




Structural Impacts, Carbon Losses, and Regeneration in Mangrove Wetlands after Two Hurricanes on St. John, U.S. Virgin Islands

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Abstract

Hurricanes Irma and Maria ravaged the mangroves of St. John, U.S. Virgin Islands, in 2017. Basal area losses were large (63–100%) and storm losses of carbon associated with aboveground biomass amounted to 11.9–43.5 Mg C/ha. Carbon biomass of dead standing trees increased 8.1–18.3 Mg C/ha among sites, and carbon in coarse woody debris on the forest floor increased 1.9–18.2 Mg C/ha, with effects varying by mangrove typology. While St. John has only ~45 ha of mangroves, they exist as isolated basins, salt ponds, and fringe mangroves; the latter sometimes support diverse marine communities. Salt pond and fringe mangroves had proportionately more organic carbon (46.3 Mg C/ha) than inorganic carbon (1.1 Mg C/ha) in soils than isolated basins. Soil organic carbon was also appreciable in isolated basins (30.8 Mg C/ha) but was matched by inorganic C (36.7 Mg C/ha), possibly due to adjacent land use history (e.g., road construction), previous storm overwash, or geomorphology. Soil nitrogen stocks were low across all typologies. Mangroves had limited regeneration 26 months after the storms, and recovery on St. John may be hindered by pre-storm hydrologic change in some stands, and potential genetic bottlenecks and lack of propagule sources for expedient recovery in all stands.

Keywords Aboveground carbon · Recovery · Soil carbon · Soil nitrogen · Total ecosystem carbon · Tropical cyclone

Introduction

Mangroves are considered disturbance-adapted ecosystems across their global range (Lugo et al. 1981). This designation relates to the influences of past tropical cyclones (hereafter,

hurricanes), and the observable recovery of structural characteristics in the years following a seemingly catastrophic disturbance (Smith et al. 1994). Mangroves are not fully resistant to hurricanes, rather, they can tolerate these events and recover if they are healthy and if hurricanes occur infrequently (Saenger 2002; Ward et al. 2016; Sippo et al. 2018; Krauss and Osland 2020). In some cases, individual hurricanes can cause severe destruction of mangroves, especially on islands, where mangrove distributions are limited (Cintrón et al. 1978) and unique associations can form (e.g., associations with coral reefs; Yates et al. 2014; Rogers 2019). Island mangrove areas are nearly always small but confer exceptional value to society (Cumick et al. 2019).

The recurrence interval is short for hurricanes within the greater Caribbean region; approximately 50 tropical storms per century for the island of Puerto Rico (Lugo 2000). The influence of hurricanes is likely to increase in the future with climate change as their numbers and intensities increase (Kossin et al. 2017). If this occurs, mangrove forest cyclical succession (Lugo 1980) will be stifled more often, with aboveground carbon stocks reduced, and the possibility of soil stocks reduced with time. Subsequent forest structure will

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provide less effective wind buffers and humans living in association with mangroves will incur greater economic and sociological costs (Lugo 2000).

Healthy mangroves tend to tolerate greater damage and are more likely to regenerate after hurricane events than stressed forests. However, stressed mangrove forests are wide spread globally (Lewis et al. 2016; López-Portillo et al. 2017; Krauss et al. 2018). While examples of persistent post-hurricane mortality from Caribbean islands may be limited to Puerto Rico, St. Croix (U.S. Virgin Islands), Guánaja/Roatan (Honduras), and Belize (Jiménez et al. 1985; Cahoon et al. 2003), circumferential road construction along the fringes of islands, coastal development across the Caribbean, location of mangroves on those islands relative to storm trajectory, and their developmental geomorphology (typology) will affect stress condition and natural vulnerabilities of mangroves to repetitive hurricanes. On the island of St. John, U.S. Virgin Islands, at least three mangrove typologies occur: (1) isolated basin (2) salt pond, and (3) fringe mangroves (typology descriptions available in [Electronic Supplemental Material](#)).

Hurricane Irma made land-fall on the island of St. John on 6 September 2017, and was followed by Hurricane Maria just 2 weeks later on 20 September 2017 to compound natural resource injury. In this study, we focus on the three mangrove habitat types (typologies) that occur on St. John to re-construct pre-hurricane forest structure, assess current forest structure, describe the influence of the hurricanes on aboveground carbon balance, assess soil carbon and nitrogen stores, and consider aspects of regeneration and recovery potential.

Methods

Study Sites

St. John is located in the U.S. Virgin Islands, a territory of the United States within the Lesser Antilles. The island comprises an area of approximately 51.8 km², and since 1956, 60% of this area has been designated protected as part of Virgin Islands National Park (additional vegetation details available in [Electronic Supplemental Material](#)). St. John is 11 km long and up to 5 km wide and is a volcanic island with a maximum elevation of 387 m. Steep slopes often transcend into rocky shorelines, beach strands, or tidal wetlands. Precipitation ranges from 890 to 1400 mm annually (Reilly 1991), with rainfall somewhat dependent upon year-to-year variability in tropical storm activity. Mangrove forests occupy approximately 45 ha on St. John (or 0.86% of total land area distributed along 11 km of coastline), mostly associated with the north eastern and eastern sides of the island (see Fig. 1a). Mangroves were heavily affected by Hurricanes Irma and Maria in 2017.

Hurricane Irma's eyewall passed just north of St. John on 6 September 2017 (Fig. 1b). Maximum sustained wind speeds were recorded as 268–278 km/h (Category 5), with an unprecedented low pressure reading of 914 mb (Cangialosi et al. 2018). Wind speeds were at least 118 km/h across much of St. John, and likely much higher (Fig. 1b). These strong winds were sustained for several hours and were compounded by orography and slopes that funneled winds in odd directions as waters surged simultaneously to deposit boats and debris into fringe mangroves. High water marks surveyed post-storm ranged from 1.6 to 3.1 m above average water level (Cox et al. 2019), substantially greater than the island's average microtidal range (NOAA Station 9751381 <https://tidesandcurrents.noaa.gov>; accessed 28 April 2020). Just 14 days later (20 September 2017), Hurricane Maria's eyewall passed approximately 90 km to the south of St. John affecting the island again with additional wind, surge, and rainfall (Browning et al. 2019) (Fig. 1c). In the year following Hurricanes Irma and Maria, mangroves on St. John were easily demarcated because they represented most of the dead vegetative biomass along the coast, contrasting to green herbaceous plants and tree re-growth of upland vegetation. Mangrove species on St. John include the red mangrove (*Rhizophora mangle* L.), black mangrove (*Avicennia germinans* (L.) L.), and white mangrove (*Laguncularia racemosa* (L.) C.F. Gaertn).

Forest Plots

We established seven sites in the mangroves of Virgin Islands National Park and Virgin Islands Coral Reef National Monument (Fig. 1a). Two sites were in isolated basin forests (Annaberg), two in salt pond forests (Francis Pond, Lameshur), and three in fringe forests (Mary Creek, Water Creek, Princess Bay). The two isolated basin forests were surveyed in July of 2018, 10 months after Hurricanes Irma and Maria and are described as “isolated” because they appear to have formed behind a natural berm, and eventually a road (by at least the late 1780s), and then culverted at some later date to promote drainage. The remainder of the sites were surveyed in November 2018, 14 months after the storms.

Each of the seven sites contained two replicate plots (>10 m apart), with each plot marked permanently with a numbered PVC pipe for future re-survey. Survey plots were circular, each with a radius of 5.65 m, equating to an area of 0.01 ha per plot, or 0.02 ha per site. Plots had to be relatively small on St. John because of the narrow width of fringe forests, but otherwise, surveys were conducted similarly to procedures outlined in Doyle et al. (1995). All live and dead trees with a diameter at breast height (*dbh*, height at ~1.4 m) of ≥1 cm were identified to species, measured for diameter with a standard diameter tape, and mapped by azimuth and distance from each plot center. We categorized each tree in four ways:

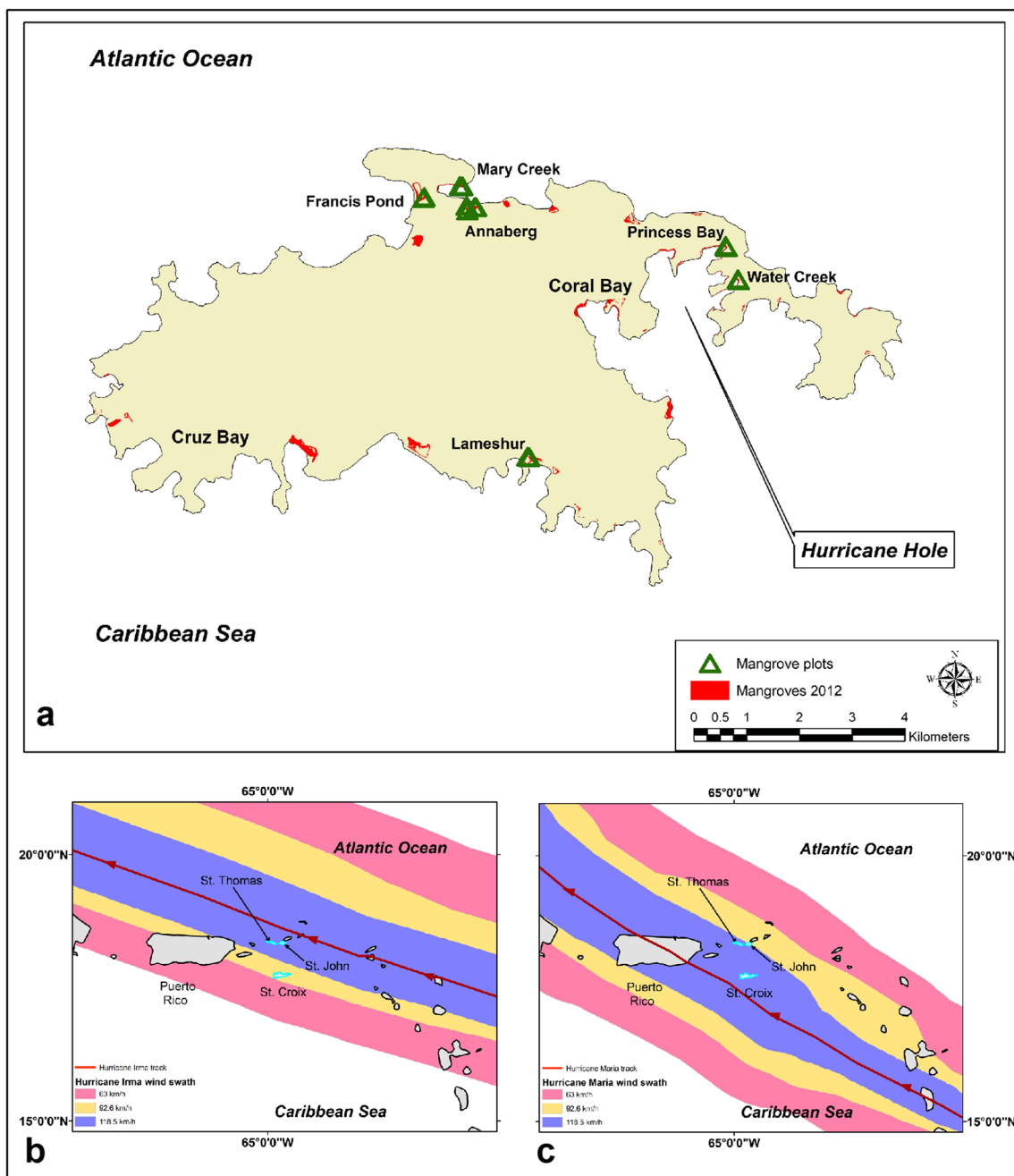


Fig. 1 (a) Distribution of mangrove wetlands on St. John, U.S. Virgin Islands based on 2012 imagery, including, (b) the track of Hurricane Irma on 6 September, 2017, and (c) the track of Hurricane Maria on 20 September, and the location of St. John relative to important wind fields. Imagery (0.5 m resolution) of St. John for mapping mangrove

area was acquired from the 2017 Hurricane Irma NOAA NGS DSS Natural Color 8 Bit Imagery, NOAA National Geodetic Survey <https://inport.nmfs.noaa.gov/inport/item/52284> (accessed, 22 July 2019). Wind field data were acquired from the NOAA National Hurricane Center, <http://www.nhc.noaa.gov/gis> (accessed, 22 July 2019)

(1) live, (2) snapped or tipped-up during the storm, (3) dead standing but not snapped from the storm, or (4) dead before the storm (standing or snapped). At times, *dbh* values were reconstructed slightly or taken from a different location on the stem if a tree was wind-snapped below *dbh* height. Each live tree with a *dbh* ≥ 5 cm was tagged with a uniquely numbered aluminum tag for future surveys. Stand height was determined

by measuring a subsample of 2–7 trees in or near each plot (4–11 trees per site) either on live trees or snags.

Forest canopy coverage was assessed at 1 m above ground at each plot center at cardinal directions (N, S, E, W) using a spherical densiometer (model A, Forest Densiometers, Bartlesville, Oklahoma, USA). Two canopy coverage assessments were made for each plot; one that included overtopping

wood and green vegetation, and the other that included only overtopping green vegetation. Distance mapping and forest height measurements were conducted with a laser range finder (model 200, Laser Technology, Inc., Englewood, Colorado, USA), and azimuths were assigned using a standard compass without magnetic declination adjustment (model KB-14/360RG, Suunto, Vantaa, Finland).

Woody debris was assessed using a line-intercept technique (cf., Van Wagner 1968) to determine coarse and fine downed woody debris volume. Three, 20-m long transects were established per plot (six per site) and run, to the degree possible, in random azimuths using a measuring tape to establish an intersect line. For some fringe locations, woody debris lines had to be segmented to fit 20-m lengths within the restricted forest area. All downed wood intersecting the transect and appearing up to 1 m above the soil surface was tallied. Coarse downed wood, defined as woody debris ≥ 7.5 cm in diameter at intersect, was diameter-measured with calipers along the entire transect, and placed into one of three decay classes: sound, intermediate, or rotten (as per Krauss et al. 2005). Fine woody debris, defined as woody debris < 7.5 -cm diameter, was recorded as numeric counts between distances of 2 to 6 m along each transect for two size classes (1–2.5-cm and 2.5–7.5 cm diameter), and between distances of 2 and 4 m only for a third size class (≤ 1.0 cm). Woody debris volume (m^3/ha) among the various categories was then calculated from an established formula (Van Wagner 1968). Based on past woody debris surveys in mangroves (Krauss et al. 2005, 2018), we assumed that coarse woody debris classified as rotten was laid down before Hurricanes Irma and Maria, while intermediate and sound wood would have been laid down by Hurricanes Irma and Maria. No such distinction could be made for fine woody debris.

Aboveground Carbon

Individual tree *dbh* values were converted to total dry biomass using allometric equations developed in south Florida, USA, but for the same mangrove species (Smith and Whelan 2006). Allometric equations included biomass estimation for prop roots of *R. mangle* trees, which we also include. Aboveground standing stocks of carbon (C) were assessed two ways: (1) pre-storm period *dbh* values were projected based on the demography of dead stumps, felled, and live trees to determine standing stocks of C pre-hurricane impact, and (2) post-storm period *dbh* values were used, as measured, to determine standing stocks of C after the storms. Biomass reduction factors that considered individual tree condition during post-storm surveys were applied to main stems (Domke et al. 2011), but not to prop roots. Woody debris biomass was determined from calculated volume based upon a mass conversion of 0.5 Mg m^{-3} for mangrove wood (Robertson and Daniel 1989). Proportional scaling factors of 0.5, 0.35, and 0.2 Mg m^{-3} were used for sound, intermediate, and rotten decay

classes, respectively (Allen et al. 2000), to convert to total dry biomass. The content of C in dry biomass of mangrove trees and woody debris was assumed to be 41.5%, as per Bouillon et al. (2008).

Belowground Carbon and Nitrogen

A single soil core was collected from each plot ($N = 2$ per site) using a 7.5-cm-diameter stainless steel split coring device driven by sledge as deep as possible; cores rarely exceeded 50 cm depth on any site without hitting hard substrates. Isolated basins and salt pond mangroves were sampled consistently to 36 cm, while fringe mangroves were sampled consistently to 48 cm. We do not assume that soil depths are consistently deeper than this, and therefore, do not normalize estimates to 50 cm or 100 cm. Compaction was minimal (< 0.5 cm). Once extracted, each core was cut manually by knife into 3-cm sections in the field, and stored individually in plastic bags each having equal volumes of soil (132.5 cm^3). Samples were kept cool either on ice during transport from the field or in a cold room prior to processing. Samples were dried within 2 weeks of collection to a constant weight at 60°C and weighed to determine bulk density (g/cm^3) (depth-specific bulk density data available in [Electronic Supplemental Material](#)). Total nitrogen (N: %) and total carbon (C: %) were determined on individual depth samples at the USGS Wetland and Aquatic Research Center, Lafayette, Louisiana on at least two analytical replicates per sample. Because some of these soils contained a high percentage of inorganic C (determined by prolific bubbling as HCl was added), we acid-fumigated soils in a desiccator containing HCl vapor to remove inorganic C (Harris et al. 2001), and re-ran all of the samples for carbon content. Organic C, inorganic C, and N densities are reported as determined with a CN elemental analyzer (model Flash EA 1112, ThermoFinnigan, Wigan, UK) and by adjusting for bulk density among the 3-cm sections.

Regeneration

Four, 1-m^2 sub-plots were established per plot to assess regeneration (eight sub-plots per site) during initial forest surveys 10–14 months after the hurricanes. Each sub-plot was established systematically starting at 2 m from each plot center at cardinal directions. All seedlings and saplings were tallied by species, classified as taller than or shorter than 50 cm, and the height of the tallest seedling/sapling in each sub-plot was measured. Saplings were defined as mangroves up to a height greater than 1.4 cm, but with a *dbh* measurement < 1.0 cm. All 1-m^2 sub-plots were re-surveyed again 26 months after the hurricanes (December 2019) by doubling the number of sub-plots – extending to 2 m and 4 m at cardinal directions from plot center – in order to canvass a larger area (16 sub-plots per site). Advance regeneration, indicated by seedlings present on

site prior to the hurricanes, was differentiated from new seedling recruitment by the presence of compressed internodes at any point along the stem, which would indicate growth in a shaded pre-storm understory versus post-storm unshaded conditions.

Statistical Analyses

Pre-hurricane and post-hurricane data on live basal area, dead basal area, as well as calculated live tree C, dead tree C, live prop root C, dead prop root C, and woody debris C were analyzed for differences among mangrove typology (isolated basin, salt pond, fringe) using ANOVA. In addition, a repeated measures ANOVA under a split-plot framework was used to determine if soil organic C, inorganic C, and total nitrogen density, as well as bulk density differed by typology with soil depth. Because there was a total of up to 17 depth increments (q) and 4–6 samples (n : number of cores per typology), the repeated measures assumption that $n + 1 > q$ (i.e., $n + 1 = 5$ to 7 and $q = 17$ in our study) was not met (Johnson and Wichern 1988). Thus, depth was assigned as the whole-plot (repeated measures) because nesting accounts for non-independence among repeated measures with core depth. Data were either normal with homoscedastic variance without transformation or were square-root transformed prior to analysis. Average separations were determined using Tukey's tests with Bonferroni adjustment. Averages ± 1 standard error (SE) are reported throughout. All analyses were conducted using SAS 9.4 Software (SAS Institute, Inc., Cary, North Carolina, USA).

Results

Reconstructed Mangrove Forest Structure before the 2017 Hurricanes

Surveyed mangrove forests in isolated basin, salt pond, and fringe typologies on St. John were intact prior to Hurricanes Irma and Maria (Fig. 2a–c). Isolated basin mangrove trees at Annaberg were > 10 m tall, had basal areas of about 19–24 m²/ha, and were comprised of 1600–2850 stems/ha (Table 1). *Rhizophora mangle* (85.8%) was the predominant species on the eastern portion of Annaberg, while *R. mangle* (46.7%) and *A. germinans* (45.7%) were co-dominant toward the western boundaries of Annaberg where tidal waters drain less efficiently. Trees on salt pond sites at Francis Pond and Lameshur were shorter (~ 5.2 m tall) than in the isolated basin mangroves of Annaberg, with basal areas of about 8–14 m²/ha and an appreciable number of stems (6750–8100 stems/ha). Species distributions in salt ponds were either completely dominated by *L. racemosa* (Francis Pond) or by *A. germinans* (Lameshur), with many of the trees at Lameshur possibly being planted after Hurricane Hugo in

1989. Trees in the fringe forests of Princess Bay, Water Creek, and Mary Creek were not dissimilar in height from salt pond mangroves, but typically had greater basal areas (about 14–22 m²/ha) supported by densely tangled stems and roots of classic fringe mangroves of the neotropics. Fringe mangroves appeared to be the most diverse among the three typologies surveyed on St. John, with a single site (Mary Creek) having representatives of all three mangrove species (Table 1). However, *R. mangle* did tend to dominate the immediate shorelines of fringe mangroves, with *A. germinans* and *L. racemosa* typically present more landward within the 11.3-m survey bands perpendicular to the water's edge. Stems were less plentiful on fringe plots of Princess Bay and Water Creek, at ~ 3200 stems/ha, than for the one fringe site at Mary Creek, at $> 13,000$ stems/ha. Statistically, live basal areas did not differ among the isolated basin, salt pond, or fringe mangroves surveyed (Table 2); however, isolated basin mangroves had a greater area of dead mangrove stems (3.7 m²/ha) prior to hurricane impact than did fringe mangroves (0.3 m²/ha), indicative of condition at the time of the storms. The lack of a small diameter class of trees (i.e., 1–5 cm *dbh*) within the isolated basin mangroves (Fig. 3a) versus salt pond (Fig. 3b) and fringe (Fig. 3c) mangroves prior to hurricane impact is noteworthy.

Component Structural and Carbon Stock Changes to Mangroves from the Hurricanes

Total ecosystem organic C stocks (aboveground live/dead; belowground live/dead) for isolated basin mangroves was 82.8 Mg C/ha, for salt pond mangroves was 46.8 Mg C/ha, and for fringe mangroves was 104.6 Mg C/ha before hurricane impact on St. John (Tables 2 and 3). However, the hurricanes resulted in a 100%, 63%, and 86% decrease in live basal area among isolated basin, salt pond, and fringe mangroves on St. John, respectively, while dead standing tree basal area increased 6.9, 12.3, and 50.3 times among those same typologies after the storm (Table 2). In short, the impact of the hurricanes to the structural integrity of St. John's mangroves could be considered catastrophic. Indeed, no live basal area remained at either of the two isolated basin mangrove sites at Annaberg.

Prior to the hurricanes, live trees accounted for 43.5 Mg C/ha in the isolated basin mangroves of Annaberg (Table 2), with this C re-distributed post-storm as dead standing (21.6 Mg C/ha), downed coarse woody debris (19.6 Mg C/ha), and downed fine woody debris (i.e., some fraction of 19.2 Mg C/ha). Approximately 6.9 Mg C/ha was accounted for by dead trees at Annaberg before the storms as well, with most of this dead tree C being represented by 5.1–10 cm diameter class trees versus the 1.0–5.0 cm diameter class trees of the salt pond and fringe mangroves (Fig. 3). Live trees in salt ponds and fringe mangroves supported 19.3 Mg C/ha and

Fig. 2 Aerial images of mangrove forest appearance before (2012) versus after (2017) Hurricanes Irma and Maria by typology for (a) isolated basin (at Annaberg), (b) salt pond (at Francis Pond), and (c) fringe (at Mary Creek) mangroves, St. John, U.S. Virgin Islands. 2012 Imagery was acquired from the U.S. Geological Survey, <https://earthexplorer.usgs.gov> (accessed 12 June 2019). 2017 imagery was acquired from the Office for Coastal Management, 2017 NOAA NGS DSS Natural Color 8 Bit Imagery, NOAA National Geodetic Survey, <https://inport.nmfs.noaa.gov/inport/item/52284> (accessed 22 July 2019)

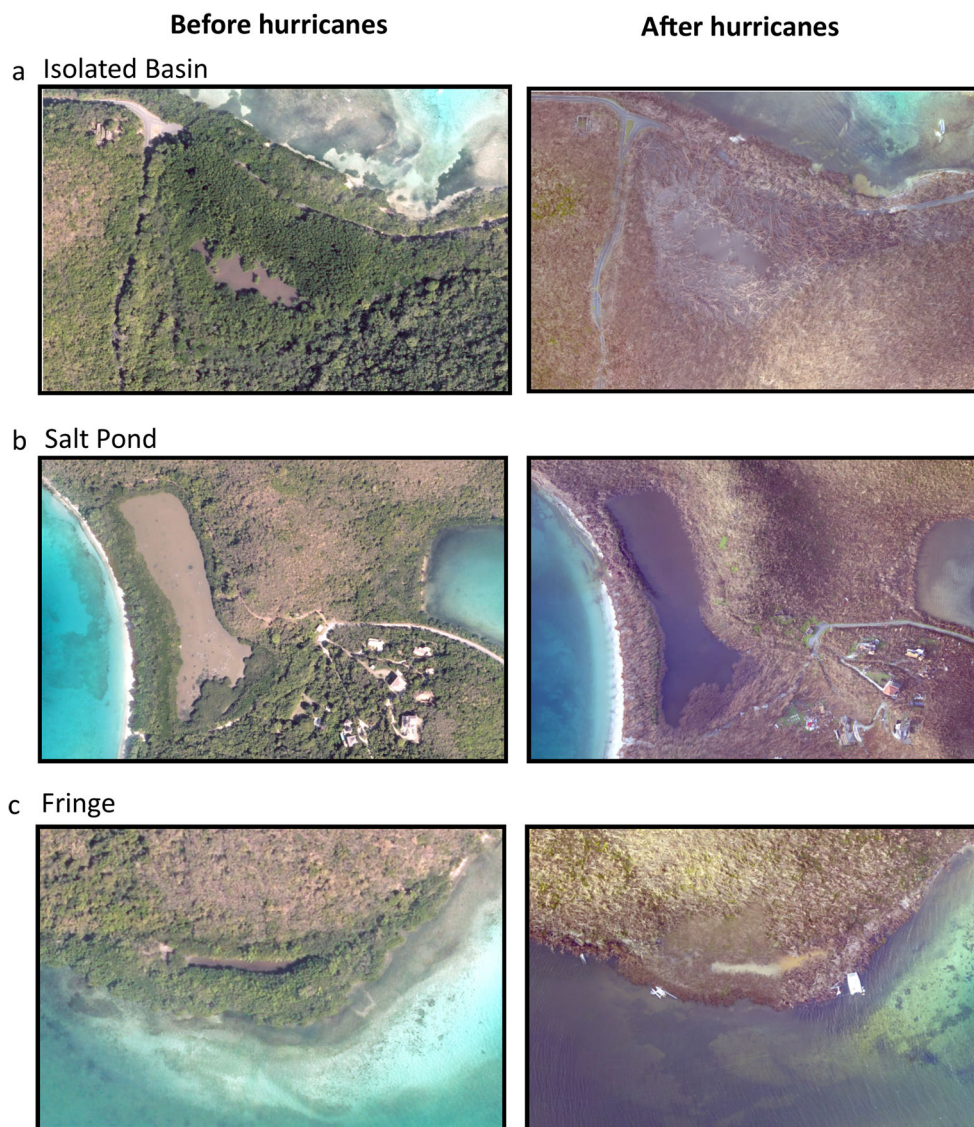


Table 1 Height, live basal area, and live stem density (± 1 SE) of mangrove forest plots ($N = 2$), and the relative distribution of species (based on live and dead basal area), on St. John, U.S. Virgin Islands, as re-constructed before Hurricanes Irma and Maria affected the island in 2017

Site	Typology	Height (m)	Basal area (m ² /ha)	Density (stems/ha)	Relative distribution of species		
					<i>R. mangle</i> (%)	<i>A. germinans</i> (%)	<i>L. racemosa</i> (%)
Annaberg East	Isolated basin	10.9 \pm 0.5	23.9 \pm 3.3	1600 \pm 0	85.8	0.0	14.2
Annaberg West	Isolated basin	10.8 \pm 1.1	19.5 \pm 2.5	2850 \pm 1150	46.7	45.7	0.0
Francis Pond	Salt pond	5.4 \pm 0.4	13.9 \pm 1.3	6750 \pm 1350	0.0	0.0	100.0
Lameshur	Salt pond	5.0 \pm 0.5	7.8 \pm 1.3	8100 \pm 300	0.0	100.0	0.0
Princess Bay	Fringe	6.1 \pm 0.6	16.5 \pm 8.0	3200 \pm 700	98.7	0.0	1.3
Water Creek	Fringe	4.4 \pm 0.3	14.0 \pm 4.5	3150 \pm 550	52.2	0.0	47.8
Mary Creek	Fringe	4.1 \pm 0.4	21.5 \pm 5.1	13,494 \pm 407	68.5	28.9	2.6

Table 2 Stand characteristics by live and dead fraction for basal area, carbon (C) content of trees, C content of prop roots, and C content of coarse woody debris (± 1 S.E.) for pre- and post-Hurricanes Irma and Maria affected mangrove stands on St. John, U.S. Virgin Islands

Component	Isolated Basin		Salt Pond		Fringe		$P > F^1$
Stand characteristics (pre-hurricanes)							
Live basal area (m ² /ha)	21.7 \pm 2.1	a	10.8 \pm 1.9	a	17.3 \pm 3.1	a	ns
Dead basal area (m ² /ha)	3.7 \pm 1.7	a	0.6 \pm 0.2	ab	0.3 \pm 0.2	b	*
Carbon, live trees (Mg C/ha)	43.5 \pm 4.8	a	19.3 \pm 2.7	a	37.5 \pm 7.5	a	ns
Carbon, dead trees (Mg C/ha)	6.9 \pm 4.2	a	0.9 \pm 0.3	ab	0.4 \pm 0.2	b	*
Carbon, live prop roots (Mg C/ha)	0.10 \pm 0.04	ab	0.00 \pm 0.00	b	0.24 \pm 0.11	a	*
Carbon, dead prop roots (Mg C/ha)	0.01 \pm 0.01	a	0.00 \pm 0.00	b	0.00 \pm 0.00	b	*
Carbon, coarse woody debris (Mg C/ha) ²	1.4 \pm 0.7	a	0.2 \pm 0.1	a	0.2 \pm 0.2	a	ns
Carbon, fine woody debris (Mg C/ha) ³	no est.		no est.		no est.		
Stand characteristics (post-hurricanes)							
Live basal area (m ² /ha)	0.0 \pm 0.0	b	4.0 \pm 0.7	a	2.5 \pm 1.1	ab	*
Dead basal area (m ² /ha)	25.4 \pm 3.8	a	7.4 \pm 2.5	b	15.1 \pm 3.6	ab	*
Carbon, live trees (Mg C/ha)	0.0 \pm 0.0	a	7.4 \pm 1.5	b	5.1 \pm 1.9	ab	*
Carbon, dead trees (Mg C/ha)	21.6 \pm 3.2	a	9.0 \pm 2.4	a	18.7 \pm 4.7	a	ns
Carbon, live prop roots (Mg C/ha)	0.00 \pm 0.00	b	0.00 \pm 0.00	b	0.02 \pm 0.00	a	***
Carbon, dead prop roots (Mg C/ha)	0.11 \pm 0.05	a	0.00 \pm 0.00	a	0.22 \pm 0.10	a	ns
Carbon, coarse woody debris (Mg C/ha) ²	19.6 \pm 2.4	a	3.1 \pm 0.6	b	2.1 \pm 1.2	b	***
Carbon, fine woody debris (Mg C/ha)	19.2 \pm 2.2	a	10.2 \pm 1.4	ab	3.7 \pm 1.2	b	***
Result of hurricanes							
Δ Carbon, live trees (Mg C/ha)	-43.5		-11.9		-32.4		
Δ Carbon, dead trees (Mg C/ha)	+14.7		+8.1		+18.3		
Δ Carbon, coarse woody debris (Mg C/ha)	+18.2		+2.9		+1.9		

¹ ns = not significant at the 0.05 level; * = significant at the 0.01–0.05 level; ** = significant at the 0.01–0.001 level; *** = significant at the <0.001 level. Values followed by the same letter among habitat condition are not significantly different at $p \leq 0.05$

² Coarse woody debris determined to be rotten was assumed to be present before the hurricanes, while coarse woody debris determined to be intermediate and sound was assumed to have fallen during the hurricanes

³ “No estimate” available for fine woody debris C biomass pre-storm

37.5 Mg C/ha prior to the hurricanes, and only 7.4 and 5.1 Mg C/ha, respectively, after the storms. Small diameter class trees (< 10 cm *dbh*) survived in salt pond and fringe mangroves (Fig. 3b,c), while no small diameter class trees were present in isolated basin mangroves at Annaberg after the hurricanes (Fig. 3a).

Depending on site, C biomass of dead trees increased 8.1–18.3 Mg C/ha, and C biomass of coarse woody debris increased 1.9–18.2 Mg C/ha after the hurricanes (Table 2). We do not know much about the dynamics of fine woody debris C before versus after the storms on St. John. A simple mass balance of all C summed before the storms versus all C summed after the storms indicates that for isolated basin and salt pond mangroves, post-hurricane surveys found 8.6–9.3 Mg C/ha more carbon, while for fringe mangroves, surveys found 8.5 Mg C/ha less carbon (Table 2). Pre- versus post-hurricane disparities are related either to export/import from surge, decomposition, or to the uncertainty of fine woody debris dynamics before the hurricanes; fine woody

debris was a significant component of total downed wood and ranged from 3.7 to 19.2 Mg C/ha among plots after the storms. Fine woody debris was incredibly prominent among larger diameter classes (2.5–7.5 cm) in isolated basin and fringe forests (Fig. 4a). Much of the large fine wood (> 1.0 cm diameter) likely represents storm debris from direct or delayed branch fall. Likewise, most of the coarse woody debris was predictably in the sound decay class, but this was especially evident on isolated basin sites (Fig. 4b).

Distribution of Nitrogen and Carbon in Mangrove Forest Soils

The total amount of N stored in the soils of isolated basin, salt pond, and fringe mangroves on St. John equated to 1.79 \pm 0.2 Mg N/ha, 1.71 Mg N/ha, and 2.50 Mg N/ha, respectively. These scaled values were fairly low, reflecting the maximum allowable sampling depth of 36–48 cm before we struck refusal. N density decreased with depth into the soil, and this was

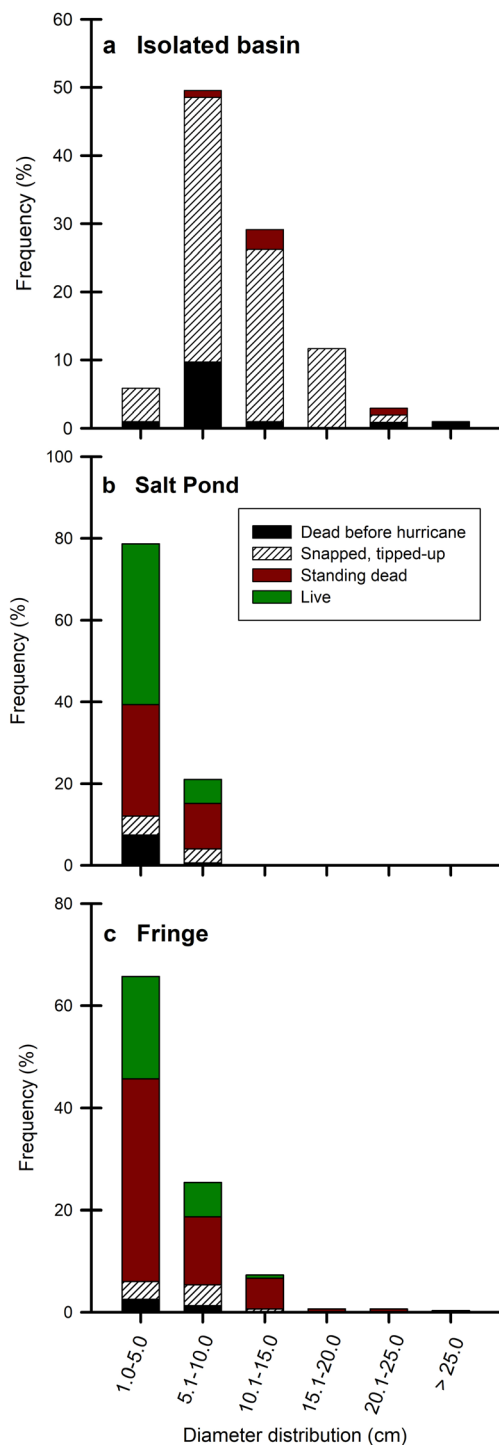


Fig. 3 Frequency distribution of stem diameters by *dbh* class (cm at 1.4 m above ground) of mangrove trees classified as dead before the hurricanes, snapped or tipped-up by the hurricanes, standing dead, or live as determined by post-Hurricanes Irma and Maria surveys in (a) isolated basin ($N = 2$), (b) salt pond ($N = 2$), and (c) fringe mangrove ($N = 3$) typologies on St. John, U.S. Virgin Islands

especially noteworthy for isolated basin mangroves (Fig. 5a). For isolated basin mangroves, N concentrations at soil depths below 9 cm were less than half of the concentrations of surface soils (0–

9 cm) because of greater association with inorganic C below 9 cm. N was more consistently distributed with soil depth in salt pond (Fig. 5b) and fringe (Fig. 5c) mangroves versus isolated basin mangroves (Fig. 5a). Significant statistical interactions for typology by depth reiterate differences among N density soil profiles, which affect area-scaled estimation (Table 3).

The balance of C in soils is divided into two components: organic C and inorganic C. Organic C in the soils of isolated basin mangroves was 30.8 ± 5.7 Mg C/ha, while inorganic C was 36.7 ± 19.7 Mg C/ha (Table 3). In contrast, inorganic C comprised only a small component of salt pond and fringe mangrove soils. Salt pond soils stored much less carbon overall, with 26.4 ± 3.1 Mg C/ha as organic C and only 6% of total C as inorganic (or 1.6 ± 1.1 Mg C/ha). Fringe mangrove soils stored 66.2 ± 14.4 Mg C/ha of organic C, of which a very small amount of total C was inorganic C (1%, or 0.7 ± 0.2 Mg C/ha) (Table 3). Typology by depth interactions were significant for organic C and inorganic C, indicating that both organic and inorganic C fractions displayed different patterns with depth into the soil among typology. For example, the inorganic C densities of isolated basins were significantly higher than for salt pond and fringe mangroves for most soil depth comparisons to 33 cm ($p = 0.05$), but organic C was higher for only a single soil depth (30–33 cm) for fringe mangroves versus the other two typologies. In general, the fraction of inorganic C to organic C increased with soil depth for isolated basins (Fig. 5a) but did not otherwise show consistent trends among salt pond or fringe mangroves except for both having consistently higher organic C at all depths (Fig. 5b,c).

Total Ecosystem Carbon Storage before and after the Hurricanes

The sum total of all aboveground C (Table 2), belowground organic C (Table 3), and belowground inorganic C (Table 3) being stored on isolated basin, salt pond, and fringe mangroves on St. John was 119.4, 48.4, and 105.2 Mg C/ha, respectively, before the hurricanes, or 82.8, 46.8, and 104.6 Mg C/ha of total organic carbon. The distribution of this C was reallocated during the storm from live aboveground C biomass to dead aboveground C biomass, with soils significantly buffering overall C losses. This also assumes that the hurricanes had no influence on the quantity and distribution of soil C.

Regeneration and Recovery Metrics

Active regeneration 10–14 months after Hurricanes Irma and Maria was fairly low across all typologies, and what was regenerating was determined to be mostly advance regeneration. For isolated basin mangroves, regeneration averaged 0.94 seedling/m² for seedlings >50 cm tall and 0.38 seedlings/m² for seedlings <50 cm tall (1.3 seedlings/m² total, ± 0.7 SE; Fig. 6). However, these data were nearly all associated

Table 3 Average bulk density across soil depth, and area-scaled values of organic carbon, inorganic carbon, and total nitrogen (± 1 S.E.) by typology (isolated basin, salt pond, fringe) along with associated statistical results for mangrove stands affected by Hurricanes Irma and Maria, St. John, U.S. Virgin Islands

Typology	g/cm ³ Bulk density	Mg/ha Organic C	Inorganic C	Total N
Isolated Basin	0.42 \pm 0.13	30.8 \pm 5.7	36.7 \pm 19.7	1.79 \pm 0.20
Salt Pond	0.52 \pm 0.05	26.4 \pm 3.1	1.6 \pm 1.1	1.71 \pm 0.22
Fringe	0.27 \pm 0.07	66.2 \pm 14.4	0.7 \pm 0.2	2.50 \pm 0.81
Source of Variation / DF _{num} , DF _{den} ¹				
Typology / 2, 11	ns	**	**	ns
Depth / 15, 118	***	***	ns	***
Typology x depth / 25, 118	**	***	***	***

¹ ns = not significant at the 0.05 level; * = significant at the 0.01–0.05 level; ** = significant at the 0.01–0.001 level; *** = significant at the <0.001 level

with the basin site on the east side of Annaberg where tides were still somewhat connected to the estuary by the presence of larger culverts that cross the road. Only a single *R. mangle* seedling (62 cm tall) was encountered on the isolated basin

site on the west side of Annaberg, and the only larger saplings or trees appearing healthy on this site were a few scattered manchineel trees (*Hippomane mancinella* L.), which are not mangroves. Presence of seedlings in both height classes within salt ponds was limited at 10–14 months (0.13 seedlings/m², ± 0.1 SE). No seedlings were discovered on fringe sites at Water Creek or Mary Creek, so all of the data from fringe mangroves in Fig. 6 for 10–14 months represent only one site (Princess Bay). There, seedling density was 0.71 seedlings/m² (± 0.5 SE), and additional larger seedlings were present but sparse in places not surveyed. Average maximum seedling heights among the advance regeneration pool for isolated basin, salt pond, and fringe mangroves were 73, 69, and 96 cm, respectively (Fig. 6).

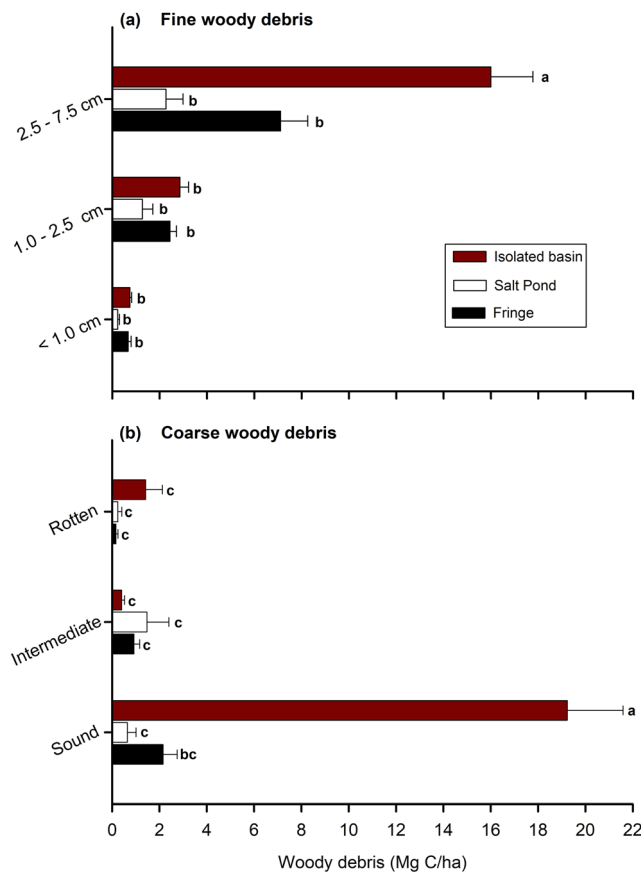


Fig. 4 (a) Distribution of fine woody debris (Mg C/ha) by size class (< 1.0 cm diameter, 1.0–2.5 cm diameter, 2.5–7.5 cm diameter) and (b) coarse woody debris (Mg C/ha) by decay class (sound, intermediate, rotten) in isolated basin, salt pond, and fringe mangrove typologies 10–14 months after the passage of Hurricanes Irma and Maria, St. John, U.S. Virgin Islands. Fine woody debris values, and separately, coarse woody debris values followed by the same letters do not differ significantly at $P \leq 0.05$

At 26 months, fewer seedlings were encountered even after doubling the number of survey sub-plots. For isolated basin, salt pond, and fringe mangroves, a total of 0.84 ± 0.3 SE, 0.09 ± 0.0 SE, and 0.35 ± 0.1 SE seedlings/m² were found (Fig. 6). Of the seedlings that survived to 26 months on the isolated basin sites of Annaberg, several advanced to the sapling stage, but still averaged only 109 cm tall across the sites. Maximum sapling height on the west side of Annaberg was approaching 2 m, and a few new manchineel tree seedlings were present (i.e., 3/m² and as tall as 76 cm on one sub-plot). Average maximum seedling height decreased to 22 cm on salt pond sites from mortality of larger seedlings between survey intervals. Maximum seedling height remained unchanged in fringe mangroves between surveys (Fig. 6). A larger number of seedlings of *L. racemosa* was found in the <50 cm height class in salt pond and fringe mangroves at 26 months versus 10–14 months, reflecting some regeneration of that species in the months since the first survey.

Cover of the residual canopy and standing structural biomass of mangroves was very low after the hurricanes. Only 11.1% of the forest floor was shielded by the canopy or standing dead wood above 1-m on isolated basin sites. This value was 26.4% and 31.4% for salt pond and fringe mangrove forests, respectively. As a reflection of the serious nature of

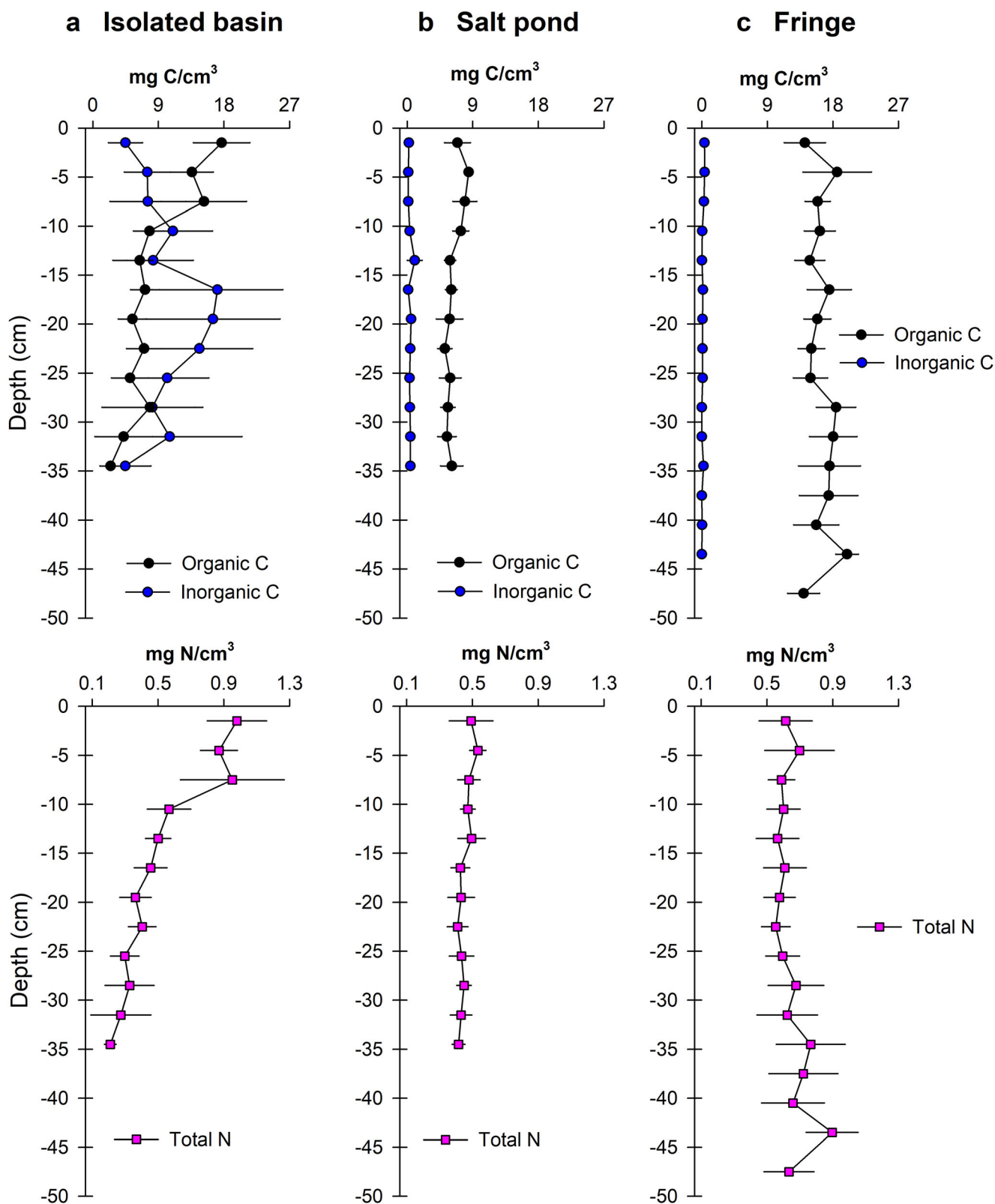
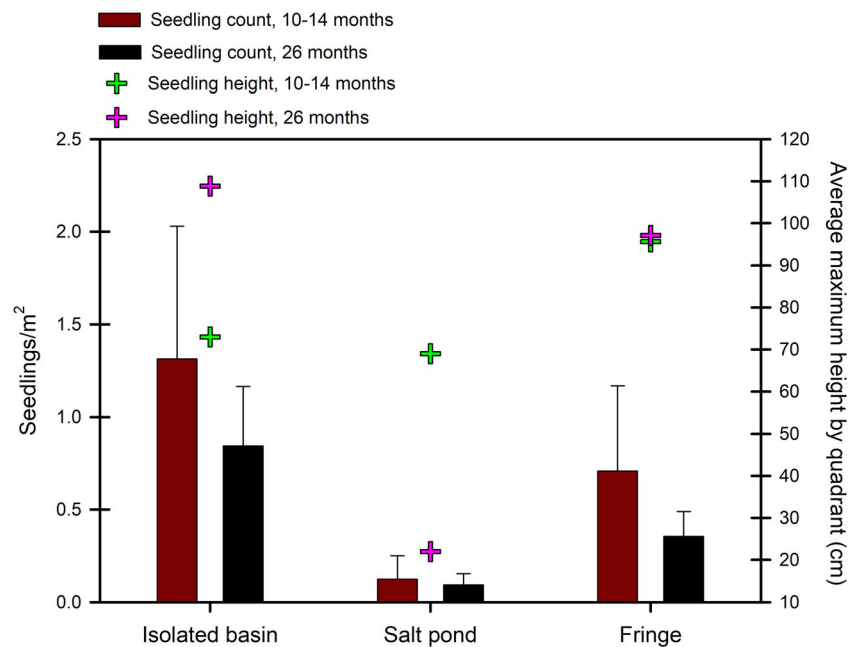


Fig. 5 Distribution of bulk-density-adjusted organic C (mg C/cm³), inorganic C (mg C/cm³), and total N (mg N/cm³) in soils at 3-cm depth increments for (a) isolated basin ($N = 4$ cores), (b) salt pond ($N = 4$ cores),

and (c) fringe ($N = 6$ cores) mangrove typologies 10–14 months after the passage of Hurricanes Irma and Maria, St. John, U.S. Virgin Islands

Fig. 6 Seedling abundance (seedlings/m²) and maximum seedling height (cm) for isolated basin, salt pond, and fringe mangrove typologies 10–14 months and 26 months after the passage of Hurricanes Irma and Maria, St. John, U.S. Virgin Islands



the damage incurred by St. John's mangroves, only 0.2% to 15.9% canopy cover was attributed to green vegetation overhead across typologies 10–14 months after the hurricanes.

Discussion

Forest Structural Attributes

Structural attributes of St. John's mangroves before the hurricanes mostly echoed data accounts from mangroves throughout the Caribbean region. For example, the basal area of mangroves with similar species ranged from 20.4 to 40.9 m²/ha in the Dominican Republic (Sherman et al. 2001), 7.8 to 47.7 m²/ha in southwest Florida (Baldwin et al. 1995; Doyle et al. 1995), and 14.8 m²/ha in Nicaragua (Roth 1992) before major hurricanes affected those mangroves. On St. John, pre-hurricane basal areas generally ranged from 13.9 to 23.9 m²/ha, with one salt pond site (Lameshur) having a basal area of only 7.8 m²/ha (Table 1). Pre-hurricane tree densities were also high on St. John, ranging from 1600 stems/ha on an isolated basin site to 31,494 stems/ha on a fringe site (Mary Creek). Sherman et al. (2001) discovered that tree densities prior to Hurricane Georges affecting mangrove forests in the Dominican Republic were 377, 1098, and 1171 stems/ha for *A. germinans*, *R. mangle*, and *L. racemosa*-dominated forests, respectively; with densities later reduced to 99, 568, and 852 stems/ha by the storm.

Caribbean mangrove forests are stress-adapted ecosystems that incur frequent tropical storm impact (Lugo et al. 1981; Smith et al. 1994). Site-specific effects can vary widely and post-storm recovery of mangrove forests is common, but

nuanced. Mangrove forests across the Everglades region in Florida, for example, experienced an average basal area reduction of 31% from Hurricane Andrew (in 1992), and basal areas in sections of the storm's eyepath were reduced by as much as 94% (Doyle et al. 1995). The average basal area reduction for St. John's mangroves was 82.8%, but this reduction was as much as 100% (isolated basin) and as low as 62.9% (salt pond). Many of the Everglades mangrove forests have been actively recovering in structural extent since Hurricane Andrew, though along different trajectories dependent upon the species distribution and size-classes that remained once the storm passed (Ward et al. 2006), as we suspect will be the case for St. John mangroves in time. Hurricane Georges (in 1998), which affected the mangroves of the Dominican Republic, also caused basal area reductions of 9–100%, averaging 42% (Sherman et al. 2001), with active recovery underway since. We suspect that fringe mangroves on St. John will recover quicker than isolated basins and salt ponds, which are incurring additional hydrologic stresses.

Recovery can be dependent upon natural hydrological connectivity; humans often modify the landscape in such ways as to prevent recovery from hurricanes (Lewis et al. 2016). The isolated basin mangrove forest at Annaberg had a pre-storm diameter distribution that indicates changes to the regeneration capabilities of those sites before the hurricanes. For one, there was a paucity of trees in the 1.0–5.0 cm diameter class and a high relative pre-storm mortality among trees in the 5.1–10.0-cm diameter class (Fig. 3a). Newly persistent flooding over the last decade or longer may be partially responsible for the added mortality. As a result, these sites do not have the typical diameter size distribution of natural mangrove forests, and can be contrasted not only to published species

distribution curves (i.e., as detailed for uneven-aged forest stands by Avery and Burkhart (1994) and for mangroves by Ward et al. (2006)), but also to the diameter distributions of salt pond and fringe mangroves on St. John (Fig. 3b,c), which have the expected relative numbers of the smallest trees often seen in mangrove forests. It is unknown exactly how the hydrology of the Annaberg sites changed over time, as it appears that the road isolating the basin from the ocean was built on a natural rock/coral berm and has been in place for a century or more, but perhaps previous culvert designs worked more efficiently than the current ones do now. Connections may have become gradually blocked over time eventually restricting tidal action. Taller trees (>10 m) in these isolated basin mangroves probably made them more vulnerable to wind-throw versus the shorter trees in salt pond and fringe mangroves (≤ 6.1 m) as is evidenced by a greater proportion of standing dead trees in the smaller diameter classes on salt pond and fringe sites versus downed trees (Fig. 3b,c). The susceptibility of taller mangrove trees to hurricane wind throw is well-documented (Smith et al. 1994; McCoy et al. 1996).

Soil Properties, Carbon, and Nitrogen

Another concern for mangroves on St. John is peat collapse (sensu, Chambers et al. 2019) from canopy stress leading to reduced root turnover (Cahoon et al. 2003; Krauss et al. 2014). We speculate, for example, that the reduced basal areas on the Lameshur salt pond site could easily be a residual influence of Hurricane Hugo in 1989, which led to forest mortality and peat collapse around dead and now missing trees that are still evident today. Lang'at et al. (2014) found that harvesting individual mangrove trees led to rapid soil surface elevation losses from peat collapse in Kenyan mangroves; hurricane-induced individual tree mortality would be similar enough but also more widespread. Thus, greater flooding from peat collapse and restricted regeneration has likely impeded recovery at Lameshur since 1989, and we might expect similar influences in other mangrove wetlands on St. John following Hurricanes Irma and Maria. However, mortality of above-ground mangrove structures would not necessarily reduce the amount of C stored in the soils initially. With forest mortality, peats instead can compact to increase C density within anaerobic soils (Krauss et al. 2018), until roots of the regenerating forest re-invade these older soils.

Mangroves of all types are important to the global carbon cycle, and C has become the new currency of mangrove forest change (e.g., Lovelock and Duarte 2019). Mangroves sequester, convey, and store C with impressive efficiency, rivaling any natural ecosystem on the planet (Donato et al. 2011). Mangroves are thus sentinel “blue carbon” ecosystems (Windham-Myers et al. 2019), stimulating research on C stock quantification and processes from a broad range of sites globally

(e.g., Bouillon et al. 2008; Breithaupt et al. 2012; Murdiyarsa et al. 2015). Total ecosystem C stocks can be high in the western Caribbean; e.g., 570 to >1000 Mg C/ha among mangroves in Honduras (Bhomia et al. 2016) and 582 to 1325 Mg C/ha for mangroves in Mexico that were similarly structured to those on St. John at 2–14 m tall (Adame et al. 2013). However, C stocks may be generally more moderate from the Caribbean region versus the globe; e.g., dwarf mangroves in Mexico registered 297 to 433 Mg C/ha (Adame et al. 2013). Projected pre-storm total ecosystem C biomass across the different mangrove typologies on St. John was only 119.4 Mg C/ha for isolated basin mangroves, 48.4 Mg C/ha for salt pond mangroves, and 105.2 Mg C/ha for fringe mangroves when live tree biomass is combined with all C from soils (organic and inorganic). This is low, but soil sample depths to refusal were shallow on St. John, where most C is stored in mangroves, and we had limited confidence that normalizing these values over 1-m depth profiles for stronger comparisons to the global literature was appropriate. Previous research in the Caribbean region has shown that 81–94% of total ecosystem C biomass is associated with soils when profiles are deep (> 1 m: Bhomia et al. 2016). On St. John, C biomass of soils was 57–64% of total ecosystem C biomass by typology before the hurricanes when both organic and inorganic C is included, but was as low as 37% among typologies (for isolated basins) when only considering organic C. Because of the protection of soil C stores from direct hurricane impact, the total amount of C lost from the mangroves on St. John would mostly be associated with aboveground biomass, with 67.5, 28.0, and 66.9 Mg C/ha still remaining in the soils after Hurricanes Irma and Maria. However, this fraction of loss will increase as recovery of mangroves on St. John is delayed.

Even compacted peats are eventually decomposable as root turnover no longer compensates for soil organic matter decomposition, leading to increased soil surface elevation collapse and carbon loss from soil through atmospheric and lateral exchange (Lovelock et al. 2011; Maher et al. 2018). Extremely high concentrations of inorganic C in the soils of the isolated basin sites at Annaberg (Fig. 5a) may speak to greater permanence of soil C at that location and may indicate that this basin has served as a sediment settling pond in the past, either from upland sources or from storm overwash. Land use activities, such as aquaculture (Sui et al. 2019), can also influence the balance of inorganic versus organic C in wetland soils. It is not likely that the inorganic C in the Annaberg soils is associated with the operations of a nearby sugar mill (18th to early nineteenth Century) but the inorganic C could be from more recent road work adjacent to the mangrove forest, or to an alternate source of weathered

upland parent material delivered through rainfall runoff or coral material deposited from storm overwash. Furthermore, some of the inorganic C in the mangrove soils on isolated basin and salt pond sites is likely from the previous history of these sites as portions of bays that have been isolated over time (Island Resources Foundation 1977).

It was also curious that the amount of N stored in the soil of all mangrove forests on St. John was relatively low. This was partly due to the shallow cores taken during sampling, but also because of low concentrations of N at all depths. Isolated basin, salt pond, and fringe mangroves had N concentrations of 0.10, 0.19, and 0.46%, respectively, equating to N densities of 0.45, 0.40, and 0.56 mg N/cm³ across all soil depths. For comparison, N concentrations from multiple mangrove forest soils in south Florida were 1.1–2.3% N (Krauss et al. 2006, 2018). However, N concentrations have been described as being comparably low to St. John in at least one mangrove forest in China (at 0.08–0.12% N; Alongi et al. 2005). Such low values of N in the mangrove soils on St. John may be related to the limited recent upland disturbance in some locations on the island, minimized by forest protections afforded by the status of much of the uplands as a U.S. National Park. These protections have prevented any large land clearings inland of the mangroves we sampled, limiting N transport down-slope from intermittent sheet flow or deposition into ephemeral streams. Even with the two hurricanes, much of the upland forest was actively recovering from structural damage incurred during the storms. Tropical forests left intact have a strong ability to re-cycle N within the forest, thus keeping N on the upland slopes (Vitousek and Sanford 1986). Similarly, Cormier et al. (2015) described low N densities of 0.48–0.71 mg N/cm³ in the mangroves on one Micronesian island (Kosrae) and vastly higher values of 1.59–1.63 mg N/cm³ from another (Pohnpei). The upland reaches of the Sapwalap River basin on Pohnpei is decidedly more disturbed from land clearing for sakau (*Piper methysticum* G. Forst.) production than the Yela River basin on Kosrae, demonstrating the potential connection between upland forest management activities and the mangroves down-slope, which would receive those sediments and nutrients.

Regeneration

Regeneration of the isolated basin typology was limited on Eastern Annaberg and almost non-existent on Western Annaberg at 10–14 months, equating to approximately 1.3 seedlings/m² across the basin typology, all from advance regeneration. This trend changed very little at 26 months, although some individual seedlings became taller. The density of mangrove seedlings averaged 1.8 to 5.3 seedlings/m² 7 months after Hurricane Andrew passed through south Florida mangroves, which was lower than for unaffected sites having 5.2 to 8.3

seedlings/m² (Baldwin et al. 1995). Thus, it is clear that mangrove seedling densities after a hurricane can be much higher than what we found on St. John; however, it should be noted that this density of seedlings on basin sites is still greatest among typologies surveyed on St. John, and many of those seedlings are growing (Fig. 6). Indeed, regeneration was low across all typologies, but it is unknown how this compares to natural regeneration present on these sites before the storms, whether acute light induction with overstory structural losses after the storms had a role in killing additional seedlings (Press et al. 1996), or other changes to the physico-chemical environments occurred as a result of the hurricanes (e.g., sediment smothering, anoxia; Paling et al. 2008).

Originally, we assumed that surveys at 10–14 months after Hurricanes Irma and Maria were perhaps too soon to understand the full regeneration potential among sites. Sherman et al. (2001) found that mangrove forest regeneration surveys conducted at 18 months after hurricane impact revealed greater densities of seedlings and saplings than surveys conducted at 7 months. For a Nicaraguan mangrove forest, 0.7 to 2.2 seedlings/m² were recorded 17 months after a hurricane (Roth 1992). Yet, our surveys at 26 months offered little optimism that natural recruitment is occurring with small delays only. Stem sprouts can be a source of regeneration (Baldwin et al. 2001), and some *L. racemosa* sprouts were noted in both isolated basin and salt pond typologies on St. John. *R. mangle* does not re-sprout, precluding this as a regeneration system for fringe mangroves dominated by that species (Gill and Tomlinson 1969). While mortality of saplings from hurricanes is often low (e.g., Smith et al. 1994) and can provide advance regeneration opportunities to facilitate post-storm recovery in some mangroves; that regeneration pool was also limited on St. John.

Developmental pressures, hydrological changes, lack of propagule sources, and other influences on recovery success are a concern on St. John. For the Francis Bay salt pond, prolific seed production of *L. racemosa* was already underway at 10–14 months but those seeds did not re-colonize this site by 26 months for some reason, probably related to persistent natural flooding in this mangrove type. In fact, this was puzzling so we conducted full plot (i.e., two, 5.65-m-radius plots per site) regeneration surveys of both salt pond sites at 26 months, and found 0 to 5 seedlings on the two individual plots at Francis Pond (or, up to 0.05 seedlings/m²) and 6–26 seedlings on the two individual plots at Lameshur (or, up to 0.26 seedlings/m²), similar to our sub-plot seedling counts (Fig. 6). Fringe mangroves will benefit from some on-site seed and propagule production in time, and by propagule drift from other sites when wind-damaged trees begin to produce propagules reliably again. The timeline for recovery is unknown, given that so many of the *R. mangle*-dominant communities on St. John and the nearby island of Tortola were also affected by Hurricanes Irma and Maria. Likewise, Hurricane Hugo affected the mangroves on St. John in 1989, and had a very

strong and adverse effect on mangroves near the Lameshur Bays on the south side of the island, including prominently restricting tidal flow (Thomas Kelley, pers. obs.). The Lameshur mangroves currently display the lowest genetic diversity among *R. mangle* on St. John, and fringing mangroves from several other sites that incurred effects from Hurricane Hugo also have low resulting genetic diversity and high inbreeding coefficients to this day (Bologna et al. 2019). This heightens concern for recovery. Do hurricanes affect the genetic structure of mangroves when they cause complete or near-complete destruction of existing forests? Would implementation of active restoration speed up recovery, and could that effort include the use of off-island propagule sources? Restricted genetic diversity may be a natural characteristic among all mangrove species on St. John (and potentially other Caribbean islands) resulting from restricted mangrove area development, connections among source populations and other islands, and recurrent damage from hurricanes.

Implications and Conclusions

Three concerns for St. John's mangrove resource emerged from this research. First, the isolated basin mangrove at Annaberg has undergone hydrologic change, leaving a potential untenable hydrologic condition to promote health and recovery across a large swath of Annaberg as it recovers from the hurricanes. Much of this site could in time fall into the category of “mangrove heart attack” (sensu Lewis et al. 2016) without hydrological rehabilitation, and endure peat collapse that could lead to expanded pond formation and subsequent C losses from chronic stress and future hurricanes. Second, while fringe mangrove forests of Hurricane Hole and Mary Creek are at elevations that would promote mangrove colonization, sources of *R. mangle* propagules to re-colonize those sites were not readily evident yet. However, *A. germinans* and *L. racemosa* trees in various damage states remained along the more landward reaches of these sites. Additional surveys and analyses would help determine whether *R. mangle* propagules are reaching these sites with adequate genetic diversity to promote healthy stand recovery. However, recovery of the unique mangrove prop root and coral assemblages that once prospered in Hurricane Hole has a less certain time line without adequate stand stocking of seedlings, the precarious subtidal positioning of *R. mangle* stems and roots that serve as coral substrates, and uncertainties surrounding coral recruitment (Rogers 2019). Third, regeneration systems that have been described for neotropical mangroves after hurricanes, e.g., Baldwin et al. (2001), apply where combinations of advance regeneration, stem sprouting and seed/propagule dispersal are possible. All three regeneration systems are currently limited on St. John.

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