

Recovery of a cultivation grazer: A mechanism for compensatory growth of *Thalassia testudinum* in a Caribbean seagrass meadow grazed by green turtles

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Funding information

Jeff and Monette Fitzsimmons Fund (through Archie Carr Center for Sea Turtle Research); Big Beards Adventure Tours; PADI Foundation; University of Florida, Department of Biology; Gumbo Limbo Nature Center; National Park Service (Buck Island Reef National Monument); Disney Conservation Fund (through Archie Carr Center for Sea Turtle Research); Mosaics in Science and Diversity; Lalita Shastry

Handling Editor: Brian Silliman

Abstract

1. Recovery of green turtles (*Chelonia mydas*), mega-herbivores that consume seagrasses, is resulting in dramatic ecosystem-wide changes as meadows are returned to a natural grazed state. The green turtle grazing strategy, with long-term cultivation of meadows and high foraging site fidelity, is distinct from other terrestrial and aquatic mega-herbivores and may affect seagrass compensatory growth responses. Identifying the mechanisms of compensatory growth responses to grazing is essential to understand the functioning of plant systems under natural grazing regimes.
2. In a naturally grazed Caribbean seagrass ecosystem, we identify a mechanism for compensatory growth responses to grazing by evaluating relationships between *Thalassia testudinum* morphology and growth, grazing intensity, and canopy light dynamics in grazed and ungrazed areas.
3. The morphological characteristics that explain variability in *T. testudinum* growth differed between grazed and ungrazed areas. In grazed areas, *T. testudinum* leaf linear growth, leaf area growth, and productivity:biomass (P:B) significantly increased as above-ground biomass decreased; P:B also increased with shoot density. Mass growth in grazed areas exhibited an increasing trend with shoot density and was maintained above a threshold of 2.5 g dry mass m⁻² above-ground biomass. In ungrazed areas, trends for mass growth and P:B with above-ground biomass and shoot density were opposite to those in grazed areas. In grazed areas, shoot density significantly increased with grazing intensity while above-ground biomass decreased and leaf area index (LAI) was not affected. Light availability at canopy height was greater in grazed areas than in ungrazed areas, and canopy light attenuation increased with shoot density in grazed areas.
4. *Synthesis.* Grazing removes above-ground biomass, which increases light availability and stimulates leaf growth and turnover (i.e. compensatory growth). Shoot density increases with grazing intensity, maintaining LAI and canopy light harvesting potential. This maximizes the potential for leaf photosynthetic activity and provides the plant with the capacity to sustain mass growth and support a compensatory growth response to grazing. This study presents novel insight for

assessing the underlying mechanisms of plant compensatory growth responses to cultivation grazing and proposes potential thresholds that may be used to evaluate the sustainability of in situ grazing pressure by a recovering mega-herbivore.

KEYWORDS

canopy light attenuation, compensatory growth, grazing, green turtle, herbivory, leaf self-thinning, plant-herbivore interactions, seagrass

1 | INTRODUCTION

Recovery of mega-herbivore populations after decades or centuries of low abundance is occurring in terrestrial and aquatic ecosystems due to long-term conservation efforts (e.g. Bakker et al., 2016; Mazaris et al., 2017; Pansu et al., 2019; Stalmans et al., 2019). For example, this phenomenon is occurring among large-bodied mammals in the post-war savannas of Mozambique (Gaynor et al., 2020), and among green turtle (*Chelonia mydas*) populations in seagrass meadows worldwide (Chaloupka et al., 2008; Mazaris et al., 2017; Weber et al., 2014). Such rebounds of mega-herbivore populations are eliciting dramatic changes to the composition (Kelkar et al., 2013; Nickell et al., 2018), productivity (Christianen et al., 2014; Gulick et al., 2020; Johnson et al., 2020; Pansu et al., 2019) and functioning (Bakker et al., 2016; James et al., 2020; Johnson et al., 2019; Scott et al., 2018; Subalusky et al., 2015) of plant communities, revealing a rare glimpse into how these ecosystems may have functioned prior to the overexploitation of mega-herbivores. However, the impacts and sustainability of increased grazing pressure by mega-herbivores in today's ecosystems that have been severely degraded by anthropogenic activities remain largely unknown.

Recovery of the green turtle (Chaloupka et al., 2008; Mazaris et al., 2017; Weber et al., 2014), a mega-herbivore that grazes on seagrasses (Bjorndal, 1980), offers a unique opportunity to evaluate plant-herbivore interactions after centuries of low mega-herbivore abundance and functional extinction (Aragones et al., 2012; Domning, 2001; Jackson et al., 2001). Although current populations are a mere fraction of historic levels, green turtles are the primary consumers of seagrass biomass worldwide (Bjorndal & Jackson, 2003;

Jackson et al., 2001; Thayer et al., 1984). In the Caribbean, green turtles exhibit a cultivation grazing strategy, in which they select and repeatedly crop distinct areas of seagrass (Figure 1) (Bjorndal, 1980; Ogden et al., 1983; Williams, 1988). Grazed areas can be maintained for at least 2 years (Gulick et al., 2020; Hernández & van Tussenbroek, 2014; Ogden et al., 1983). Green turtles exhibit high site fidelity to foraging areas (Bjorndal et al., 2005), sometimes forming resident aggregations that graze in the same area year-around (Hart et al., 2017). Cultivation grazing, albeit for shorter durations compared to green turtles, is relatively common among grazers in marine ecosystems (e.g. reef fishes (Ceccarelli et al., 2005), urchins (Valentine et al., 1997), dugongs (Preen, 1995)). This grazing strategy is not well documented among terrestrial herbivores (see Gibson & Hamilton, 1983). Long-term cultivation grazing by green turtles, combined with their high foraging site fidelity and low metabolic requirements, is distinct from other terrestrial and aquatic mega-herbivores and may affect seagrass compensatory growth responses as green turtle populations recover. In light of green turtle recovery and the global decline of seagrasses due to anthropogenic threats (Grech et al., 2012; Orth et al., 2006; Waycott et al., 2009), evaluating how seagrass morphology and growth respond to increases in grazing pressure is essential to assessing the sustainability of grazing and understanding the ecology and habitat characteristics of grazed ecosystems.

Plants that have co-evolved with large vertebrate herbivores have developed a myriad of adaptations that allow for tolerance of defoliation (McIntire & Hik, 2002; McNaughton, 1979). Compensatory growth, or the stimulated production of photosynthetic tissue following a grazing event, is an important adaptation

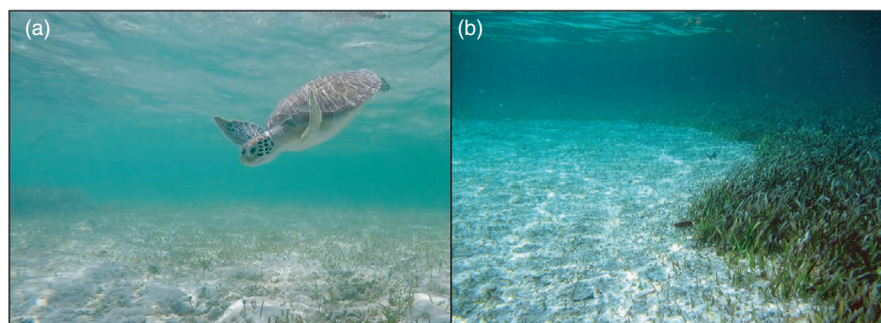


FIGURE 1 (a) A juvenile green turtle *Chelonia mydas* swims above a naturally grazed area of *Thalassia testudinum* in a Caribbean seagrass ecosystem; (b) A border of a grazed (left) and ungrazed (right) area—note the reduced above-ground biomass in the grazed area and the light reflection at the water surface. Photos: A. Gulick (left), R. Johnson (right)

that allows terrestrial and aquatic plants to sustain grazing pressure (LaMontagne et al., 2003; McIntire & Hik, 2002; McNaughton, 1983; Oesterheld & McNaughton, 1991; Ramula et al., 2019; Van der Graaf et al., 2005). Internal mechanisms that alter plant metabolism and external mechanisms that modify the plant's environment in favour of growth interact to support compensatory growth responses (de Mazancourt et al., 1998; Jaremo et al., 1996; McNaughton, 1979; Van der Graaf et al., 2005). The reduced leaf self-shading and increased light availability that stimulates photosynthetic activity in leaf tissue following a grazing event is an underlying mechanism of this compensatory response (Häsler et al., 2008; Jaremo et al., 1996; McNaughton, 1992). Compensatory responses to grazing can be sustained through changes to plant morphology, including the stimulated production of secondary shoots to maximize the area of photosynthetic tissue as grazing intensity increases (e.g. McIntire & Hik, 2002; McNaughton, 1979, 1992). This mechanism for compensatory growth to grazing in terrestrial grasslands has been quantified by evaluating relationships between plant morphology (e.g. leaf biomass, shoot density, leaf area index) and growth/turnover under natural grazing regimes (Jaremo et al., 1996; McIntire & Hik, 2002), an approach that would also be applicable to marine vascular plant-based systems like seagrass meadows because of the strong allometric relationships between leaf morphology and growth (Enríquez et al., 2019).

Plant compensatory growth responses to grazing have also been documented in aquatic vascular plant-based systems like seagrass meadows (e.g. Cebrián et al., 1998; Valentine et al., 1997; Vergés et al., 2008), including those grazed by green turtles (Gulick et al., 2020; Moran & Bjorndal, 2005). However, the underlying mechanisms of compensatory growth responses to green turtle grazing and the effects of a range of grazing intensities on leaf morphology and canopy light dynamics have not been quantified. Understanding these dynamics in naturally grazed ecosystems will be critical to assessing the capacity of seagrass compensatory growth responses under long-term cultivation grazing regimes and to identifying potential thresholds for evaluating the sustainability of grazing as populations of this mega-herbivore continue to rebound.

Through a previous experiment, we documented a significant compensatory growth response to green turtle grazing in a tropical Caribbean seagrass ecosystem where productivity of the dominant seagrass, *Thalassia testudinum*, was regulated by both grazing intensity and abiotic factors (Gulick et al., 2020). In this manuscript, we identify a mechanism for compensatory growth responses of *T. testudinum* to cultivation grazing by green turtles, by addressing the following: (a) Evaluating relationships between *T. testudinum* morphology and growth for comparison between naturally grazed and ungrazed areas; (b) Assessing changes in *T. testudinum* leaf morphology over a gradient of grazing intensity; and (c) Comparing light availability and light attenuation in grazed and ungrazed *T. testudinum* canopies, and assessing the dynamics of leaf self-shading in grazed areas by exploring relationships between canopy light attenuation and leaf morphology. This study offers an approach for assessing the underlying mechanisms of plant compensatory growth responses to

cultivation grazing and for identifying potential thresholds that may be used to evaluate the sustainability of increased grazing pressure by recovering mega-herbivore populations.

2 | MATERIALS AND METHODS

2.1 | Study design and data collection

This study was conducted in a tropical, naturally grazed seagrass ecosystem at Buck Island Reef National Monument (BIRNM), St. Croix, U.S. Virgin Islands (17°47.4'N, 64°37.2'W). Seagrass meadows at this site are dominated by *Thalassia testudinum* and support an increasing foraging aggregation of juvenile and adult green turtles throughout the year (Hart et al., 2017; National Park Service, unpublished data). Green turtles at BIRNM maintain large grazing areas (>1,000 m²; Figure 1) located in both shallow (3–4 m) and deep (9–10 m) habitats, many of which had been grazed consistently for at least 2 years (Gulick et al., 2020). Locations of grazed areas were determined by surveying all seagrass meadows at the study site (depth range, 3–10 m).

We selected grazed and ungrazed study sites at both depths and measured *T. testudinum* morphology and growth during August–October 2017 (shallow and deep) and January–February 2018 (deep only). These sampling periods correspond to the summer and winter season at this site (NOAA Coral Reef Watch, 2018), during which a 3°C difference in seafloor water temperature was recorded. Due to limited field site access during January–February 2018, winter measurements of *T. testudinum* morphology and growth in deep meadows were prioritized over shallow meadows given the lack of previous work conducted in deep (>6 m) *T. testudinum* habitats.

Green turtle enclosures (0.5 m × 0.5 m × 0.3 m; mesh size 2.5 cm) were established for 7–10 day intervals in grazed ($n = 65$) and ungrazed ($n = 64$) areas throughout the duration of this study (Table 1). Enclosures were constructed from 2 cm PVC conduit and durable 20-gauge galvanized wire mesh and anchored to the sediment using 25 cm stainless steel stakes. We constructed 30 enclosures and deployed them in groups of 10 (5 in grazed, 5 in ungrazed) for 7–10 day intervals; the number of enclosures deployed in grazed and ungrazed areas by depth and season is summarized in Table 1. Each enclosure was treated as a single site, and measurements of *T. testudinum* growth and morphology were collected a single time from the inside of each enclosure; repeated measures were not conducted.

Enclosures were fitted with a HOBO Pendant Logger (Model UA-002-08; Onset Computer Corporation) that recorded hourly irradiance ($\mu\text{mol}/\text{m}^2/\text{s}$) for the duration of the 7–10 day growth period. Mean irradiance for the growth period of each enclosure was determined using irradiance values collected between 08:00 and 16:00 (period of peak irradiance) because the hourly reading interval did not sufficiently capture the change in irradiance associated with sunrise and sunset. Light availability in the *T. testudinum* canopy was assessed for each enclosure using values of mean irradiance at canopy height. Light attenuation coefficients within the seagrass canopy

TABLE 1 Summary of *Thalassia testudinum* morphology and growth parameters (mean \pm SD) in grazed and ungrazed areas, across water depth and seasonal temperature. Mass growth, above-ground biomass and below-ground biomass were determined on a dry matter (DM) basis. P:B is the ratio of mass growth to above-ground biomass. LAI denotes leaf area index. Values borrowed and modified from tables 1 and 2 in Gulick et al. (2020)

	Shallow (3–4 m) Summer (28.9–29.2°C)		Deep (9–10 m) Summer (29.0–29.6°C)		Deep (9–10 m) Winter (26.6–26.8°C)	
	Grazed n = 25	Ungrazed n = 25	Grazed n = 25	Ungrazed n = 24	Grazed n = 15	Ungrazed n = 15
Linear (mm leaf ⁻¹ day ⁻¹)	5.7 \pm 1.0	3.5 \pm 0.3	5.2 \pm 0.8	4.7 \pm 0.6	4.9 \pm 0.4	3.9 \pm 0.4
Area (mm ² leaf ⁻¹ day ⁻¹)	32.8 \pm 5.9	21.9 \pm 2.7	37.2 \pm 8.4	34.4 \pm 6.6	32.3 \pm 4.0	25.0 \pm 3.2
Mass (g DM m ⁻² day ⁻¹)	0.7 \pm 0.2	4.0 \pm 1.4	0.4 \pm 0.2	1.3 \pm 0.9	0.3 \pm 0.1	0.9 \pm 0.4
P:B (%/day)	39.1 \pm 15.4	16.4 \pm 2.1	11.0 \pm 3.1	11.4 \pm 3.4	13.2 \pm 4.1	12.5 \pm 0.1
LAI	1.6 \pm 0.5	8.4 \pm 1.9	1.7 \pm 0.7	3.1 \pm 1.4	1.1 \pm 0.4	2.8 \pm 1.4
Shoot density (shoots/ m ²)	505.3 \pm 150.9	791.7 \pm 137.7	242.9 \pm 84.6	154.0 \pm 60.2	215.5 \pm 62.9	172.5 \pm 70.4
Above-ground biomass (g DM/m ²)	3.8 \pm 1.3	24.2 \pm 6.5	4.0 \pm 2.0	10.6 \pm 6.2	2.4 \pm 0.7	6.8 \pm 3.4
Below-ground biomass (g DM/m ²)	32.5 \pm 11.4	50.9 \pm 19.3	22.8 \pm 12.3	24.6 \pm 8.8	16.7 \pm 7.9	14.9 \pm 9.6

(Canopy- K_d , m⁻¹), a metric for the degree of leaf self-shading, were calculated for each enclosure (see Enríquez et al., 2019; Enríquez & Pantoja-Reyes, 2005). In situ grazing intensity was calculated at the time of enclosure placement, using the following index (ranges from 0 to 1, or 0%–100% removal of blade biomass; Gulick et al., 2020):

$$\text{Grazing intensity} = \left(\frac{\# \text{ Grazed shoots} / \text{m}^2}{\# \text{ Total shoots} / \text{m}^2} \right) \times \left(\frac{\text{Ungrazed blade length} - \text{Grazed blade length}}{\text{Ungrazed blade length}} \right). \quad (1)$$

Grazing intensity ranged from 0.1 to 0.7 at our study site (Gulick et al., 2020); allowing for a thorough assessment of relationships between *T. testudinum* growth and morphology and the canopy light environment over a gradient of in situ grazing pressure in this study.

Thalassia testudinum morphology and growth were measured a single time in each enclosure (Table 1); repeated measures were not conducted. Morphology was evaluated by measuring total shoot density (shoots/m²), length (mm) and width (mm) of 30 randomly selected leaves, number of leaves per shoot of 10 randomly selected shoots, and above-ground and below-ground biomass (g dry mass (DM)/m²) within each enclosure. Above-ground biomass consisted of all leaf materials above the leaf-sheath junction and below-ground biomass consisted of roots and rhizomes. For each enclosure, leaf surface area per unit substrate (m² per m² of meadow) was calculated as a one-sided leaf area index (LAI) (Enríquez & Pantoja-Reyes, 2005; Watson, 1947) to integrate four important morphological characteristics:

$$\text{LAI} = \frac{(\text{leaf length} \times \text{leaf width}) \times \text{leaves per shoot} \times \text{shoot density}}{1,000}.$$

Below-ground biomass (g DM/m²), consisting of *T. testudinum* roots and rhizomes, was determined from a single 1,140 cm³ core (7.62 cm inner diameter, 25 cm depth) taken from inside each enclosure at the

end of the deployment interval. Dry mass of above- and below-ground biomass was determined by rinsing samples with fresh water and drying to a constant weight at 60°C.

To measure growth and above-ground biomass while maintaining the distinctive canopy conditions associated with grazed

(low leaf biomass) and ungrazed (high leaf biomass) areas, we used different methods to establish the initial point on the leaves from which we measured growth. Measures of growth using these two methods are comparable (Gulick et al., 2020; Moran & Bjorndal, 2005). At the time of enclosure establishment, *T. testudinum* leaves in grazed enclosures were trimmed to the leaf-sheath junction to provide a consistent initial leaf length and the small amount of leaf biomass was removed. This initial trimming did not affect growth in grazed enclosures because these areas were being maintained by natural grazing (Gulick et al., 2020; Moran & Bjorndal, 2005). In ungrazed enclosures, *T. testudinum* leaves were left intact and marked at the leaf-sheath junction using the needle-point method (Fourqurean et al., 2010), an adaptation of the staple marking technique (Zieman, 1974). Upon enclosure removal in both grazed and ungrazed areas, all leaves were clipped at the leaf-sheath junction and collected to quantify growth and biomass.

Thalassia testudinum leaf growth in each enclosure was quantified using four metrics: leaf linear growth (mm leaf⁻¹ day⁻¹), leaf area growth (mm² leaf⁻¹ day⁻¹), mass growth (g DM m⁻² day⁻¹) and the ratio of mass growth to above-ground biomass (%/day, hereafter referred to as P:B). Further details of growth methodology can be found in Gulick et al. (2020).

2.2 | Statistical analyses

Generalized additive models (GAM) were used to evaluate relationships between *T. testudinum* morphology and growth in grazed areas ($n = 65$) and ungrazed areas ($n = 64$), and to test our predictions listed in Table 2. Models were fit using thin-plate regression splines to evaluate the effects of nonlinear covariates. Data were analysed in R version 4.0.1 (R Core Team, 2020) using the 'mgcv' package (Wood, 2011) with smoothness parameters estimated using REML (Wood, 2006).

We evaluated four response variables in our models (leaf linear growth, leaf area growth, mass growth and P:B), and data were evaluated separately for grazed and ungrazed areas. Each model included four fixed effects: above-ground biomass, below-ground biomass, shoot density and LAI. Raw data values for growth and morphology were used in each model. Given that water depth (shallow and deep; treated as a two-level factor) was a significant factor in regulating *T. testudinum* productivity at this study site (Gulick et al., 2020), we also included depth as an ordered smooth-factor interaction in addition to a separate component smooth, for each covariate. This allowed us to determine how much variation in *T. testudinum* growth was explained by morphology alone while still

accounting for the effects of depth on each covariate. We used the following statement format for each model, where 'growth_metric' corresponds to the response variable and 'meadow_type' to grazed or ungrazed areas:

```
gam(growth_metric ~ s(above-ground_biomass) +
s(above-ground_biomass, by = depth_category) +
s(below-ground_biomass) + s(below-ground_biomass,
by = depth_category) + s(shoot_density) + s(shoot_
density, by = depth_category) + s(lai, k = 5) + s(lai,
k = 5, by = depth_category), data = meadow_type,
method = 'REML')
```

Note that we did not include irradiance or season in the GAMs for this study because they were not significant regulating factors of growth at our study site (Gulick et al., 2020). Summary statistics for all morphology and growth parameters collected during this study are provided in Table 1.

Linear regression models were used to evaluate relationships between grazing intensity (Equation 1) and *T. testudinum* leaf morphology to test whether a shift in growth allocation towards stimulated shoot production occurs in grazed areas (Table 2). We assessed

TABLE 2 Summary of predictions for the analysis of relationships between *Thalassia testudinum* morphology and growth, canopy light dynamics and grazing intensity to identify mechanisms for seagrass compensatory growth responses to cultivation grazing by green turtles. Predictions were tested based on results from generalized additive models (Table 2; Figures 2–4) and linear regression (Figures 5 and 6). Significant compensatory growth responses occurred in grazed areas at our study site via stimulated leaf linear growth, leaf area growth and productivity:biomass (P:B) (Gulick et al., 2020). GR, grazed areas; LAI, Leaf area index; UG, ungrazed areas

Predictions	Model results	Conclusions
<p>Because leaf biomass is reduced in GR:</p> <p>1. Relationships between <i>Thalassia testudinum</i> morphology and growth will change in GR such that shoot density will increase with grazing intensity, as above-ground biomass is removed.</p> <p>2. Compensatory growth of <i>T. testudinum</i> in GR will result from stimulated photosynthetic rates in leaf tissue.</p>	<p>1. Mass growth ($\text{g dry mass (DM) m}^{-2} \text{ day}^{-2}$) in GR exhibits an increasing trend with shoot density (Figure 3). P:B ($\%/ \text{day}^{-1}$) in GR significantly increases with shoot density, and significantly decreases with above-ground biomass (Figure 4). Trends for opposite effects occur in UG for both growth metrics (Figures 3 and 4).</p> <p>Shoot density significantly increases and above-ground biomass significantly decreases with increasing grazing intensity (Figure 5). Irradiance ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) at canopy height is higher in GR than UG while canopy light attenuation does not differ (Figure 6).</p> <p>2. Linear ($\text{mm leaf}^{-1} \text{ day}^{-1}$) and area growth ($\text{mm}^2 \text{ leaf}^{-1} \text{ day}^{-1}$) in GR significantly increase with shoot density and reduced above-ground biomass (Figure 2). Mass growth in GR is maintained above a threshold of 2.5 g DM/ m^2 above-ground biomass (Figure 3a). P:B in GR significantly increases with reduced above-ground biomass and significantly increases with shoot density (Figure 4). Shoot density significantly increases with grazing intensity while LAI is maintained (Figure 5). Canopy light attenuation increases with shoot density (Figure 6).</p>	<p>Prediction supported</p> <p>1. Grazing removes aboveground biomass and increases light availability, which results in stimulated shoot production</p> <p>Prediction supported</p> <p>2. Increased light availability in GR increases photosynthetic activity per leaf and per unit leaf area, thereby stimulating leaf growth and turnover and resulting in compensatory growth. Increased shoot production (see Conclusion 1) in GR maintains the light harvesting potential of the seagrass canopy. This allows LAI to be maintained as grazing intensity increases, thereby maximizing the potential for leaf photosynthetic activity and providing the plant with the capacity to sustain mass growth and support a compensatory growth response</p>

the effects of grazing intensity on three response variables: above-ground biomass, shoot density and LAI. Analyses were performed in R version 4.0.1 (R Core Team, 2020) using the 'DPLYR' package (Wickham et al., 2020).

To test whether the light environment of the *T. testudinum* canopy is affected by grazing (Table 2), we compared light availability (irradiance at canopy height) and canopy light attenuation coefficients (Canopy- K_d) between grazed and ungrazed areas, using a nonparametric test of group differences (Mann-Whitney). We also assessed the dynamics of leaf self-shading in grazed *T. testudinum* canopies using linear regression models to explore relationships between Canopy- K_d and *T. testudinum* leaf morphology (i.e. above-ground biomass, shoot density and LAI).

3 | RESULTS

The morphological characteristics that explain variability in *Thalassia testudinum* growth differed between naturally grazed areas and ungrazed areas (Table 3), providing support for our predictions in Table 2. Because the primary objective of this study is to identify the mechanisms of compensatory growth by evaluating relationships between *T. testudinum* morphology and growth, the results from depth-factor interactions are not emphasized here but are accounted for in Table 3. Please note that the effects of depth on *T. testudinum* morphology and growth in grazed and ungrazed areas were assessed in a separate study (Gulick et al., 2020).

The generalized additive models (GAMs) for leaf linear growth and leaf area growth of *T. testudinum* in grazed areas explained 53.3% and 55.2% of model deviance, respectively (Table 3). The following morphological characteristics were significant fixed effects (Table 3, Figure 2): above-ground biomass, shoot density and LAI. In contrast, none of the morphological characteristics were significant in the models for linear growth and area growth in ungrazed areas.

The GAM for mass growth of *T. testudinum* in grazed areas explains 79.0% of model deviance (Table 3), with none of the morphological characteristics as significant fixed effects (see depth-factor interactions in Table 3). In contrast, the GAM for mass growth of *T. testudinum* in ungrazed areas explains 95.7% of model deviance, with above-ground biomass and shoot density as significant fixed effects (Table 3). The insignificance of morphological parameters in the mass growth model for grazed areas is likely due, in part, to the low variation in mass growth (Table 1). Mass growth in grazed areas was maintained once above-ground biomass reached ~2.5 g DM/m² (Figure 3a), whereas mass growth in ungrazed areas exhibited a significant positive linear relationship with above-ground biomass (Figure 3c). Mass growth was positively related to shoot density in grazed areas (Figure 3b), whereas a trend for an opposite relationship was found in ungrazed areas (Figure 3d).

The GAM for P:B of *T. testudinum* in grazed areas explains 90.2% of model deviance, with above-ground biomass and shoot density as significant fixed effects (Table 3; Figure 4a,b). The GAM for P:B in ungrazed areas explains 71.6% of model deviance, with none of

the morphological characteristics as significant fixed effects (although there was a significant depth-factor interaction for above-ground biomass; Table 3). Above-ground biomass and shoot density were not significant in the model for P:B in ungrazed areas (Table 3; Figure 4c,d); however, trends for both variables in ungrazed areas were opposite to those in grazed areas (Figure 4a,b).

Grazing intensity (Equation 1) had a significant effect on the morphology of *T. testudinum* leaves (Figure 5), providing support for our prediction that growth allocation would shift towards increased shoot production, as above-ground biomass is removed with increasing grazing intensity (Table 2). Shoot density significantly increased with grazing intensity (Figure 5b; $R^2 = 0.37$; $p < 0.001$) while above-ground biomass significantly decreased (Figure 5a; $R^2 = 0.29$; $p < 0.001$) and LAI was not affected (Figure 5c; $R^2 = 0.00$; $p = 0.627$).

The light environment of *T. testudinum* canopies differed between grazed and ungrazed areas (Figure 6), which provided context for our supported predictions in Table 2. Light availability, quantified by the irradiance at canopy height ($\mu\text{mol m}^{-2} \text{s}^{-1}$), was significantly higher in grazed areas than in ungrazed areas (Figure 6a; $p = 0.001$; $U = 2,800$) while canopy light attenuation coefficients (Canopy- K_d (m^{-1})) tended to be lower and less variable in grazed areas than in ungrazed areas (Figure 6b; $p = 0.08$; $U = 1,683$). Canopy- K_d in grazed areas exhibited positive linear relationships with leaf morphology metrics, with shoot density (log-transformed) explaining most of the variation in Canopy- K_d (Figure 6c; $R^2 = 0.93$; $p < 0.001$); Canopy- K_d also increased with LAI (Figure S1; $R^2 = 0.33$; $p < 0.001$). There was no relationship between Canopy- K_d and above-ground biomass in grazed areas (Figure S1; $R^2 = 0.00$; $p = 0.62$).

4 | DISCUSSION

Cultivation grazing by green turtles reduces above-ground biomass of *Thalassia testudinum* (Figures 1 and 5a), which increases light availability at canopy height relative to ungrazed areas (Figure 6a) and stimulates leaf growth and turnover (i.e. compensatory growth) (Figures 2a,b, and 4a). Our analysis of the dynamics between *T. testudinum* morphology and growth, the canopy light environment and grazing intensity has allowed us to identify an underlying mechanism of this compensatory growth response to grazing in a Caribbean seagrass ecosystem (Table 2). Shoot density increases with grazing intensity (Figure 5b), which maintains the light harvesting potential of the canopy (Figure 6b,c), despite the removal of leaf biomass. This shift in growth allocation allows LAI to be maintained within the range of grazing intensity values of our study (0.1–0.7; i.e. 10%–70% leaf biomass removal; Figure 5c), thereby maximizing the potential for leaf photosynthetic activity and providing the plant with the capacity to sustain mass growth and support a compensatory response. While a combination of factors may underlie this compensatory response to cultivation grazing by green turtles, the light dynamics in grazed canopies clearly have a relevant role.

TABLE 3 Summary of GAM output for grazed areas ($n = 65$) and ungrazed areas ($n = 64$). p values for significant covariates are indicated in bold. Water depth (shallow, deep) is included as an ordered smooth-factor interaction (denoted 'by = depth'), in addition to a separate component smooth, for each covariate. Models were fit using thin-plate regression splines with smoothness parameters estimated using REML. Mass growth and biomass were evaluated on a dry matter (DM) basis. Raw values for response variables and covariates are summarized in Table 1

	Response variable (<i>Thalassia testudinum</i> growth)			
	Linear	Area	Mass	P:B
	(mm leaf ⁻¹ day ⁻¹)	(mm ² leaf ⁻¹ day ⁻¹)	(g DM m ⁻² day ⁻¹)	(%/day)
Grazed areas				
Covariate				
Above-ground biomass (g DM/m ²)	0.015	0.048	0.229	< 0.001
Below-ground biomass (g DM/m ²)	0.872	0.636	0.165	0.363
Shoot density (# shoots/m ²)	0.004	< 0.001	0.084	0.013
LAI	0.028	0.004	0.401	0.563
Above-ground biomass (by = depth)	0.004	0.002	0.449	< 0.001
Below-ground biomass (by = depth)	0.214	0.035	0.070	0.147
Shoot density (by = depth)	0.023	0.294	0.138	0.395
LAI (by = depth)	0.020	0.007	0.978	0.845
R ²	0.533	0.552	0.790	0.902
Ungrazed areas				
Covariate				
Above-ground biomass (g DM/m ²)	0.686	0.406	< 0.001	0.338
Below-ground biomass (g DM/m ²)	0.740	0.984	0.089	0.169
Shoot density (# shoots/m ²)	0.883	0.828	0.033	0.052
LAI	0.387	0.535	0.123	0.151
Above-ground biomass (by = depth)	0.003	0.012	< 0.001	< 0.001
Below-ground biomass (by = depth)	0.416	0.338	0.420	0.577
Shoot density (by = depth)	< 0.001	< 0.001	0.057	0.117
LAI (by = depth)	0.340	0.008	0.978	0.418
R ²	0.675	0.763	0.957	0.716

4.1 | A mechanism for compensatory growth under a green turtle grazing regime

Plant compensatory growth responses to mega-herbivore grazing can be supported by a combination of internal and external mechanisms, with the increase in light availability that occurs following removal of biomass as one such mechanism that alters the plant's environment in favour of growth (Häsler et al., 2008; Jaremo et al., 1996; McNaughton, 1992). Increased light availability to younger, previously shaded leaf tissue can elicit changes in plant growth allocation, towards the stimulated production of leaf tissue and secondary shoots, particularly as grazing intensity increases (McIntire & Hik, 2002; McNaughton, 1979, 1992; Van der Graaf et al., 2005). It is well established that grazing by green turtles can dramatically alter the morphology and growth of seagrasses (e.g. Christianen et al., 2014; Fourqurean et al., 2010; Hernández & van Tussenbroek, 2014; Kelkar et al., 2013; Moran & Bjorndal, 2005; Rodriguez & Heck, 2020; Scott et al., 2018; Williams, 1988; Zieman et al., 1984), and can result in compensatory growth (Gulick

et al., 2020; Moran & Bjorndal, 2005). However, potential underlying mechanisms of seagrass compensatory growth responses to green turtle grazing have not been evaluated prior to this study.

In ungrazed meadows, light access explains substantial variation in the morphology, growth and degree of leaf self-shading that occurs in *T. testudinum* canopies (Enríquez et al., 2002, 2019; Enríquez & Pantoja-Reyes, 2005; Lee & Dunton, 1997; Major & Dunton, 2002). Reductions in leaf self-shading allow for increased absorption of photosynthetically active radiation on a per leaf basis (Enríquez et al., 2019; Hedley & Enríquez, 2010; Zimmerman, 2006), and more consistent durations of supersaturating irradiance for all leaves within each shoot (Enríquez et al., 2002). Canopy light attenuation coefficients (Canopy- K_d), or the degree of leaf self-shading, are largely regulated by shoot density in ungrazed *T. testudinum* canopies (Enríquez et al., 2019; Enríquez & Pantoja-Reyes, 2005). *Thalassia testudinum* can simultaneously increase shoot density and decrease shoot size (or above-ground biomass) to achieve the optimal LAI for maximizing light harvesting and net assimilation rates (Enríquez et al., 2019). Such a response is consistent with the

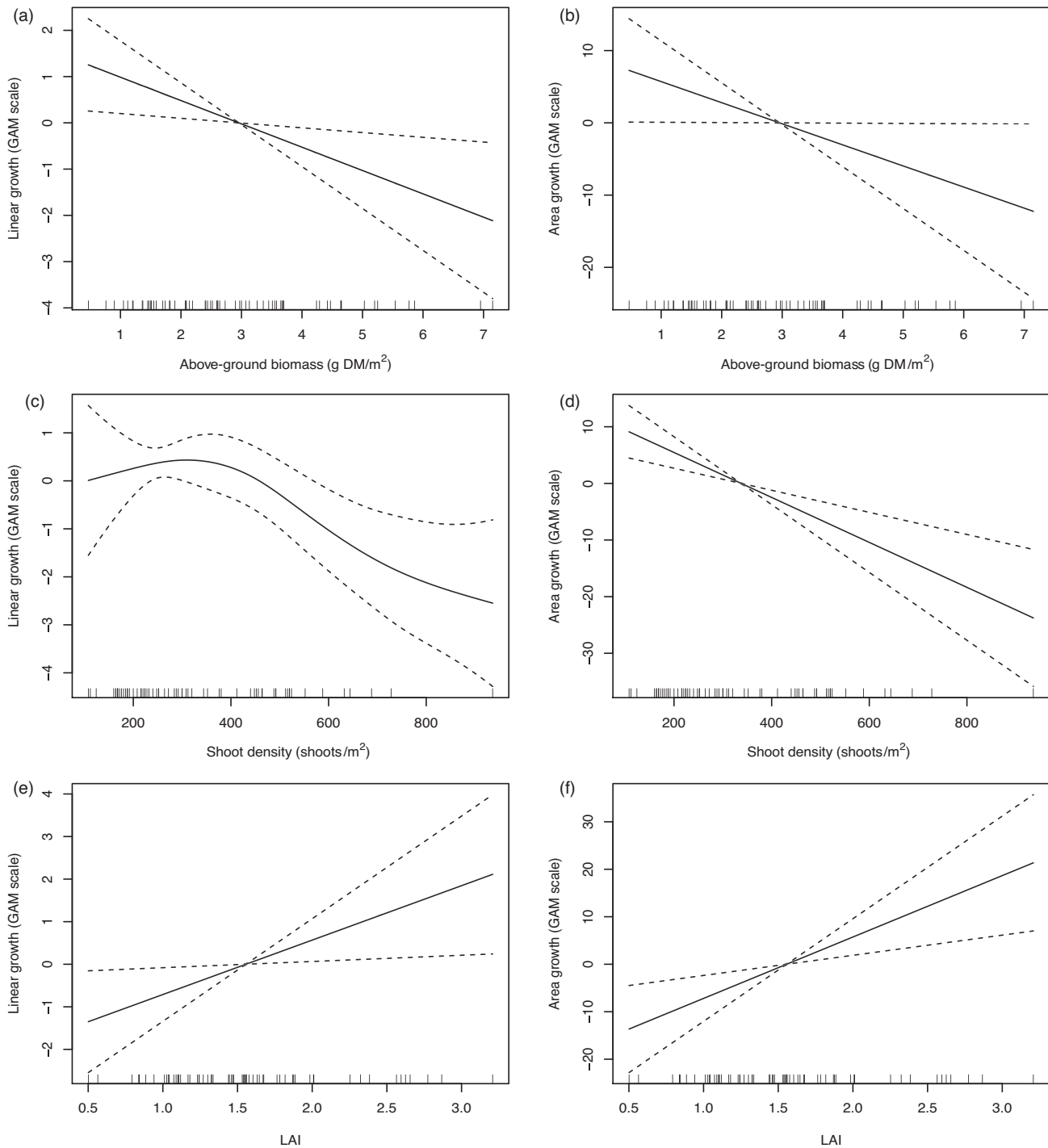


FIGURE 2 Graphical summary of GAM analysis for evaluating the relationship between morphology and leaf linear growth ($\text{mm leaf}^{-1} \text{day}^{-1}$) (a, c, e) and leaf area growth ($\text{mm}^2 \text{leaf}^{-1} \text{day}^{-1}$) (b, d, f) of *Thalassia testudinum* in grazed areas. Response variables are unitless and are shown on the y-axis as a centred smooth function scale. Significant covariates are shown on the x-axis with the rug plot corresponding to the sample distribution. Above-ground biomass was evaluated on a dry matter (DM) basis. Solid curves are smoothing spline fits conditioned on all other covariates and dashed lines are 95% CI. The convergence of 95% CI lines at zero is a result of the identifiability constraint applied to the smooth terms and indicates that there is no uncertainty about this point (see Wood, 2006)

universal leaf self-thinning law (Westoby, 1984) documented in seagrasses (Enríquez et al., 2019), and has been observed only in environments where light availability does not limit growth (i.e. shallow depths).

One might assume that leaf self-shading should decrease with the removal of above-ground biomass by green turtles, and potentially result in a stimulated growth response. However, Canopy- K_d did not differ between grazed and ungrazed areas in our study (Figure 6b),

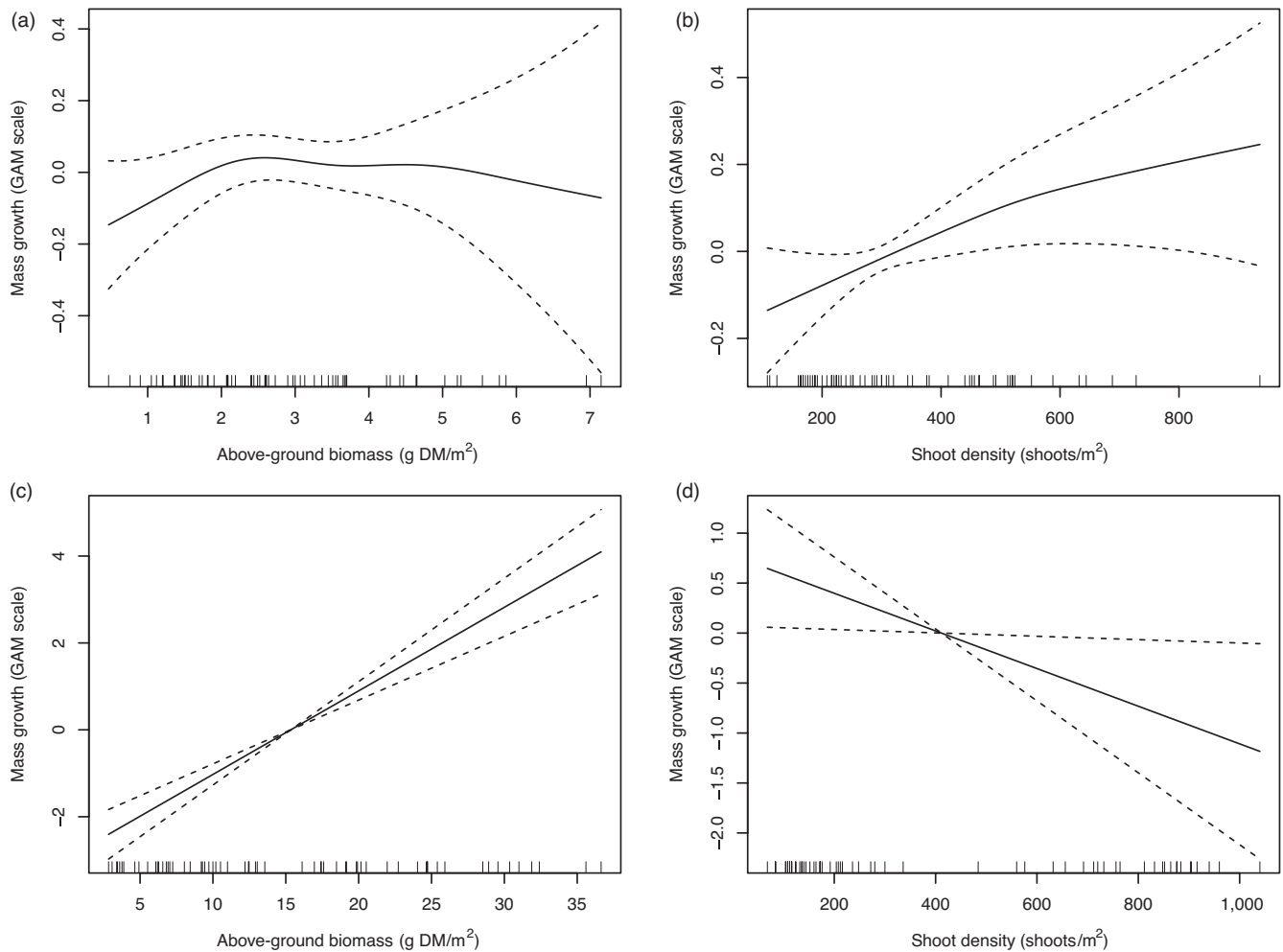


FIGURE 3 Graphical summary of GAM analysis for evaluating the relationship between morphology and mass growth ($\text{g DM m}^{-2} \text{ day}^{-1}$) of *Thalassia testudinum* in grazed areas (a, b) and ungrazed areas (c, d). The response variable is unitless and shown on the y-axis as a centred smooth function scale. Covariates are shown on the x-axis with the rug plot corresponding to the sample distribution; note the difference in range of x-values (a, c). Only the covariates in the ungrazed model (c, d) were significant. Mass growth and above-ground biomass were evaluated on a dry matter (DM) basis. Solid curves are smoothing spline fits conditioned on all other covariates and dashed lines are 95% CI. The convergence of 95% CI lines at zero is a result of the identifiability constraint applied to the smooth terms and indicates that there is no uncertainty about this point (see Wood, 2006)

indicating that leaf self-shading was not dramatically reduced with the removal of above-ground biomass. Canopy- K_d in grazed areas is strongly regulated by shoot density (Figure 6c), similar to results reported by Enríquez and Pantoja-Reyes (2005) for ungrazed *T. testudinum* canopies. Because shoot density significantly increases with grazing pressure (Figure 5b), while LAI is not affected (Figure 5c), the light harvesting potential of the canopy is maintained and any self-shading effects that would result from an increase in shoot density are counteracted by the removal of biomass. The combined effects of increased light availability (Figure 6a) and the self-thinning response via increased shoot density (Figure 5b) in grazed areas, thereby allowing rates of leaf linear and area growth and P:B to increase as above-ground biomass is reduced (Figures 2a,b and 4a).

Morphological thresholds to compensatory growth and releases from growth constraints are apparent in grazed areas at our study site. For example, leaf linear growth ($\text{mm leaf}^{-1} \text{ day}^{-1}$) in grazed areas

declines after shoot density reaches ~ 400 shoots/ m^2 (Figure 2c), whereas mass growth ($\text{g DM m}^{-2} \text{ day}^{-1}$) is maintained above a release threshold of 2.5 g DM/m^2 above-ground biomass (Figure 3a). Because the percentage of photosynthetically active radiation (PAR) absorbed by seagrasses increases with above-ground biomass (Enríquez et al., 2019; Hedley & Enríquez, 2010; Zimmerman, 2006), scattering of PAR and access to PAR should increase for the low levels of leaf biomass present in grazed areas (Figure 1). Increased light availability and access to PAR in grazed areas likely support a self-thinning response while releasing the plant from constraints to mass growth that result from the accumulation of above-ground biomass. These thresholds in grazed areas could also be a partial manifestation of the leaf self-thinning law (Westoby, 1984) in seagrasses (Enríquez et al., 2019), which establishes a limit for the maximum biomass that a photosynthetic organism can accumulate. However, because above-ground biomass is significantly reduced in grazed

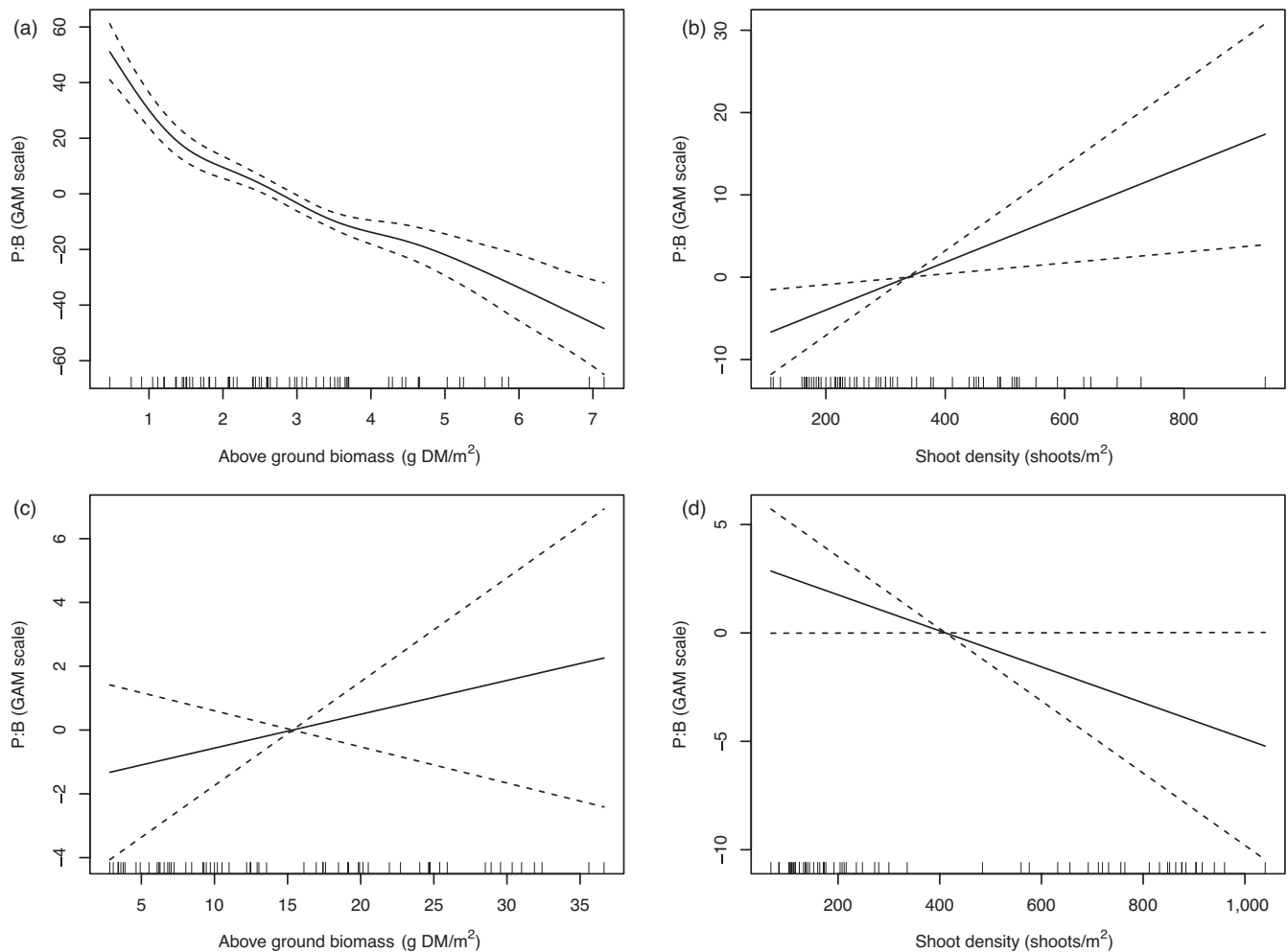


FIGURE 4 Graphical summary of GAM analysis for evaluating the relationship between morphology and P:B (%/day) of *Thalassia testudinum* in grazed areas (a, b) and ungrazed areas (c, d). The response variable is unitless and shown on the y-axis as a centred smooth function scale. Covariates are shown on the x-axis with the rug plot corresponding to the sample distribution; note the difference in range of x-values (a, c). Above-ground biomass was evaluated on a dry matter (DM) basis. Solid curves are smoothing spline fits conditioned on all other covariates and dashed lines are 95% CI. The convergence of 95% CI lines at zero is a result of the identifiability constraint applied to the smooth terms and indicates that there is no uncertainty about this point (see Wood, 2006). Both covariates were significant in the grazed model, but not significant in the ungrazed model

areas compared to ungrazed areas, the thresholds in grazed areas likely reflect the maximum biomass that can support a mass growth and compensatory response under grazing pressure, not the maximum biomass that accumulate before limiting growth via leaf self-shading. Theoretically, as long as sufficient leaf tissue is available for photosynthesis (~ 2.5 g DM/m², Figure 3a), mass growth in grazed areas should be maintained—providing a critical starting point for evaluating the sustainability of grazing pressure by recovering green turtle populations in tropical naturally grazed seagrass ecosystems.

4.2 | Other mechanisms for seagrass compensatory growth responses

Results from our study provide evidence that increased light availability in grazed areas is an underlying mechanism for compensatory

growth of *T. testudinum* in response to cultivation grazing by green turtles. A combination of factors may be at work to support compensatory responses in seagrasses. Mobilization of carbohydrate stores (Holzer & McGlathery, 2016; Vergés et al., 2008), nutrient input via herbivore urine/faeces (Bakker et al., 2016; McNaughton, 1979; Subalusky et al., 2015), reduced rates of leaf senescence (Tiffin, 2000) and redistribution of growth hormones (Tiffin, 2000) are additional mechanisms that can support compensatory growth responses in terrestrial and aquatic plants. These additional mechanisms warrant further study in seagrass ecosystems that support green turtles and should be considered when evaluating compensatory growth responses to grazing in aquatic and terrestrial systems.

Mobilization of carbohydrate reserves has been documented in seagrass meadows grazed by green turtles (Fourqurean et al., 2010; Holzer & McGlathery, 2016) and could be an additional mechanism for supporting compensatory growth. Below-ground biomass did

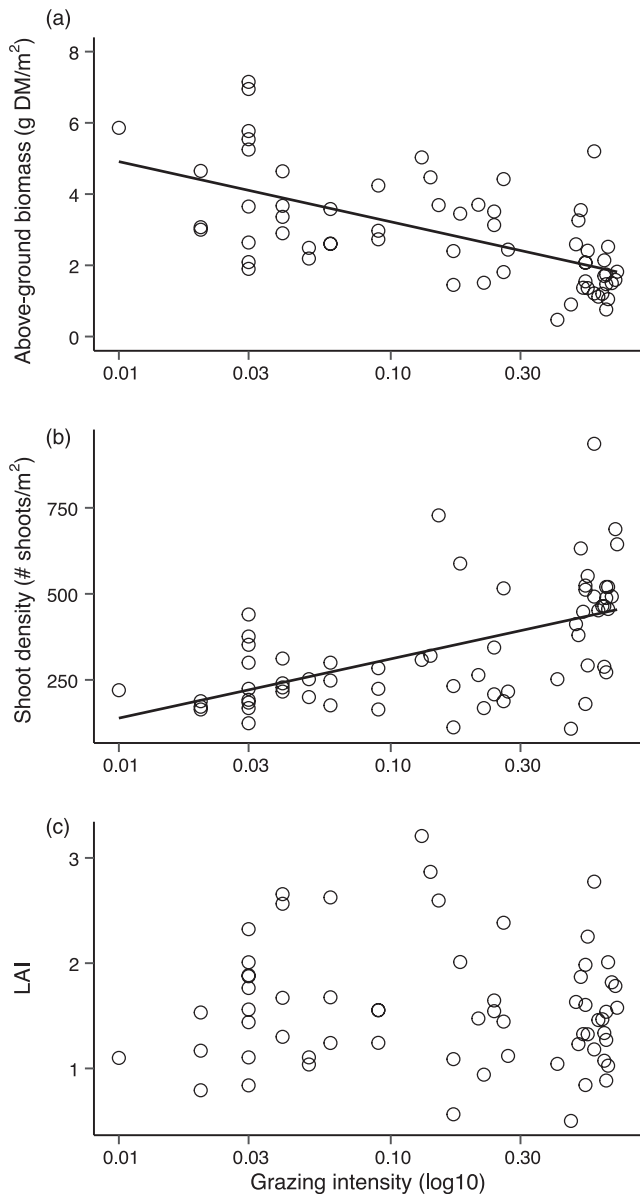


FIGURE 5 Graphical summary of linear regression analysis for evaluating relationships between grazing intensity (log transformed) and *Thalassia testudinum* leaf morphology to assess shifts in growth allocation in grazed areas: (a) Above-ground biomass ($R^2 = 0.37$; $p < 0.001$); (b) shoot density ($R^2 = 0.29$; $p < 0.001$); (c) photosynthetic leaf area per unit substrate (leaf area index, LAI) ($R^2 = 0.00$; $p = 0.627$). Above-ground biomass was determined on a dry matter (DM) basis. Grazing intensity was calculated using Equation 1

not have a significant role in any of the models for grazed areas in our study. This result was unexpected, given that declines in below-ground biomass (Hernández & van Tussenbroek, 2014) and storage levels of rhizome soluble carbohydrates (Fourqurean et al., 2010; Holzer & McGlathery, 2016) have been observed in grazed areas when compared to ungrazed areas. However, some of these studies were conducted at subtropical/temperate latitudes, near the northern limit of the *T. testudinum* range (Fourqurean et al., 2010; Holzer & McGlathery, 2016). Other studies from tropical Caribbean locations

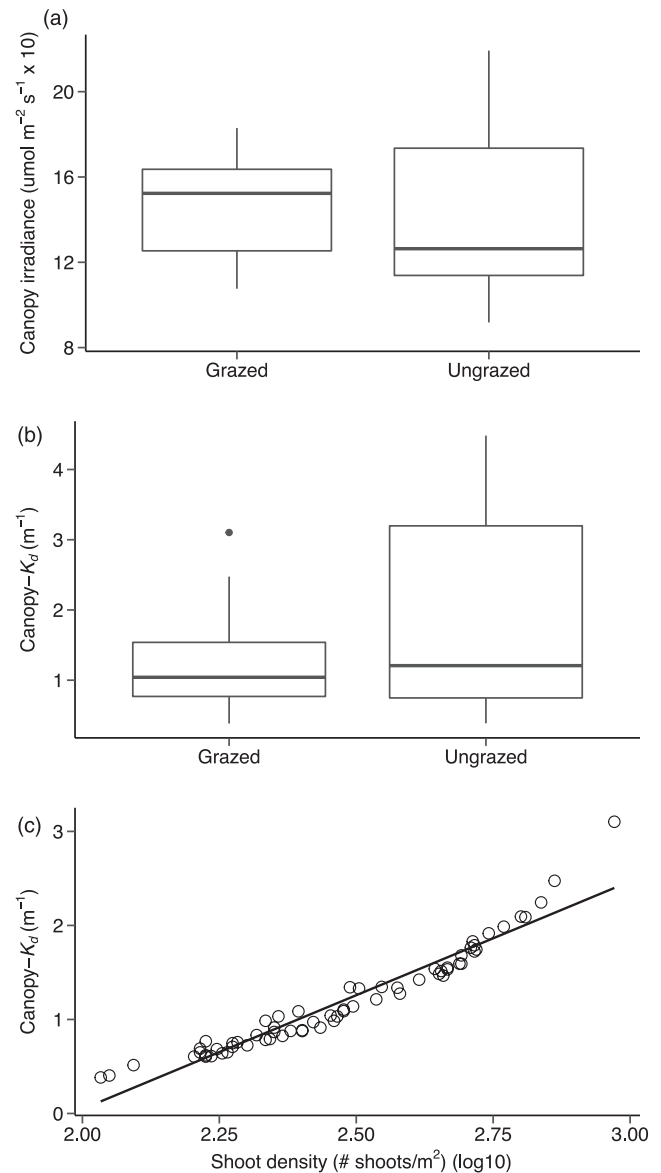


FIGURE 6 Graphical summary for comparing (a) light availability ($p = 0.001$; $U = 2,800$) and (b) canopy light attenuation coefficients ($p = 0.08$; $U = 1,683$) of *Thalassia testudinum* between grazed and ungrazed areas. (c) Canopy- K_d in grazed areas increased with shoot density (log transformed) ($R^2 = 0.93$; $p < 0.001$). Relationships between Canopy- K_d and both above-ground biomass and LAI are provided in Figure S1. Canopy- K_d was calculated using the model provided by Enríquez and Pantoja-Reyes (2005) and Enríquez et al. (2019) for *T. testudinum* canopies

found no difference in below-ground biomass (Gulick et al., 2020; Johnson et al., 2017) or storage of rhizome soluble carbohydrates (Gulick et al., 2020) between naturally grazed and ungrazed areas. Since light availability and depth are critical to supporting below-ground biomass (Enríquez et al., 2019) and the storage of carbohydrates in seagrasses (Alcoverro et al., 2001; Lee & Dunton, 1997), we propose that the increase in light availability in grazed areas and the tropical latitude could collectively play a role in the sustained below-ground biomass in grazed areas at our study site. However, further study of these dynamics in grazed systems throughout the

geographical range of *T. testudinum* is warranted because of seasonal effects on light access and carbohydrate storage.

Nutrient input from herbivores is another mechanism for supporting compensatory growth responses in plants (Bakker et al., 2016; McNaughton, 1979), with recovery of herbivore populations capable of eliciting dramatic changes to ecosystem nutrient dynamics (e.g. Subalusky et al., 2015). However, nutrient input from green turtle urine and faeces is an unlikely mechanism for supporting stimulated growth of seagrasses (Thayer et al., 1984) for the following reasons: (a) It is unlikely that urine makes a large contribution to nitrogen budgets in grazed areas because seagrasses absorb the bulk of required nitrogen via below-ground sediment pore water pools, not directly from the water column through the leaves (Lee & Dunton, 1999); (b) Green turtle faeces may not be deposited in grazed areas because turtles often defecate in resting areas each morning, prior to moving into grazed areas (Bjorndal, 1980); (c) Faeces likely float away from grazed areas (Balazs et al., 1993) due to trapped gasses produced during hindgut fermentation (Bjorndal, 1979).

4.3 | Sustaining compensatory growth under cultivation grazing

Caribbean green turtles can maintain grazed areas for at least 1–2 years (Bjorndal, 1980; Hernández & van Tussenbroek, 2014; Ogden et al., 1983). Long-term cultivation grazing by Caribbean green turtles, combined with their high site fidelity to foraging areas (Bjorndal et al., 2005) and low metabolic requirements, may affect the capacity for seagrass compensatory growth responses as green turtle populations recover. The morphological thresholds and releases from growth constraints, identified during our analysis of *T. testudinum* morphology and growth, are potential starting points for assessing the sustainability of increased grazing pressure in tropical seagrass ecosystems. Our analytical approach provides a tangible management tool for assessing the status of naturally grazed seagrass ecosystems and the underlying mechanisms of seagrass compensatory growth responses, which should be of value in other aquatic and terrestrial systems subjected to cultivation grazing regimes. A myriad of biological and environmental factors (e.g. grazing intensity, resource availability, plant morphological plasticity), and the significant degradation of plant systems due to anthropogenic threats, could impact these threshold values, and the capacity of plants to support and sustain compensatory growth responses to grazing.

Seagrasses experienced much greater levels of green turtle grazing pressure historically, and the coevolution of seagrasses and green turtles has undoubtedly influenced ecosystem properties (Jackson et al., 2001; Thayer et al., 1984). A historical perspective, an integrated approach to conservation (Sievers et al., 2019; Unsworth et al., 2019), and an increased integration of the literature on freshwater, marine and terrestrial herbivory (Bakker et al., 2016), will be essential to advancing future research efforts and informing the

management of ecosystems that are experiencing the recovery of a once functionally extinct mega-herbivore.

ACKNOWLEDGEMENTS

We thank the staff of the National Park Service (NPS) in St. Croix, U.S. Virgin Islands, for providing staff and logistical support for field operations. We also thank Laura Palma, Ashley Meade, and Rich Bery for their assistance with the field and laboratory components of the project. This project was funded by the NPS at Buck Island Reef National Monument in St. Croix, PADI Foundation, Mosaics in Science and Diversity, UF Department of Biology, Gumbo Limbo Nature Center, and the UF Archie Carr Center for Sea Turtle Research through funds from Lalita Shastri, the Disney Conservation Fund, and the Jeff and Monette Fitzsimmons Fund. Big Beards Adventure Tours in St. Croix also supported our work.

AUTHORS' CONTRIBUTIONS

A.G.G., A.B.B. and K.A.B. conceived and designed the study; A.G.G., R.A.J., C.G.P., Z.H.-S., A.B.B. and K.A.B. contributed to the planning and implementation of the study; A.G.G., R.A.J. and C.G.P. collected the data; A.G.G., A.B.B. and K.A.B. analysed the data; A.G.G. wrote the manuscript with contributions and final approval from all authors.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13718>.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kwh70rz3t> (Gulick et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Gulick, A. G., Johnson, R. A., Pollock, C. G., Hillis-Starr, Z., Bolten, A. B., & Bjorndal, K. A. (2021). Recovery of a cultivation grazer: A mechanism for compensatory growth of *Thalassia testudinum* in a Caribbean seagrass meadow grazed by green turtles. *Journal of Ecology*, 109, 3031–3045. <https://doi.org/10.1111/1365-2745.13718>