The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida

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Abstract

The interplay between mangroves and saltmarshes at the temperate to subtropical transition in Florida results in dramatic changes to the appearance of the coastal landscape. In the 1980s, freezes killed entire mangrove forests dominated by black mangroves, *Avicennia germinans* (L.). Following the freezes, saltmarshes dominated by smooth cordgrass, *Spartina alterniflora* Loisel, revegetated the intertidal zone. After a decade of mild winters, however, mangroves are beginning to reclaim the area. The rate of mangrove expansion was determined by comparing aerial photography (change from 1995 to 1999), and from monitoring transects (over a 3 year period) on three of the Cedar Keys, Florida (Lat. 29°08'). The rate of mangrove expansion varied among islands, and the mechanism of expansion ranged from propagule-trapping by saltmarshes along the edges of mangrove clumps to widespread dispersal and growth of existing or newly imported propagules. A freeze occurred during the study, which may have set back mangrove expansion by defoliating mangrove trees and resetting mangrove reproduction. Mangrove expansion was projected to take 20–30 years for complete seedling cover. Given the possibility of global climate change and its potential influence on the distribution of coastal vegetation, the timeframes and implications to coastal wetland ecosystems involved in this regular interplay will provide valuable baseline information for future studies.

Introduction

The distribution of mangroves in the northern Gulf of Mexico is controlled primarily by freezing temperatures (Davis 1940; Lugo and Patterson-Zucca 1977; Kangas and Lugo 1990). Saltmarshes dominate intertidal zones in more temperate climates, but mangroves replace saltmarshes at lower latitudes where warm temperatures allow mangrove survival and growth. At the transition between temperate and subtropical climate, however, an interplay occurs between mangroves dominated by black mangroves, *Avicennia* germinans (L.), and saltmarshes dominated by smooth cordgrass, *Spartina alterniflora* Loisel. Freezes favor the marsh, but mangroves prevail during periods of mild winters. In Florida, this transition zone occurs along the east coast north of Cape Canaveral to St. Augustine, and along the west coast north of Tampa Bay to the Cedar Keys (Kangas and Lugo 1990).

During periods of mangrove succession, a variety of factors influence the distribution of mangrove and saltmarsh ecotones. Saltmarsh vegetation cannot grow in the shade of mangrove trees (Kangas and Lugo 1990). Freezes open the forest floor to light, which allows fast pioneering saltmarsh species to vegetate the intertidal zone (Patterson et al. 1993). In the process, saltmarshes remove available nutrients, possibly causing root competition for nutrients among the saltmarsh species and new mangrove seedlings (Patterson et al. 1993). Saltmarshes, however, may also facilitate mangrove colonization by trapping mangrove propagules (Lewis and Dunston 1975). The combination of propagule trapping and nutrient competition makes the overall effect of the marsh on mangrove recolonization unclear. Other factors influencing the distribution of mangrove and saltmarsh ecotones at local scales are hydroperiod, salinity, sediment characteristics, and propagule predation (e.g., Patterson and Mendelssohn 1991; Clarke and Allaway 1993; Clarke and Myercough 1993; Patterson et al. 1993). At regional scales, mangrove transgressions into saltmarshes occurring in South Florida (Wanless et al. 1994) and Australia (Saintilan and Williams 1999) have been explained by changes in precipitation patterns, increases in nutrient levels and sedimentation, revegetation of disturbed areas, altered tidal regimes, and sea-level rise; however, the overall distribution of mangroves in the northern Gulf of Mexico appears to be dominated by freeze frequency (Kangas and Lugo 1990), with other factors explaining local variation (e.g., Patterson and Mendelssohn 1991).

Recent climate history in Florida provides an opportunity to investigate the interplay between mangroves and saltmarshes. Hard freezes during the 1980s killed entire mangrove forests in the northern Gulf of Mexico (McMillan and Sherrod 1986; Watson 1986; Montague and Weigert 1990; Montague and Odum 1997). Saltmarshes replaced the intertidal zone within 4–5 years. However, 6 years of mild winters have allowed mangroves to begin reclaiming the area. Mangroves now grow in clumps among saltmarsh vegetation. Given the possibility of global climate change and its potential influence on the distribution of coastal vegetation, quantifying the timeframes involved in this regular interplay would provide valuable baseline information for future studies. The purpose of this study is to document the ongoing succession from saltmarshes to mangrove forests within the temperate to subtropical transition in Florida and to estimate the time frame for mangrove replacement.

Materials and methods

Study location

The Cedar Keys are located in the Big Bend region of Florida (Lat. 29°08' N; Figure 1), which has a low-energy coastline with a mean tidal range of 1 m (NOAA 1988). Salinity is influenced by the Gulf of Mexico, local rainfall, surface runoff, and freshwater discharge from the Suwannee River (average 296 m³ s⁻¹) 26 km to the north (NOAA) 1985). Mangrove forests persist on the Cedar Keys because the intensity of freezes is reduced by the surrounding water (Laessle and Wharton 1959; Lugo and Patterson-Zucca 1977; Montague and Odum 1997). Patches of closed-canopy mangrove forest on the Cedar Keys exist as nearly monospecific stands of A. germinans. Red mangrove, Rhizophora mangle L., and white mangrove, Laguncularia racemosa (L.), only occur as scattered individuals, probably because they do not tolerate low-temperatures as well as A. germinans (Markley et al. 1982; McMillan and Sherrod 1986). The canopy height of A. germinans forests prior to the mangrove kill in the 1980s was approximately 3-4 m (Lugo and Patterson-Zucca 1977; Watson 1986).

Small intertidal wetlands on Snake Key, North Key, and Seahorse Key (Figure 1) were selected for study. Sites on Snake Key and North Key were in pockets of marsh nearly surrounded by upland forests and naturally occurring sand berms. These barriers effectively block wind in the marshes. Water enters these pocket marshes via creeks. The site on Seahorse Key, on the other hand, was fully exposed to open water and north wind; water filled and drained the marsh from an adjacent lagoon. The saltmarsh vegetation on the islands consisted almost entirely of *S. alterniflora* except on Seahorse Key, which had a mixture of *S. alterniflora*,



Figure 1. Map of the Cedar Keys showing study sites.

saltwort, *Batis maritima* L., and glasswort, *Salicornia virginica* L.

Aerial photography/change analysis

Gross changes in vegetation were determined by comparing 1995 and 1999 digital orthophotos. Digital orthophotos (1-m resolution digital orthoquads) taken by US Geological Survey National Aerial Photography Program at the Cedar Keys were obtained from the Florida Land Boundary Information System (www.labins.org). For each study site, the digital orthophotos were displayed at 1:1000 scale in ArcMap 8.3. Mangrove and saltmarsh vegetation were digitized based primarily on height, color and texture variance (e.g., Higinbotham et al. 2004). The vegetation was easily distinguished in the orthophotos; marsh vegetation appeared black, mangrove vegetation appeared dark red, upland vegetation appeared pink, and beach and spoil appeared white. Hard copies of the same US Geological Survey aerial photography were obtained from local resource managers and placed under a stereoscope to further assist in the delineation of the vegetation.

From the digitizing process, maps were generated depicting mangrove and saltmarsh distribution within the study area for 1995 and 1999. Mangrove area for each study site was calculated for each year based on the total area digitized for each vegetation class. Change analyses were performed in ArcMap using the Union feature, which computes a geographic intersection of the input features from both years producing output features attributed with the vegetation class of both time periods. The changes in mangrove distribution that occurred over the 5-year period were displayed in ArcMap using symbology based on the attribution for both time periods (e.g., persistent mangrove, mangrove expansion, mangrove loss). For example, mangrove areas present in both 1995 and 1999 aerial photographs were termed persistent mangroves, and mangrove expansion referred to areas where mangroves were present in 1999 but not in the earlier 1995 photos. Polygons less than 10 m² were dropped from the change analyses because these small areas were considered to be within the error of the digitizing process. The results of the change analyses were used to provide a mangrove expansion rate (new mangrove area year⁻¹) at each study site.

Ground level transects

Thirty-meter transects oriented perpendicular to mangrove/saltmarsh ecotones were established at the Cedar Keys to provide a finer scale for monitoring changes in mangrove and saltmarsh densities, and to supplement results of GIS analyses. A total of five transect locations were established, which were placed in areas where definitive mangrove and saltmarsh ecotones were apparent from 1995 aerial photography. The approximate elevations along transects with respect to Mean Lower Low Water (MLLW) ranged between 65 and 88 cm, which resulted in daily inundation by the 1-m tides characteristic of the area.

Increases in mangrove tree and seedling densities were important indicators of mangrove expansion, and saltmarsh stem densities were expected to decrease as mangroves expanded and shaded the underlying saltmarsh. Mangrove trees and seedlings (identified by lack of branching) were counted in 4-m² quadrats at 5-m intervals along the transects for 2 years (1995 and 1996) in May and November, which approximate the usual growing season for this region. Densities were also measured in May 1997 along Seahorse Key and North Key transects and in November 1997 along transects on Snake Key. Densities of saltmarsh stems were counted in 0.25-m² quadrats at 5-m intervals along the transects. Saltmarsh stem densities within the seven 0.25-m^{-2} quadrats along each transect were summed to give number of stems 1.75 m⁻². Seasonal and annual changes in saltmarsh stem density was calculated for each transect by subtracting May values from November values (seasonal) or November values from subsequent November values (annual). The five transects were used as replicates (for non-parametric analysis) to evaluate statistical significance of regional differences (Wilcoxon signed rank test, 0.05 level of significance).

An estimate of mangrove seedling recruitment was used as an indicator of mangrove expansion along the transects to supplement results from aerial photography. The estimate of seedling recruitment was determined by the following equation: Seedling Recruitment = Δ seedling density + Δ tree density + tree death + seedling death. Changes in seedling and tree densities were calculated by subtracting densities in November of one year from densities in November of the following year. Tree death was easily measured by counting the number of leafless trees within a quadrat, but seedling death was not measured. As a result, seedling recruitment was underestimated.

Results

Freeze observations

A severe winter occurred between the 1995 and 1996 growing seasons (minimum air temperature of -8 °C in January 1996 at a station near the Cedar Keys; NOAA 1915–1997). Many trees had lost some or all of their leaves when measured in May 1996, but most recovered by November 1996. Tree mortality along transects following the freeze was 12% on Seahorse Key, 5% on North Key, and 4% on Snake Key. Although mangroves in this region typically flower during spring and drop propagules during fall, flowering and propagule drop was not observed on the islands during 1996. Mangroves were flowering again by May 1997.

Aerial photography/change analysis

The study sites were at different stages of mangrove succession at the beginning of the study period in 1995 (3% cover on Seahorse Key, 20% cover on North Key, and 33% cover on Snake Key, Table 1). Mangrove cover expanded to occupy ca. another 20% of the intertidal zones at each study site during the 5-year period. From the change analyses, the site on North Key expanded at a rate of about 300 m² year⁻¹, and the sites on Seahorse Key and Snake Key expanded at rates exceeding 840 m² year⁻¹. Mangrove expansion on North Key and Snake Key occurred along the boundaries of persistent mangrove clumps (Figure 2). The mangrove expansion on Seahorse Key also occurred along the boundaries of persistent mangrove clumps, but much of the expansion at this site was represented by many small mangrove clumps distributed widely throughout the marsh (Figure 2). Some mangrove loss was evident at the North Key and Snake Key study sites, but this loss was greatly outweighed by mangrove expansion.

Ground level transects

Initial canopy height (used simply as an indicator of where mangrove and saltmarsh boundaries occur) and seedling recruitment for the five transects are shown in Figure 3. Seedling recruitment along the two Snake Key transects was highest around mangrove clumps and declined with distance. Mangrove seedling recruitment along Snake Key-Transect 2 occurred up to 5 m from mangrove clumps into saltmarsh areas. Seedling recruitment along Snake Key-Transect 1 was as high as 76 seedlings $m^{-2} year^{-1}$ and seedlings recruited at least 15 m into saltmarsh areas. Although seedling recruitment on Seahorse Key occurred, it primarily occurred within the mangrove clump (Transect 1), and along the area fringing the lagoon (Transect 2). On the North Key transect, seedling recruitment did not occur. Seedling recruitment did not occur along any transect in 1997.

Seasonal changes in saltmarsh stem density along transects were not significant during 1995 (p = 0.35), but were significant during 1996 (p = 0.04). Annual changes in saltmarsh stem density along transects were higher in 1996 than in 1995 (p = 0.04). These increases occurred along transect locations that were farthest from mangrove clumps.

Discussion

Frequency of freezes in Northern Florida

Freeze cycles in Florida have been explored by scientists interested in the risks associated with citrus production. In one such study, Miller and Downton (1992) defined a local killing freeze as winters in which the minimum temperature fell below -6.7 °C, and a regionwide severe freeze

season was defined as winters in which the minimum temperature fell below -5 °C at several temperature stations within an area. During 1932–



Figure 2. GIS change analysis between 1995 and 1999 on Snake Key (a), North Key (b), and Seahorse Key (c). White refers to upland or beach, blue refers to water, pink refers to persistent mangrove, red refers to mangrove expansion, opaque refers to mangrove loss, grey refers to remaining intertidal zone, dark grey refers to change in intertidal zone (low tide in 1995 aerial photography vs. high tide in 1999 aerial photography). Locations of 30-m transects are also shown.

Aerial photography						
Location	Intertidal area (m ²)	1995		1999		Change analysis
		Mangrove area (m ²)	Mangrove cover (%)	Mangrove area (m ²)	Mangrove cover (%)	mangrove expansion rate (m ² year ⁻¹)
Snake Key	15,333	5114	33	9044	59	862
North Key	6948	1356	20	2565	37	300
Seahorse	21,186	609	3	4822	23	842
Key						

Table 1. Total intertidal area, mangrove area, and percent mangrove cover at each study site for 1995 and 1999 determined from aerial photography. Also shown are mangrove expansion rates at each study site determined from GIS change analysis.

1980, a regionwide severe freeze season occurred approximately every 8 years in Florida. The freeze frequency changed substantially during the 1980s as tree killing freezes occurred in 4 out of 5 years between 1981 and 1985 (Miller and Downtown 1992).

The freezes that affect the citrus industry appear to coincide with freezes that affect mangroves and probably subtropical species in general. Major impacts to mangroves resulting from freezes occurred in 1962 (Dr Frank Maturo, University of Florida, personal communication), 1977 (Lugo and Patterson-Zucca 1977), 1981, 1983, 1985, 1989 (personal observation) and 1996 (this study). These accounts are consistent with an annual minimum temperate of less than -6.7 °C (definition of a local killing freeze for citrus; Miller and Downtown 1992) recorded at the Cedar Key temperature station (NOAA 1915-1997). However, temperatures on the outermost islands (Snake Key, North Key, and Seahorse Key) are slightly warmer than Cedar Key (Laessle and Wharton 1959). Therefore, the lowest temperature that can be tolerated by mangroves at this latitude may be close to Davis' (1940) original suggestion of -4 °C.

A single severe winter, however, may only set back mangrove development without killing a substantial number of trees. At the Cedar Keys, mangroves have recovered within one year following a severe freeze (Lugo and Patterson-Zucca 1977; personal observation 1981). However, a series of severe freezes is catastrophic, as evidenced by the mangrove kill in the 1980s. Such a catastrophic series of severe winters may recur only once every century in Florida (Winsberg 1990; Miller and Downton 1992). The catastrophic freeze in the 19th century, for example, involved a series of severe winters during 1895–1905, and the series of severe winters during 1977–1989 comprised the catastrophic freeze of the 20th century.

Impact of freezes on mangroves

According to Lugo and Patterson-Zucca (1977), freeze damage to mangroves is greatest in areas more exposed to cold wind. The Seahorse Key marsh is exposed to cold north winds that follow cold fronts in this region. This may explain the high mangrove mortality (12%) at Seahorse Key following the January 1996 freeze (compared to 5% on North Key and 4% on Snake Key). The marshes on Snake Key and North Key, where mangroves are more extensive, are isolated from north wind by natural barriers such as berms and upland forests. Even on these islands, however, some mortality was evident from direct observations along transects and from results of the change analyses that show some small net losses of mangrove, which likely occurred from areas affected by freeze that had not yet fully recovered.

Although Seahorse Key appears to be the most vulnerable to freezes, the impacts of the January 1996 freeze reset mangrove development on all three islands. The failure of mangroves to flower and produce propagules during the 1996 growing season presumably resulted from depletion of the plants' resources during recovery from the previous winter. The lack of seedling recruitment in 1997 suggests that mangrove expansion at the Cedar Keys depends largely on a local source of propagules rather than imports from more



Figure 3. Canopy height and seedling recruitment along each transect.

southerly locations, such as Tampa Bay (a net northward transport of Gulf of Mexico waters occurs in this region; Clarke 1997). Hence, freezes that impact mangrove reproduction at the Cedar Keys cause a major setback to mangrove succession.

Freezes that impact mangroves, however, may indirectly affect saltmarshes. Saltmarsh stem densities at the Cedar Keys were higher in 1996 than in 1995, even though mangrove expansion was expected to result in lower saltmarsh stem densities. Although the increases followed a freeze that defoliated mangroves, increased light availability cannot explain the changes in saltmarsh stem density because they occurred primarily in areas away from mangrove clumps. However, recycled nutrients from fallen mangrove leaves might explain the increase. Freezes may have resulted in greater amounts of detritus as mangrove biomass was defoliated or killed, and subsequent detrital breakdown increased nutrients available for plant growth.

Mangrove expansion

The mechanism of mangrove seedling recruitment and expansion appeared to differ among the study sites. On Snake Key, trapping of mangrove propagules by saltmarsh (Lewis and Dunston 1975) could account for the high seedling recruitment near mangrove clumps. Propagules produced by the mangrove clumps on Snake Key were immediately trapped in saltmarsh within 5–15 m of their source. Without the adjacent saltmarsh, more mangrove propagules may have been exported rather than being retained in the vicinity of the parent trees. High rates of seedling recruitment along the edges of the mangrove clumps and subsequent growth of these mangroves into trees probably explains why Snake Key has the greatest mangrove cover and highest expansion rates among the study sites.

On Seahorse Key, mangrove seedling recruitment occurred within the existing mangrove clump and along the transect adjacent to the lagoon also suggesting that mangrove seedlings may remain near parent trees (Blanchard and Prado 1995; McKee 1995). However, numerous mangrove clumps on Seahorse Key appeared to 'sprinkle in' throughout the marsh (apparent from change analysis), particularly at the southern end of the study site adjacent to the lagoon. This mechanism of expansion may result from single seedlings scattered throughout the marsh that grew to become trees during the study period. Some of the smallest 'clumps' apparent in the digital orthophotos may result from one or two trees that developed a broad canopy (possibly an advantageous strategy when competing alone with saltmarsh). Some of these small clumps among saltmarsh vegetation were also evident on Snake Key.

Time-frame for mangrove succession

The freezes in 1983 and 1985 killed 98% of mangroves at the Cedar Keys (Montague and Odum 1997), which may have eliminated the local mangrove propagule source. It is not known whether local seedlings survived, which would have provided a seed bank for subsequent mangrove succession, or if new recruitment was initially dependent on propagules from areas further south. Regardless, as more mangroves continue to reach reproductive maturity at the Cedar Keys, the rate of mangrove colonization should increase. In the absence of major freezes, the time it will take for mangroves to completely cover the marsh on Snake Key is another 8 years (15,333 m² total area – 9044 m² 1999 mangrove area/mangrove expansion rate of 862 m^2 year⁻¹). Thus, the time frame for complete mangrove recolonization on Snake Key since the freeze kill during the 1980s is nearly 20 years. Using the same calculation for North Key and Seahorse Key, these study sites will take 25–30 years for mangroves to again reclaim the marsh. Periodic freezes, however, ensure that some saltmarsh cover will persist. This mixture of mangrove forests and saltmarshes may continue for several decades until another catastrophic series of freezes kill mangrove forests, and allow saltmarshes to once again occupy the intertidal zone.

Implications for coastal wetland communities

As the intertidal zone changes between mangrove forests and saltmarshes, faunal changes should occur. Both mangroves and saltmarshes provide food and refuge for fiddler crabs, periwinkles, clams, and oysters (Odum et al. 1982; Stout 1984). However, the greater volume and structural complexity of mangroves supports additional fauna such as the mangrove tree crab, *Aratus pisonii* (Milne Edwards), the coffee-bean snail, Melampus coffeus (Linnaeus), the mangrove crab, Goniopsis cruentata (Latreille), the ladder-horn snail, Cerithidea scalariformis (Say), the mangrove rivulus fish, Rivulus marmoratus Poey, and the mangrove cuckoo, Coccyzus minor (Gmelin) (Odum et al. 1982; Davis et al. 1995; Taylor et al. 1995). In mangroves, the periwinkle Littoraria angulifera (Lamarck) replaces the Littoraria irrorata (Say) of saltmarshes (Odum et al. 1982). Also, mangrove forests may attract nesting colonial birds (Watson 1986). Conversely, saltmarsh-dependent bird species such as seaside sparrows, Ammospiza maritima (Wilson), and long-billed marsh wrens, Cistothorus palustris (Wilson), may leave the area when saltmarsh is overtaken by mangroves (Post and Greenlaw 1994).

During the present study, saltmarsh-dependent A. maritima and C. palustris were only encountered at the Seahorse Key study site where saltmarsh cover remains extensive (personal observation). Although pelicans were observed nesting in mangroves on Seahorse Key prior to the catastrophic freezes in the 1980s (Watson 1986), colonial birds were not observed in the developing mangroves of the present study. The only fauna unique to mangroves on the islands was A. pisonii. Aratus pisonii reached densities of 1 crab m^{-3} prior to the 1996 freeze (unpublished data), which are within the range reported for mature mangrove forests of South Florida (1-4 crabs m⁻³; Beever et al. 1979). Mangrove fauna may not only be dependent on the habitat present, but also on other environmental factors, especially temperature (e.g., R. marmoratus, Taylor 1993). A long period of time without freezes may allow a richer mangrove fauna to develop. Alternatively, the lag in development of mangrove fauna may exceed the frequency of freezes at this latitude.

Implications for coastal wetland ecosystems

Odum (1983) describes succession and retrogression as 'the self-organizational process by which ecosystems develop structure and processes from available energies.' In the absence of freezes, mangroves succeed saltmarshes perhaps because they are able to channel more energy into greater stature and biomass, thereby shading out saltmarshes (Kangas and Lugo 1990). During periods of severe winters, however, the combined energy drains of salinity and frost limit the amount of structure that can be maintained. As a result, mangroves are killed and the coastal wetlands rapidly retrogress to saltmarshes. Following a mangrove kill, saltmarshes occupy the intertidal zone within a period of only 5-10 years. The saltmarsh vegetation, however, may stabilize marsh soils and maintain certain wetland functions (e.g., juvenile fish habitat, detritus production). Whether the overall effect of saltmarshes facilitates mangrove colonization by trapping mangrove propagules or retards mangrove reestablishment by outcompeting mangrove seedlings remains equivocal. Nevertheless, saltmarshes maintain emergent habitat in the intertidal zone in the interim between occupations by mangroves. Although coastal wetlands alternate between mangroves and saltmarshes at the temperate to subtropical transition in Florida, overall production and survival of wetland-dependent biota are maintained despite periodic disturbances.

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