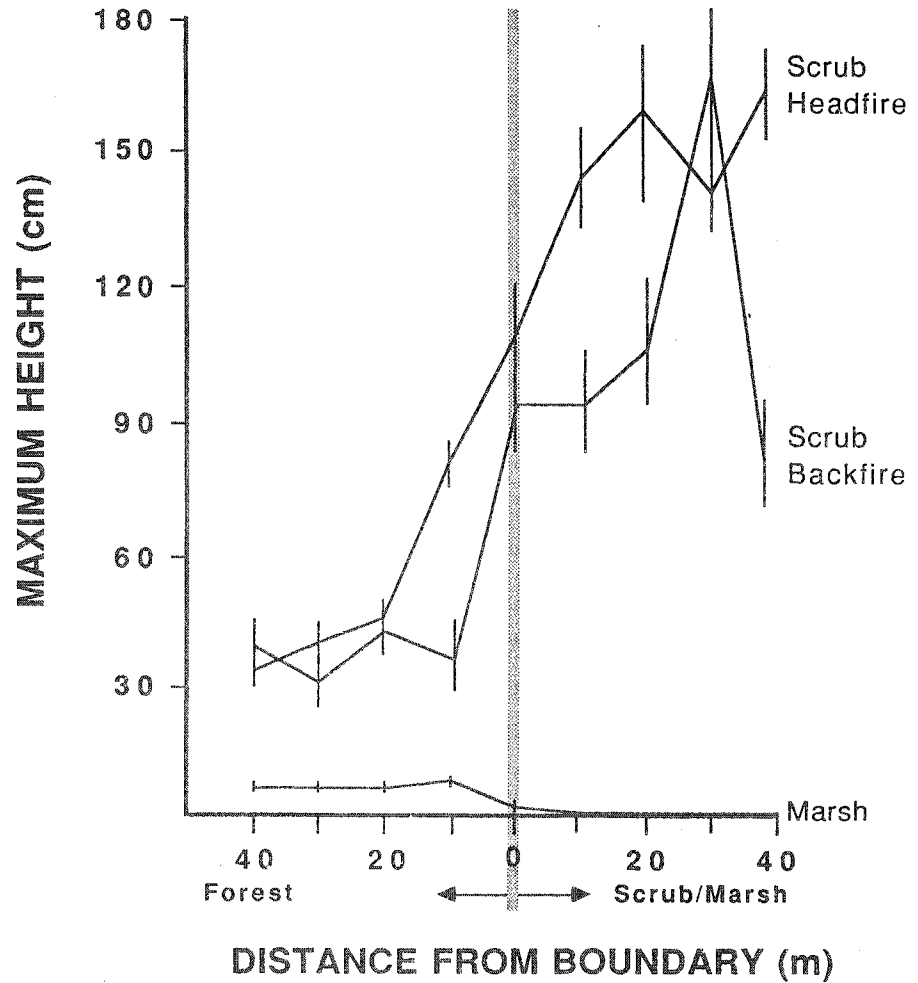
Type of fire affected few other species. Dwarf blueberry (all attributes, scrub/forest macroplots) and stagger-bush (basal area and density, marsh/forest macroplots; density, scrub/forest macroplots) were more common in areas which burned as headfires than in areas which burned as backfires. Conversely, wax myrtle (basal area and density, scrub/forest macroplots) was more common in backfire macroplots than in headfire macroplots.

Macroplot position affected ($P < 0.01$) live oak seedling height on scrub/forest macroplots, but not ($P > 0.25$) on marsh/forest macroplots. Interactions between fire type \times macroplot position were not significant ($P > 0.05$) for either community. However, live oak seedlings in headfire-burned areas were significantly ($P < 0.01$) taller than seedlings in backfire-burned areas (Fig. 4).

Mean relative elevation decreased along marsh/forest transects from 1.05 m (boundary elevation = 0.0 m) in the forest (45 m from boundary) to -0.46 m in the marsh (45 m from boundary). Elevational difference between the boundary and the highest point along the transect varied from 0.65 to 1.51 m. Difference between the boundary and the lowest point varied from 0.27 to 0.68 m. Relative elevation was not consistently directional on scrub/forest transects. Forest elevation was greater than scrub elevation on three of four transects; scrub was elevationally higher than forest on the fourth. Relative elevation varied little on scrub/forest transects; average slope along transects was 0.6%.

Depth of litter and soil horizons (A1, A2) did not vary ($P > 0.05$) along transects. However, the organic (O) horizon was deeper ($P < 0.01$) at the

Figure 4. Relationship between *Quercus* spp. seedling height and distance from community boundary for forest/scrub and forest/marsh communities on Cumberland Island, Georgia. Height represents the mean of the tallest seedling in 2x2-m quadrats (n = 10 quadrats/plot). Vertical bars are standard errors.



marsh/forest boundary (mean \pm S.E. = 5.3 ± 0.4 cm) than in forest plots (mean \pm S.E. = 1.4 ± 0.2 cm). Depth of the 0 horizon did not vary ($P > 0.10$) along scrub/forest transects.

Soils under scrub and oak-palmetto forest were characterized by a dark organic layer at a depth of about 50 cm. The Mandarin series is the only soil on the island with a zone of accumulation (Rigdon and Green 1980). Sampling from forest to marsh, the B horizon disappeared from soil profiles 5-25 m (mean = 13.8 m) from the marsh/forest boundary. Other soil physical characteristics were not influenced by transect position or community.

Interactions between community and transect position were not significant ($P > 0.05$) for soil chemical characteristics. Soils on marsh/forest transects had higher ($P < 0.05$) values of macronutrients (P, K, Ca, Mg) than did scrub/forest transects in subsoil (sampled at a depth of 30 cm to top of B horizon) (Table 2). Marsh/forest macroplots had higher values of K at all depths than did scrub/forest macroplots. No other comparisons yielded significant ($P < 0.05$) differences. Especially noteworthy was the absence of soil chemical differences between transect positions along community gradients.

Response of soil moisture content to transect position differed between communities. Date x transect position interaction was not significant ($P > 0.10$) on marsh/forest transects, indicating that moisture content responded to transect position similarly across dates. Subsoil (15-30 cm) moisture content decreased ($P < 0.05$) with increasing distance into the forest from the marsh/forest boundary. Subsoil moisture content along scrub/forest transects was dependent on sampling date (i.e., date x transect position interaction was significant [$P < 0.05$]). Moisture content was higher ($P < 0.01$) in scrub 20, 30, and 40 m from the scrub/forest boundary than at other transect locations on the first sampling date, 1 February 1988 (Fig. 5). This date represented the only sampling period during which soil moisture content exceeded 20%, indicating that the water table dropped below the deepest sampling depth in

Table 2. Soil chemical characteristics (mean \pm S.E.) on transects perpendicular to marsh/forest and scrub/forest boundaries, Cumberland Island, Georgia. Measured attributes did not differ ($P > 0.05$) between transect positions.

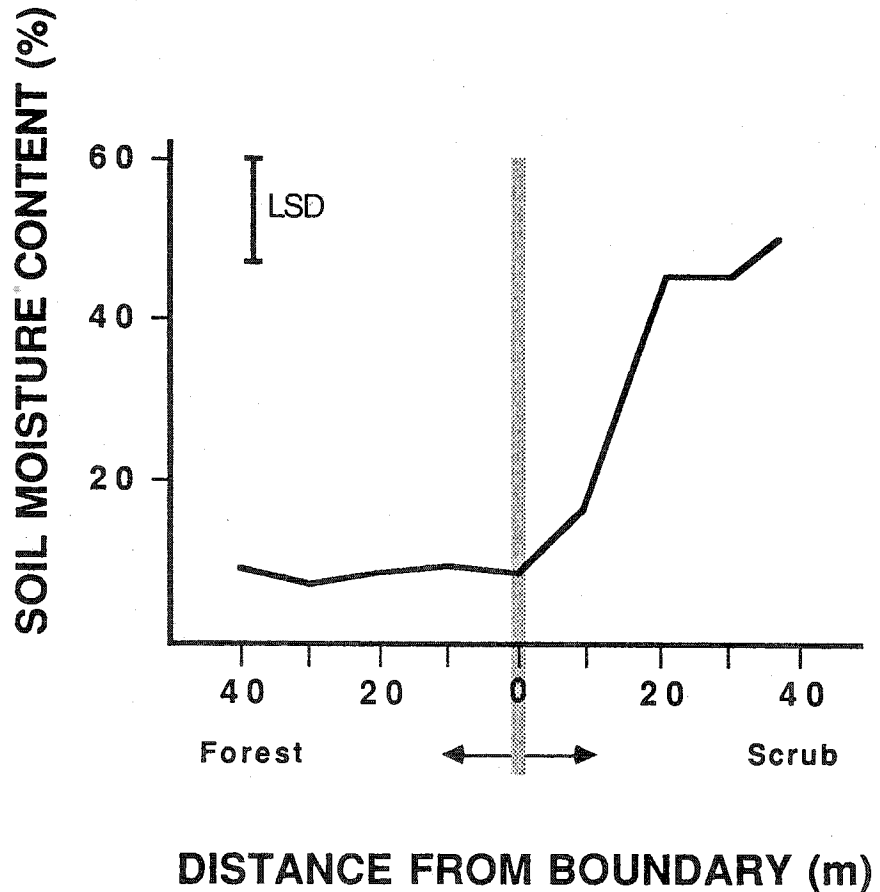
Attribute	Community ²	Soil depth ¹		
		1	2	3
pH	Marsh	4.0 \pm 0.0	4.1 \pm 0.0*	4.3 \pm 0.1
	Scrub	3.9 \pm 0.0	4.2 \pm 0.0	4.3 \pm 0.0
Buffer pH	Marsh	7.5 \pm 0.0	7.7 \pm 0.0	7.3 \pm 0.1
	Scrub	7.5 \pm 0.0	7.8 \pm 0.0	7.4 \pm 0.0
P (kg/ha)	Marsh	10.2 \pm 1.0	11.6 \pm 2.2*	183.0 \pm 33.6
	Scrub	7.3 \pm 0.4	5.1 \pm 0.4	101.0 \pm 11.1
K (kg/ha)	Marsh	51.6 \pm 5.3*	30.4 \pm 3.1*	41.2 \pm 6.8*
	Scrub	32.6 \pm 2.5	15.0 \pm 1.4	20.7 \pm 1.9
Ca (kg/ha)	Marsh	186.5 \pm 26.6	90.0 \pm 5.7*	75.3 \pm 4.4
	Scrub	150.9 \pm 14.8	65.7 \pm 2.7	65.1 \pm 3.6
Mg (kg/ha)	Marsh	85.9 \pm 10.1	35.0 \pm 2.7*	29.9 \pm 4.7
	Scrub	70.5 \pm 9.0	12.5 \pm 1.3	21.6 \pm 2.8

¹Depths: 1=0-30 cm, 2=30 cm-top of B horizon, 3=upper 15 cm of B horizon.

²Marsh=transects perpendicular to marsh/forest boundary, Scrub=transects perpendicular to scrub/forest boundary.

*Significantly greater ($P < 0.05$) than value on scrub/forest transect.

Figure 5. Mean soil moisture content along a transect from oak-palmetto (*Quercus* spp.-*Serenoa repens*) forest to scrub on 1 February 1988, Cumberland Island, Georgia.

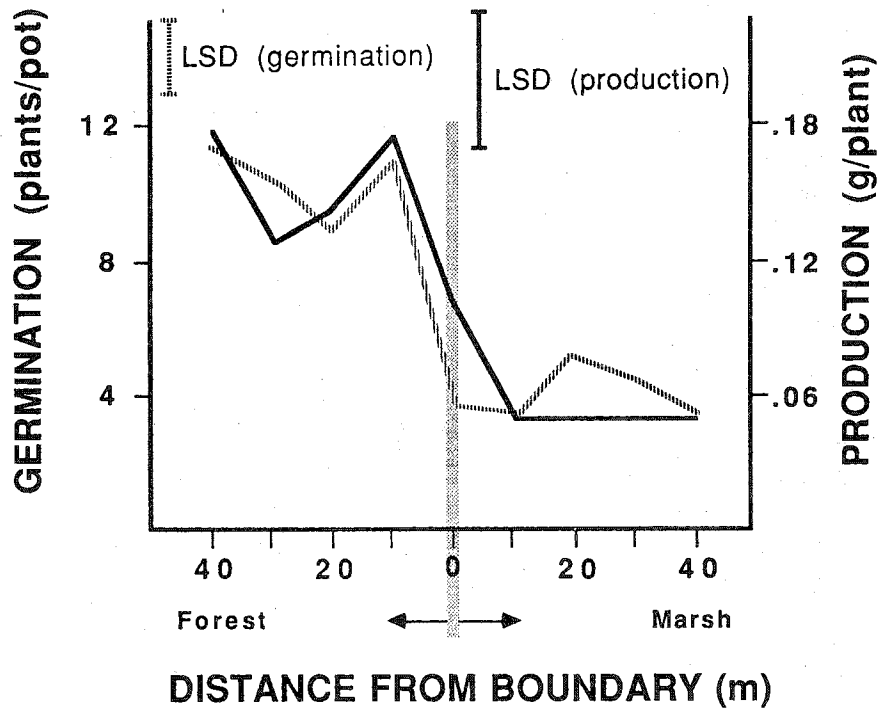


subsequent samples. After 1 February, soil moisture was relatively dry and was not influenced by transect position.

Soil Fertility Bioassay

Germination and production of sorghum-sudangrass were affected ($P < 0.05$) by relative position along marsh/forest macroplots. Germination was highest in soils collected from forest plots and declined sharply at the marsh/forest boundary (Fig. 6). Production followed a similar pattern. Germination and production did not differ ($P > 0.25$) between locations along scrub/forest macroplots. Germination averaged 11 plants/pot; mean production averaged 1.0 g per pot and 0.1 g per plant, respectively.

Figure 6. Mean germination and production of an annual warm season grass in soils collected along forest/marsh transects on Cumberland Island, Georgia. Germination and production did not differ ($P > 0.25$) along forest/scrub transects ($n = 16$ pots per transect position, 4 pots per position on each of 4 transects).



DISCUSSION

Disturbance did not have a direct, marked influence on boundary dynamics. Despite periodic high-intensity disturbance (fire) and chronic low-intensity disturbance (grazing), marsh and scrub communities have failed to replace oak forest at the boundary, and fluctuations in areal extent of marsh and scrub patches have occurred independently of disturbance events. Furthermore, patch boundaries are relatively discrete—landscape heterogeneity has been maintained despite periodic disturbances. Since disturbance does not regulate scrub/forest and marsh/forest boundaries, an obvious question is “what does?”

These data suggest that the marsh/forest boundary is controlled by water level. Forest species typically are intolerant of anaerobic conditions associated with standing water. Soil fertility, reflected by differences in germination and production, varied on either side of the marsh/forest boundary. However, soil fertility differences are not causal with respect to tree production. Davison

(1984) noted that shrubs and trees from adjacent oak forest germinated in marsh soils after an extended drought lowered water levels. These species did not survive subsequent flooding. It should be noted that periodic fires remove peat accumulations in freshwater marshes, thereby lowering marsh elevation and precluding succession to forest (Christensen 1988 and references therein). Thus fire plays an indirect role in maintaining marshes; fire maintains an elevational gradient, which regulates flooding, and, subsequently, distributions of woody species.

Bertness (1988) reported that peat accumulations inhibited colonization and growth of native species in Rhode Island, and attributed the reduced performance to the hard physical texture and adverse chemical composition of peat-loaded sediments. Heavy peat loads reduced production to a greater extent than light peat loads. This factor may explain the intermediate production at the marsh/forest boundary (moderate peat accumulation) compared to production in forest plots (peat absent) and marsh plots (heavy peat accumulation) in the current study.

These data imply that scrub/forest boundaries are also controlled by soil moisture, specifically the underground water table. Water table depth is a complex product of several factors, including surface profile, soil texture, localized precipitation, and vegetation (Birkeland and Larson 1978, Pritchett 1979). Scrub area increased during long-term periods of above average precipitation, and decreased during dry periods. Soil moisture content data collected from scrub/forest transects further support this hypothesis. No other measured factors elucidated boundary dynamics between scrub and oak forest; relative elevation, soil pH, macronutrients, and fertility did not vary between scrub and oak forest. Scrub/forest boundaries did not follow elevational contours, possibly because slopes were relatively gentle.

Due to the absence of ungrazed controls on Cumberland Island, the impact of grazing was not tested explicitly in the current study. However, the rejection of other potential causal mechanisms, combined with supporting animal behavior and food habits data, lead us to believe that grazing was at least partially responsible for some differences in community structure.

Disturbance, especially grazing, appeared to have a marked effect on live oak regeneration. Density and size of live oak seedlings in oak forest adjacent to marshes were reduced considerably compared to seedling density and size in forest plots adjacent to scrub plots. Productivity differences did not favor scrub sites, as evidenced by basal area of mature oak trees, soil chemical differences, and germination and productivity of a warm-season grass in soils from both sites. Well-developed trails around marsh edges indicate that large herbivores spend a disproportionate amount of time in and around marshes. Marshes, therefore, act as an energy source for propagation of grazing, with oak forests serving as recipients of the disturbance. That is, large herbivores attracted to marshes "spill over" into adjacent oak forests, impacting these forests to a greater degree than forests further away from marshes. M. Turner and Bratton (1987) discussed the importance of landscape heterogeneity in

facilitating energy transfer across community boundaries and concluded that the presence of tidal marshes increases grazing on adjacent forest habitats on Cumberland Island. There is no reason to believe that freshwater marshes are not capable of propagating similar energy transfers.

Energy transfer from marsh to forest did not precipitate measurable changes in community boundaries for at least two reasons. Marsh water levels, produced by differences in relative elevation and long-term precipitation patterns, restricted flood-intolerant woody species to upland sites. Additionally, recruitment from surviving live oak seedlings into the overstory is probably adequate to fill canopy gaps as they open. For example, proximity to saw palmetto may offer grazing protection to some live oak seedlings. Live oak's long life span (Preston 1976), rapid growth rate, and episodic fruit production (Elias 1980) allow self-replacement by exploiting gaps in its own canopy.

Grazing by large herbivores caused energy to flow in the opposite direction at the scrub/forest boundary than at the marsh/forest boundary. Oak seedling density did not differ along scrub/forest boundaries; greater cover and height of oak seedlings at the scrub end of the scrub/forest gradient indicated preferential grazing by large herbivores in forest compared to scrub. Behavior and diet data from studies of feral horses (Lenarz 1983) and white-tailed deer (Harlow and Jones 1965, Harlow and Hooper 1972) further indicate that large herbivores prefer live oak forest to scrub vegetation. Thus, scrub protects oak seedlings from grazing. The net result is an absence of disturbance-induced boundary change. Protection from grazing, coupled with relatively long fire-free intervals, provides oak forest an opportunity to encroach into scrub at the boundary. As the water table retreats from the scrub/forest boundary, oak forest advances into area formerly occupied by scrub (i.e., succession converts scrub to oak forest). These results agree with the hypothesis that scrub is a seral stage of oak-palmetto forest (Monk 1968, Hillestad et al. 1975, Veno 1976, Davison and Bratton 1988). However, the current study indicates that succession is primarily limited by edaphic characteristics (soil moisture content) rather than fire, as proposed by Hillestad et al. (1975) and Davison and Bratton (1988) (also Monk 1968, Abrahamson 1984a for Florida scrub).

Although fire did not affect the location of community boundaries, differential fire intensity between backfires and headfires influenced live oak seedling response. Greater cover, density, basal area, and height of live oak seedlings at headfire boundaries than at backfire boundaries may reflect differences in grazing pressure associated with structural boundary differences produced by different types of fires. Alternatively, low-intensity backfires may expose less mineral soil (thus, fewer "safe sites") than high-intensity headfires. Backfire boundaries were relatively discrete and straight compared to headfire boundaries, which were wavy and diffuse. Variations in fire intensity at headfire fronts caused variable fire penetration into oak forest, with a subsequently variable ("patchy") vegetation response. Headfire boundaries were characterized by "fingers" of scrub extending into oak forest. These

fingers did not produce significant increases in scrub area (as evidenced by aerial photographs), but tended to homogenize the scrub/forest boundary. By contrast, relatively low-intensity backfires killed few live oak trees, thereby producing a discrete scrub/forest boundary. The wavy, diffuse headfire boundary apparently protected oak seedlings from grazing by large herbivores to a greater degree than did the discrete, straight backfire boundary. These findings are consistent with the hypothesis of Wiens et al. (1985) that high-intensity disturbance blurred patch boundaries to a greater extent than low-intensity disturbance.

Most authors agree that fire is a normal environmental feature in scrub and marsh communities of the southeastern United States (see especially Abrahamson 1984b, Christensen 1988). The current study indicates that the influence of fire on scrub/forest and marsh/forest boundaries is minimal compared to climatic influences. It should be noted that, whereas fire does not directly regulate community boundaries, the boundaries are primarily responsible for determining which areas will burn. Finally, grazing by large herbivores apparently has not affected community boundaries. Consistent with the hypothesis of Wiens et al. (1985), we conclude that the physical environment is of primary importance in controlling patch boundaries. Disturbance played a minor role in community dynamics and boundary phenomena of these communities.

MANAGEMENT IMPLICATIONS

Intense scrub and marsh fires are difficult, if not impossible, to suppress. These fires have no apparent negative impacts on community structure or function; communities recover to preburn levels within two years (Davison and Bratton 1988). Most authors agree that fire is a normal environmental feature in these communities (see especially Abrahamson 1984b, Christensen 1988). Furthermore, the current study indicates that the influence of fire on scrub/forest and marsh/forest boundaries is minimal compared to climatic influences. Since fires in adjacent communities are relatively easily controlled, it is inadvisable to attempt suppression action on marsh or scrub fires when typical wildfire conditions prevail. Risks to personnel and economic costs associated with fire suppression can be extremely high, especially in scrub vegetation. It is doubtful whether benefits (which appear to be negligible) exceed suppression costs in marsh and scrub communities.

Grazing by large herbivores has not affected community boundaries to date. However, the density and height of oak sprouts in forests adjacent to marshes indicate the potential detrimental impact of large grazers on oak regeneration. Comparing exclosures which exclude deer, wild hogs, and horses to those which exclude only horses and to controls in open live oak forest (which produces fewer sprouts and has less shrub cover than live oak forest adjoining scrub) indicates oak sprouts on Cumberland Island respond immediately to

the elimination of browsing deer. Although response varied by individual trees and locations, some oak sprouts in deer-hog-horse exclosures exceeded 150 cm four years after cessation of grazing, averaging 30 to 40 cm around the most prolific parent trees. Sprouts in horse exclosures and controls rarely exceeded 15 cm in height, and averaged less than 10 cm (S.P. Bratton, unpublished data). Twenty months after a 1986 wildfire at the marsh/forest boundary, oak sprouts had been browsed by deer and were generally less than 15 cm tall. By contrast, red bay sprouts frequently exceeded 50 cm in height and occasionally reached 250 cm (S.P. Bratton, unpublished data). Reducing populations of herbivores, particularly white-tailed deer, would provide insurance against loss of live oak forest at the marsh/forest interface.

ACKNOWLEDGMENTS

Sheila Merrigan provided assistance with project logistics, data collection and analysis, and manuscript editing. Additional field assistance was provided by Christi Lambert, Valerie Sewell, and Tom Engelsma. Their help is gratefully acknowledged. Frank Golley, Carl Monk, Carolyn Sieg, and Tom Boutton provided helpful reviews of an earlier draft of the manuscript. Greenhouse space was provided by the Southern Piedmont Conservation Research Center, Watkinsville, Georgia. Funding was provided by a contract (10-21-RR271-189) from the U.S. National Park Service, Department of Interior, through the Center for Coastal Studies, Rutgers University to S. P. Bratton, Institute of Ecology, University of Georgia.

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