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Effects of Ocean Acidification on Seagrass Ecosystems

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Abstract. The ecological effects of ocean acidification are among the central issues in contemporary global change research. As a key component of blue carbon ecosystems, seagrass beds were once simplistically framed as "carbon-limited beneficiaries" of rising CO_2 concentrations. However, evidence accumulated over the past two decades has revealed a far more complex picture.This review synthesizes major advances in seagrass acidification research from 2008 to 2026, organizing core findings and controversies across three levels: individual physiology, interspecific interactions, and ecosystem function.It shows that direct physiological responses of seagrasses to acidification are markedly species-specific, time-dependent, and environmentally contingent, enhanced photosynthesis does not necessarily translate into enhanced growth, and short-term responses are not equivalent to long-term effects. By weakening phenolic chemical defenses and restructuring epibiont communities, acidification may trigger indirect effects across trophic levels that partially offset its direct "carbon fertilization" benefits.Seagrass beds can provide localized acidification buffering during the day, but this capacity declines markedly under multiple co-occurring stressors. This review argues that casting seagrasses simply as climate change "winners" or "losers" is misleading, a more accurate understanding treats them as "conditional responders" whose ecological fate depends on the interaction of species identity, stressor combinations and spatiotemporal scale.

Keywords: ocean acidification, seagrass ecosystems, blue carbon, species specificity, ecological cascades

1. Introduction

Since the Industrial Revolution, the global ocean has absorbed approximately one-third of anthropogenic CO_2 emissions, causing surface seawater pH to decline by 0.1 units. A further decline of 0.3-0.4 units is projected by the end of this century. This process, known as "ocean acidification", is fundamentally altering the chemical equilibrium of the marine carbonate system. Against this backdrop, sustained attention has focused on the fate of seagrass ecosystems, which cover less than 0.2% of the seafloor yet contribute approximately 15% of oceanic carbon storage.

Seagrasses have become a focal taxon in ocean acidification research because of an apparently simple logic: as carbon-limited plants, their photosynthesis is constrained by the low diffusion rate and low concentration of CO_2 in seawater, and CO_2 enrichment should relieve this constraint, stimulating photosynthesis and growth. This hypothesis received substantial support in early studies:

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increased shoot density in seagrasses at natural CO_2 vents, elevated photosynthetic rates in laboratory experiments, and consistent positive responses in multi-species comparisons all seemed to point to a single conclusion-that seagrasses would be among the few "winners" under climate change. However, as research has advanced, this narrative has encountered increasing challenges. Response patterns differ markedly among species, photosynthetic enhancement does not necessarily translate into biomass accumulation, Conclusions attenuate or even reverse over longer timescales. Seagrasses respond to acidification not only through photosynthesis but also through indirect pathways, generating complex feedbacks across multiple levels of ecosystem organization.

This review systematically summarizes research progress on the effects of ocean acidification on seagrass ecosystems, summarizing core findings, major controversies, and research gaps across three levels-individual physiological responses, interspecific interactions, and ecosystem function to provide a theoretical reference for subsequent mechanistic research, risk prediction, and conservation management of seagrass ecosystems under ocean acidification.

2. Direct physiological responses of seagrasses to ocean acidification

2.1. Enhanced photosynthetic physiology and growth

The theoretical expectation that seagrasses are carbon-limited plants received substantial empirical support in early studies. A two-week experiment showed that net productivity and maximum photosynthetic rate increased linearly with rising pCO_2 in all three species, with no significant differences in response slopes among species (as shown in figure 1) [1]. The key contribution of this study lies in providing a quantitative multi-species comparison within a single experimental framework, confirming a generalized photosynthetic response of tropical seagrasses to CO_2 enrichment. However, despite similar photosynthetic responses, leaf growth rates of C. serrulata did not increase with rising pCO_2, whereas H. uninervis and T. hemprichii exhibited significant growth enhancement. This difference reflects "carbon allocation strategy": whether photosynthate is used for leaf expansion or stored in belowground tissues plays a key role in determining the ultimate phenotypic response.

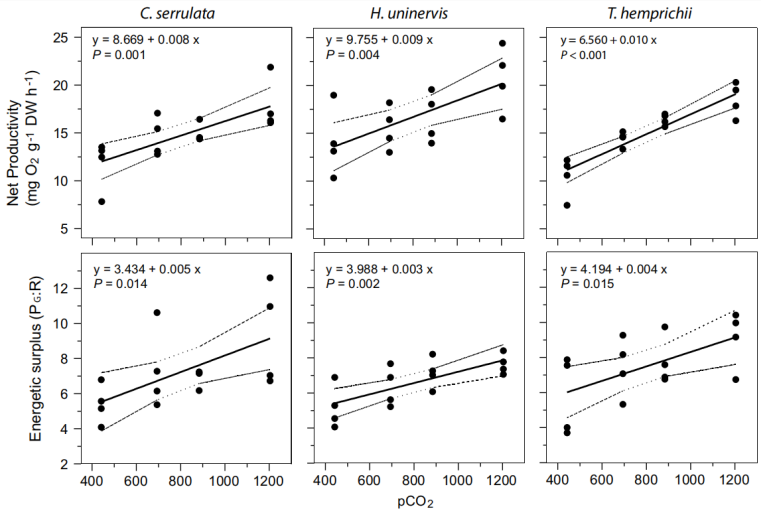


Figure 1. Linear model fits (dotted lines indicate 95 % confidence intervals) for net productivity and energetic surplus (PG:R)of C. serrulata , H. uninervis and T. hemprichii in response to pCO_2 enrichment. N = 44

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This "carbon allocation strategy" is not an isolated case. Viana et al. found that under combined warming at 32 °C and elevated pCO_2, C. serrulata exhibited only limited biochemical responses-decreased rhizome carbon content and increased sucrose concentration-with no significant changes in morphological or photophysiological traits [2]. The authors interpreted 32 °C as a temperature "below the species' thermal tolerance threshold," implying that under conditions not yet reaching stress limits, C. serrulata may tend to allocate extra fixed carbon to storage rather than immediately to growth.

Taken together, these studies reveal that seagrasses benefit photosynthetically under acidification, though the extent and nature of these benefits differ by species, developmental stage, and environmental conditions. Photosynthetic enhancement is relatively common, but whether it translates into gains at the growth, biomass, or population level depends on the species "carbon allocation strategy" and other limiting factors in its environment.

2.2. Differences in responses across temporal scales

If "photosynthetic enhancement" is a common finding in short-term experiments, then "attenuation of growth enhancement" is the other side revealed by long-term observations.Pansini et al.'s study provides a classic example of temporal-scale effects [3]: by comparing plants transplanted from control-pH sites to low-pH sites (short-term acidification, 3 months) with untransplanted plants at naturally low-pH sites.

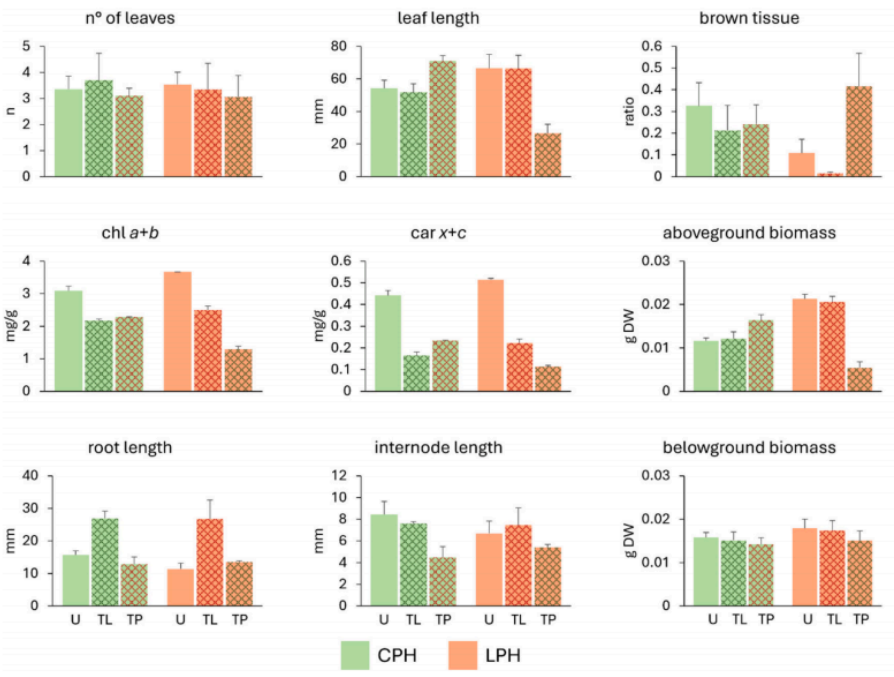


Figure 2. Mean (+SE) of Z.noltii above and belowground variables at the CPH (control) and LPH (acidified) sites: untouched (u), translocated (TL), and transplanted (TP) plants

The study found that short-term acidification significantly increased leaf length, pigment content, and aboveground biomass, whereas under long-term acidification these morphological advantages were no longer significant, with only photosynthetic pigment content remaining elevated (as shown in figure 2). This "short-term promotion, long-term attenuation" pattern suggests that seagrasses may

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initially benefit from CO_2 enrichment through rapid plastic responses, but as exposure time lengthens, adaptive compensatory mechanisms or metabolic reconfiguration may offset early gains.

3. Joint responses of seagrasses and epibionts

3.1. Ocean acidification drives structural restructuring of epibiont communities

Calcareous epibionts on seagrass leaves, especially coralline algae, are key contributors to carbonate production and carbon cycling in seagrass ecosystems. Martin et al.'s study showed that at normal-pH (8.0-8.2) sites, coralline algae reached 18-69% cover and were the overwhelmingly dominant calcareous epibiont group, at sites with a mean pH of 7.7, coralline algae disappeared completely, and $CaCO_3$ mass per leaf declined from 41 mg to 3 mg, a reduction of approximately 90%. A laboratory transplantation experiment further confirmed causality: when leaves bearing coralline algae were transferred from normal pH to seawater at pH 7.0, the coralline algae dissolved completely within two weeks [4].

This disappearance is not simply a case of "all calcareous organisms disappearing". Martin et al. also observed that bryozoans survived under low-pH conditions (cover 1-6%). Their skeletons have lower Mg content (0.1-3 %) and are more resistant to dissolution than the high-magnesium calcite of coralline algae (Mg 3.5-6 %). This implies that acidification will drive a shift in seagrass epibiont communities from "coralline-algae-dominated" to "bryozoan-dominated", a community reorganization based on mineralogical differences.

3.2. Feedback effects of altered epibiont communities on seagrasses

This restructuring may generate complex feedback effects on seagrasses themselves.As "pioneer colonizers", the disappearance of coralline algae may affect the subsequent colonization of a suite of epibionts, altering the structure of the epibiont food web. On the other hand, the presence of calcareous epibionts shades light, increases leaf mass, and impedes carbon uptake, so their disappearance may actually benefit seagrass photosynthesis. Hall-Spencer et al. observed at Ischia that shoot density increased by approximately 30% at pH 7.6, where calcareous epibionts had completely disappeared [5]. This raises a hypothesis warranting rigorous testing: part of the "promotional" effect of acidification on seagrasses may arise from indirect mechanisms involving the removal of competitors or shade casters, rather than solely through the direct pathway of increased carbon substrate.

4. Chemical defenses and trophic cascades

4.1. Decline in phenolic chemical defenses

The primary chemical defenses of seagrasses and most estuarine vascular plants are phenolics, including simple phenolic acids, condensed tannins, and lignin, which play important roles in anti-herbivore, anti-pathogen, and anti-fouling defense.Arnold et al.'s study at natural CO_2 vents off Vulcano found that along a pH gradient from 8.1 to 7.3, proanthocyanidins in Cymodocea nodosa leaves declined by 25% and total phenolic acids by 59%, with no phenolic compound increasing under acidification. Similar responses were verified in an in situ FOCE experiment in Chesapeake Bay, USA: under a pH reduction of approximately 0.5 units, Ruppia maritima showed a 45-60% decline in proanthocyanidins and a 45% decline in total active phenolics [6].

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The pattern of acidification-induced phenolic reduction contrasts sharply with the accumulation of phenolics in terrestrial plants under elevated CO_2. The authors proposed two possible mechanistic explanations: first, a "growth–defense trade-off", in which acidification promotes photosynthesis and growth, leading plants to allocate carbon preferentially to growth (protein synthesis) rather than defense (phenolic synthesis), second, direct inhibition of the shikimate–phenylpropanoid pathway by acidification, although the exact mechanism remains to be elucidated. This conclusion has major implications for the ability of seagrasses to resist herbivory and pathogens, and is a core element of how seagrasses cope with biotic and environmental stresses.

4.2. Controversies and drivers of acidification–herbivory interactions

Existing conclusions regarding the effects of acidification on seagrass–herbivore relationships are contradictory. Jiménez-Ramos et al. tested the combined effects of acidification, warming, and eutrophication on C. nodosa and found that acidification alone reduced leaf phenolic content and biomechanical resistance, while multi-factor combinations significantly increased sea urchin feeding rates, supporting the hypothesis that "multi-factor disturbances enhance herbivory pressure by altering palatability" [7]. In contrast, Hughes et al. observed a quadratic response of herbivore biomass and exponential growth of macroalgae, while Z. marina remained resilient across all pH levels, with some metrics even increasing linearly, indicating that seagrasses may compensate for algal competition through acidification-driven physiological enhancement [8].

The root of this disagreement lies in differences in experimental design: large sea urchins consume far more than mesograzers (sea hares, isopods), and the latter can be compensated for by physiological enhancement of seagrasses. Moreover, differences in seagrass species, experiment duration (1 month vs. 24 days), and stressor combinations (single-factor vs. multi-factor) alter the direction of effects.

5. The function of seagrass ecosystems

5.1. Buffering capacity of seagrass beds against localized ocean acidification

Seagrass beds can modulate the local carbonate system through photosynthetic carbon fixation and alkalinity generation, buffering seawater acidification.Scott-Askin et al.'s in situ experiment showed that seagrass beds are a net source of total alkalinity (TA), increasing Ω_{arg} within the meadow by 13% and reducing the Revelle factor by 14% during the day, significantly enhancing seawater buffering capacity, although the buffering effect disappeared at night [9].

Compared with mangroves and salt marshes, seagrass beds have inorganic carbon export fluxes an order of magnitude lower but higher buffering efficiency.This is because subtidal seagrass beds lack strong tide-driven porewater exchange, mass transport is dominated by diffusion and advection, making water-column carbonate chemistry more readily regulated by seagrass metabolism.

5.2. Limitations of seagrass buffering capacity

FOCE experiments have further revised the understanding of seagrass bed buffering effects: acidification weakens the buffering capacity of seawater itself, increasing the diel pH fluctuation amplitude to 2–3 times that of controls [10]. The two effects—acidification-driven photosynthetic gains in seagrasses and reduced seawater buffering capacity—can offset each other. This study did

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not detect acidification-enhanced seagrass productivity, so the hypothesis that "acidification drives seagrass production, thereby strengthening local acidification buffering is not supported.

In addition, the buffering effect of seagrasses is clearly constrained in time and space. In some cases it operates only during photosynthetically active daytime hours, while nocturnal respiration releases CO_2 and the buffering effect disappears [11]. Meanwhile, hydrodynamic exchange dilutes alkalinity within the meadow, weakening the ability of seagrass beds to regulate acidification in surrounding waters.

6. Conclusion

The effects of ocean acidification on seagrass ecosystems cannot be captured by a simple "winner" versus "loser" dichotomy.The evidence indicates that seagrass photosynthetic physiology benefits from CO_2 enrichment in most cases, but the extent to which this benefit translates into growth and biomass gains varies with species, developmental stage, and environmental context. By weakening phenolic defenses and restructuring epibiont communities, acidification may trigger indirect effects across trophic levels that partially offset direct "carbon fertilization" benefits. Seagrass beds can provide localized acidification buffering during the day, but this function may decline under multiple co-occurring stressors.

Overall, the literature reveals several structural limitations. First, most experiments last weeks to months, whereas the shoot lifespan of seagrasses can reach decades, the asynchrony between carbon storage and growth means that short-term photosynthetic stimulation may require seasonal or even multi-year timescales to translate into population-level gains. Second, research has concentrated on a few species from the Mediterranean (P. oceanica, C. nodosa) and the tropical Great Barrier Reef (T. hemprichii, H. uninervis, C. serrulata), while data for cold-temperate and polar species are extremely scarce, the study by Scott-Askin et al. on Z. marina in Sweden is one of the few exceptions. Third, although studies have examined acidification×warming, acidification×low salinity, and acidification×eutrophication, the interactive effects of acidification×hypoxia, acidification×heavy metals, and acidification×pathogens are almost entirely unexplored.

This research highlights that acidification does not necessarily enhance seagrass carbon sinks, instead, net effects should be evaluated considering specific species, locations, and combinations of stressors, directly impacting blue-carbon-based conservation and restoration strategies.

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