Global dataset on seagrass meadow structure, biomass and production

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Abstract. Seagrass meadows provide valuable socio-ecological ecosystem services, including a key role in climate change mitigation and adaption. Understanding the natural history of seagrass meadows across environmental gradients is crucial to decipher the role of seagrasses in the global ocean. In this data collation, spatial and temporal patterns in seagrass meadow structure, biomass and production data are presented as a function of biotic and abiotic habitat characteristics. The biological traits compiled include measures of meadow structure (e.g., percent cover and shoot density), biomass (e.g., above-ground biomass) and production (e.g., shoot production). Categorical factors include bioregion, geotype (coastal or estuarine), genera and year of sampling. This dataset contains data extracted from peer-reviewed publications published between 1975 and 2020 based on a Web of Science search, and includes 11 data variables across 12 seagrass genera. The dataset excludes data from mesocosm and field experiments, contains 14,271 data points extracted from 390 publications, and it is publicly available on the PANGAEA® data repository (https://doi.org/10.1594/PANGAEA.929968). The top five most studied genera are *Zostera*, *Thalassia*, *Cymodocea*, *Halodule* and *Halophila* (84% of data), and the least studied genera are *Phyllospadix*, *Amphibolis* and *Thalassodendron* (2.3% of data). The data hotspot bioregion is the Tropical Indo Pacific (25% of data) followed by the Tropical Atlantic (21%), whereas data for the other four bioregions are evenly spread (ranging between 13 and 15% of total data within each bioregion). From the data compiled, 57% related to seagrass biomass and 33% to seagrass structure, while the least number of data were related to seagrass production (11% of data). This data collation can inform several research fields beyond seagrass ecology, such as the development of nature-based solutions for climate change mitigation, which include readership interested in blue carbon, engineering, fisheries, global change, conservation and policy.

1 Introduction

Approximately 65 million years ago, a group of marine angiosperms called seagrasses adapted to life within the coastal zone, and now, they rank among the most valuable ecosystems globally. Seagrasses encompass ~72 species within 12 genera spread across all continents except Antarctica (Short et al., 2011). Seagrasses are recognised as highly productive habitats that provide multiple ecosystem services relevant to human wellbeing, such as biodiversity, fisheries, sediment stabilisation and nutrient cycling across the coastal zone (Ascioti et al., 2022; Lamb et al., 2017; McMahon et al., 2013; Nordlund et al., 2016; Unsworth et al., 2018). Furthermore, the high primary production rates and capacity of seagrasses to sequester carbon is relevant to mitigating climate change, while their role in stabilising the substrate, ameliorating hydrodynamic energy and nourishing beaches with biogenic sands contributes to climate change adaptation against storms and sea-level rise (Duarte et al., 2013).

Seagrass research initially focussed on understanding biology, distribution, ecology, taxonomy, and phenology. More recently, the socio-ecological value of seagrass ecosystem services has received recognition, in part owing to the extensive losses of seagrasses globally. Since the beginning of the 20th century, widespread loss of seagrass meadows has been estimated at 0.9% yr^{-1}, linked to a variety of factors including impacts associated with alterations to key drivers of growth (e.g., irradiance and temperature) resulting from sediment loading, eutrophication, extreme climate events and flooding (Hall et al., 1999; Short et al., 2011; Strydom et al., 2020; Waycott et al., 2009). Recent conservation and management actions have resulted in the deceleration and reversal of declining trends in some locations (de los Santos et al., 2019).

Duarte and Chiscano (1999) conducted a review on seagrass biomass and production, which has greatly contributed to the advancement of seagrass research. Information on seagrass meadows structure, production, biomass and reproduction is essential to understand the role of seagrasses in the global ocean, while providing insights for developing restoration initiatives, informing management and ultimately contributing to their conservation (Unsworth et al., 2018). Therefore, understanding global patterns in the functioning of threatened natural ecosystems such as seagrass meadows, is crucial to inform management strategies to protect natural assets (Cullen-Unsworth et al., 2014; Hoegh-Guldberg and Bruno, 2010). Since Duarte and Chiscano (1999), new information across hundreds of peer-reviewed manuscripts (past 24 years, 1996-2020) has not been synthesised and made available online, which precludes gathering new knowledge around seagrass natural history based on data synthesis studies. Indeed, data on seagrass reproduction has never been compiled.

In this review, data on key variables on seagrass meadow structure, biomass and production published between 1975 and 2020 (data collected between 1972 and 2020) are presented as a function of biotic and abiotic habitat characteristics. The main goals of this review are to synthetize current literature on seagrass ecology to facilitate further multidisciplinary research, and to identify research gaps and provide recommendations for future research. The dataset provides baseline data that can inform science, management and policy. In particular, it provides critical and basic knowledge to inform traditional seagrass biology and ecology fields, but also can contribute to advance knowledge in other disciplines including fisheries, biodiversity, conservation, coastal biogeochemistry, and emerging fields such as the Blue Economy.

2 Data compilation

2.1 Literature search

In order to create a global seagrass database containing relevant data on seagrass meadow structure, biomass and production, a Web of Science (www.webofknowledge.com) search was conducted in June 2020 using these search terms for the growth, production and biomass variables: ((TS=((Seagrass* OR eelgrass OR SAV OR Amphibolis OR Cymodocea OR Enhalus OR Halophila OR Halodule OR Posidonia OR Phyllospadix OR Ruppia OR Thalassia OR Thalassodendron OR Zostera) AND (product* OR biomass OR growth OR exten))))

Only data from peer-reviewed manuscripts was included and thereby, the dataset compiled excludes data from non-peer reviewed manuscripts and reports. We acknowledge that our search has likely missed a small portion of the peer-reviewed data published to date, owing to the use of different terms across research fields, and the use of a single search engine WOS to conduct the review. Data for 11 variables (mean values) were extracted (Table 1, see 2.2) and compiled in a database (https://doi.org/10.1594/PANGAEA.929968). These variables were selected based on their widespread study among seagrass habitats, and to their usefulness for quantifying seagrass condition across papers with different aims (Short & Coles, 2001). Standardised units (spatially i.e., m^{-2} and temporally i.e., day^{-1}) are reported. Note that data from mesocosm experiments, field experiments with the exception of control sites, or meadows altered by direct anthropogenic disturbances (i.e., aquaculture, anchoring or dredging) were dismissed as these were considered as impacted meadows and were unlikely to reflect meadows in a ‘natural’ condition. Note that seagrass species were recorded following accepted convention as per Short et al. 2011 (e.g., *Zostera capricorni*, *Z. mucronata*, *Z. novazealandica* were named as *Z. muelleri*).

2.2. Seagrass structure, biomass, production and reproduction variables

The 11 variables extracted from the peer-reviewed literature were classified within three categories: seagrass meadow structure (three variables), biomass (three variables) and production (five variables).

- Seagrass meadow structure: percent cover (%), shoot density (no. shoots m^{-2}), leaf density (no. leaves m^{-2}).
- Seagrass biomass: above-ground biomass dry weight (DW) (g DW m^{-2}), below-ground biomass (g DW m^{-2}) and total biomass (g DW m^{-2}).
- Seagrass production: shoot production (g DW m^{-2} day^{-1}), leaf production (g DW m^{-2} day^{-1}), and above-ground production (g DW m^{-2} day^{-1}), below-ground production (g DW m^{-2} day^{-1}) and total production (g DW m^{-2} day^{-1}).

For all these 11 variables, relevant data points were extracted from results text, tables and when appropriate from figures using a web based tool that allow the extraction of data from plots, images and maps (WebPlotDigitazer: https://automeris.io/WebPlotDigitizer/). Datapoint in an individual row can be a mean of multiple replicates or a single unique measurement point for that variable and location. Other relevant spatial and site information was also extracted including the latitude and longitude (decimal degrees), seagrass bioregion according to Short et al. 2007 (Fig. 1), geotype (coastal or estuarine geomorphology), seagrass genera, the year of sampling when reported, and the doi of the publication containing the data. When sampling site coordinates were not reported in the publication, study location maps were consulted if applicable and corresponding coordinates estimated using *Google Earth*. Similarly, geotype was classified as estuarine if the study site was on close proximity to riverine input or within a coastal lagoon, conversely if there were no rivers nearby or the study site was located within an embayment then it was considered coastal. If publications included data on above-ground biomass and below-ground biomass for the same study site, these two values were summed to estimate a value of total seagrass biomass. Publications that reported growth or production expressed as grams of carbon were excluded. When sampling was conducted over multiple years, the year of sampling was left blank and not reported in the dataset.

The seagrass natural history information reported and the way it was reported has evolved during the 45 years of research compiled. Overall, early publications provided comprehensive details regarding meadow structure and production, while sampling procedures were not clearly described. Later on, the sampling strategies and data reporting became more standardized and comprehensive.

2.3 Statistical analyses

Descriptive parameters (e.g., count of data and publications, minimum, maximum and median values) for all 11 variables were compiled. Median values are reported instead of mean values because the data for most of the variables studied is not normally distributed. Boxplots for four key variables sorted by bioregion and genera were produced in R using the ggplot2 package (Wickham, 2016) (version 4.0.1, R Core Team 2020). In order to spatially illustrate the dataset, maps were also created in R, using the leaflet package (Graul, 2016).

3 Results and discussion

The highest number of data points were collected in year 2018, while the lowest occurred in 1975 (Fig. 2). Overall, all data categories were represented well over time (1972–2020), with biomass data present in the majority of papers consistently over time, meadow structure data encompassing a larger proportion of data over the last decade, and production data being the least studied category. Data was extracted from a total 390 peer-reviewed publications, with 66% of the studies conducted in coastal marine areas (n = 263), 32% conducted in estuarine areas (n = 120), and 7 studies conducted in both coastal and estuarine areas (2%).

3.2 Spatial distribution of seagrass data

The seagrass database includes information collected across 11 variables on seagrass structure, biomass and production from all 12 seagrass genera described to date, spanning all continents except Antarctica (Fig. 3). Based on the count of data, the top five most studied genera making up to 84% of the database were *Zostera* (n = 5,736), *Thalassia* (n = 2,081), *Cymodocea* (n = 1,456), *Halodule* (n = 1,416) and *Halophila* (n = 1,343). The least studied genera were *Amphibolis* (n = 86), *Thalassodendron* (n = 115), and *Phyllospadix* (n = 126). The predominance of *Zostera* data could be related to their broad global distribution, including European countries which were the pioneers of seagrass science, while the least studied genera are more geographically restricted (Fig. 3). The bioregion with highest number of data was the Tropical Indo Pacific (n = 3,612), which also included 10 of the 12 genera, illustrating the seagrass biodiversity of this bioregion. The number of data across the Temperate North Pacific (n = 2,121; four genera), Mediterranean (n = 1,965; five genera), Temperate North Atlantic (n = 1,837; five genera), Temperate Southern (n = 1,790; seven genera), and Tropical Atlantic (n = 2,946; six genera) bioregions was similar. There was up to 67-fold difference between the most and least studied seagrass genera, but only a 2-fold difference between bioregions. Overall, data for the production category was the least reported (n = 1,536; 11%) followed by structure (n = 4,643; 32%), whereas biomass variable types were the most reported (n = 8,092; 57%) (Fig. 4).

3.3 Variability in seagrass data among variables

The dataset compiled includes data on shoot density (n = 3,212), percent cover (n = 1,285), leaf density (n = 146), above-ground biomass (n = 3,389), below-ground biomass, (n = 2,008), total biomass (n = 2,695), shoot production (n = 151), leaf production (n = 737), above-ground production (n = 265), below-ground production (n = 125) and total production (n = 258). Across all dataset, shoot density ranged from 0.08 to 28,682 shoots m^{-2} (median = 675), percent cover from 0.3 to 100% (median = 33), leaf density from 5.1 to 48,978 leaves m^{-2} (median = 3,287), above-ground biomass from 0.01 to 1,509 g DW m^{-2} (median = 52), below-ground biomass from 0.03 to 5,635 g DW m^{-2} (median = 69), total biomass from 0.01 to 3,393 g DW m^{-2} (median = 134), shoot production from 0.001 to 24 g DW m^{-2} day^{-1} (median = 0.34), leaf production from 0.001 to 165 g DW m^{-2} day^{-1} (median = 1.5), above-ground production from 0.001 to 23 g DW m^{-2} day^{-1} (median = 1.5), below-ground production from 0.015 to 34 g DW m^{-2} day^{-1} (median = 1.3) and total production from 0.002 to 39 g DW m^{-2} day^{-1} (median = 2.5).

There was high variability in most variables using pooled data across bioregions and genera, and in the amount of data for each variable across bioregion, geotype and genera (Table 1). The values of some variables varied substantially across the six bioregions (Fig. 5). Median total biomass was highest in the Mediterranean bioregion (283 g DW m^{-2}), while the lowest was in the Tropical Indo Pacific bioregion

(61 g DW m^{-2}). The highest median shoot density values were recorded in the Temperate Southern bioregion (967 shoots m^{-2}) and the lowest in the Temperate North Pacific bioregion (466 shoots m^{-2}), whereas the highest median total production values were recorded in the Temperate Southern bioregion (6.6 g DW m^{-2} day^{-1}). Of all genera, total biomass was generally highest for seagrasses with persistent life history stages, such as *Posidonia* and *Enhalus* (Kilminster et al., 2015). *Phyllospadix* had the highest median total biomass (1,056 g DW m^{-2}), followed by *Amphibolis* (845 g DW m^{-2}) (Fig. 6). Median shoot density values were highest for *Phyllospadix* (6,593 shoots m^{-2}) followed by *Halodule* (6,343 shoots m^{-2}). Total production was highest for *Phyllospadix* (median 22 g DW m^{-2} day^{-1}), followed by *Syringodium* (median 9.3 g DW m^{-2} day^{-1}).

3.4 Significant gaps

This global collation of seagrass data has illustrated some gaps in our collective peer-reviewed knowledge. Across seagrass' worldwide distribution, limited peer-reviewed data were found for the eastern Mediterranean, and the coastlines of South America and Africa. Data for some seagrass variables were spatially depauperate, such as seagrass production at high latitudes (<50°N and S), including the Temperate North Atlantic. Overall, seagrass production variables were the least reported. When considering data among seagrass genera, the least studied were *Amphibolis* (n = 86), *Thalassodendron* (n = 115), and *Phyllospadix* (n = 126), with gaps in most variables.

4 Conclusions

This database encompassing peer-reviewed data collected over the last 48 years provides an overview of seagrass distribution, biomass, production and structure on a global scale. The top five most prevalent studied genera encompassing 84% of data were *Zostera* (mostly from the Temperate North Pacific), *Thalassia and Halodule* (Tropical Atlantic), *Cymodocea* and *Halophila* (Tropical Indo Pacific and Mediterranean), and the least studied genera *Amphibolis*, *Thalassodendron* and *Phyllospadix* (2.3% of data). Data hotspots include the Tropical Indo Pacific bioregion (25% of dataset), whereas the Temperate Southern bioregion had the least amount of data (13% of data). The strengths on seagrass natural history knowledge focus on seagrass biomass (57% of data). Our review can inform several research fields beyond seagrass ecology, such as the development of Nature-Based Solutions for climate change mitigation and adaptation and Blue Economy, which include readership interested in blue carbon, engineering, fisheries, global change, conservation and policy.

5 Data availability

Data archived in the data repository PANGAEA (https://doi.pangaea.de/10.1594/PANGAEA.929968) (Strydom et al., 2022)

6 Code availability

R scripts used to generate figures and maps can be found in the supplementary information.

7 Team list

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8 Author contribution

OS conceived the idea. SS and OS lead the project, curated data and wrote the paper. SS, JR, SM, RB, MJH and OS conducted literature searches. SS, RM, KI, CW, NS, CS, SB, AL, CO, CC, CG, CMP, ND, AW, AF, RB, SM, FV, VP, AD, KM, JR, MJH, GH and OS contributed to the manuscript and/or extracted data from papers. SS, CW, RM, CMP and OS wrote scripts and created figures and tables. All authors reviewed the manuscript.

9 Competing interests

The authors declare that they have no conflicting interest.

10 Disclaimer

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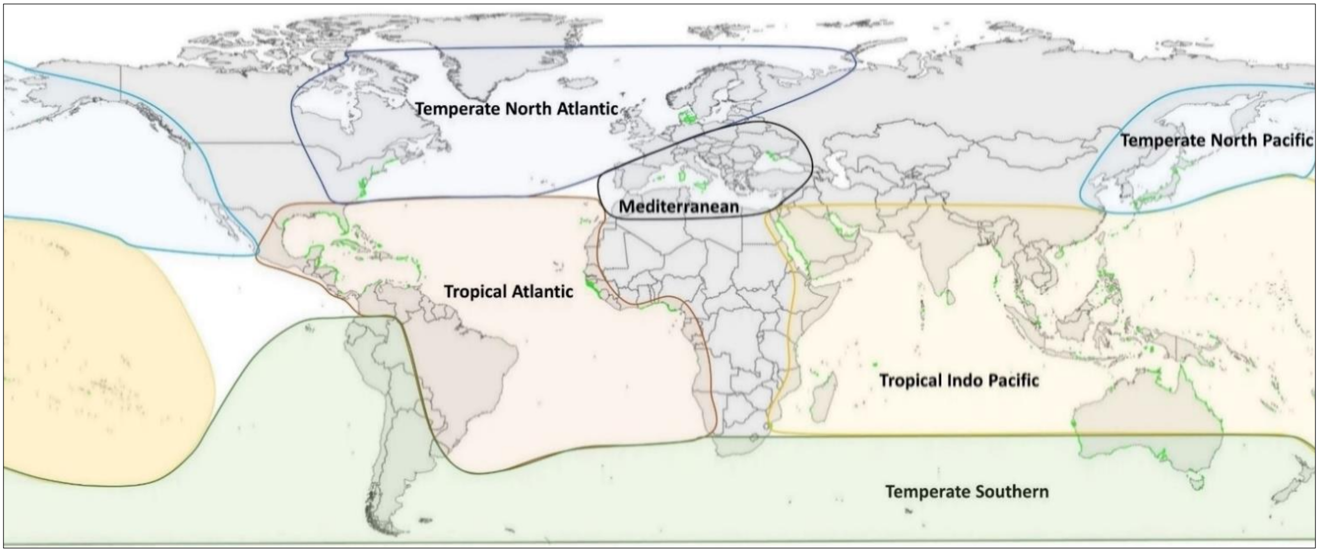

Figure 1. Global distribution of seagrass meadows (green) overlaid within six seagrass bioregions. Seagrass distribution data sourced from UNEP-WCMC & Short, (2018). Seagrass bioregions adapted from Short, Carruthers, Dennison, & Waycott (2007).

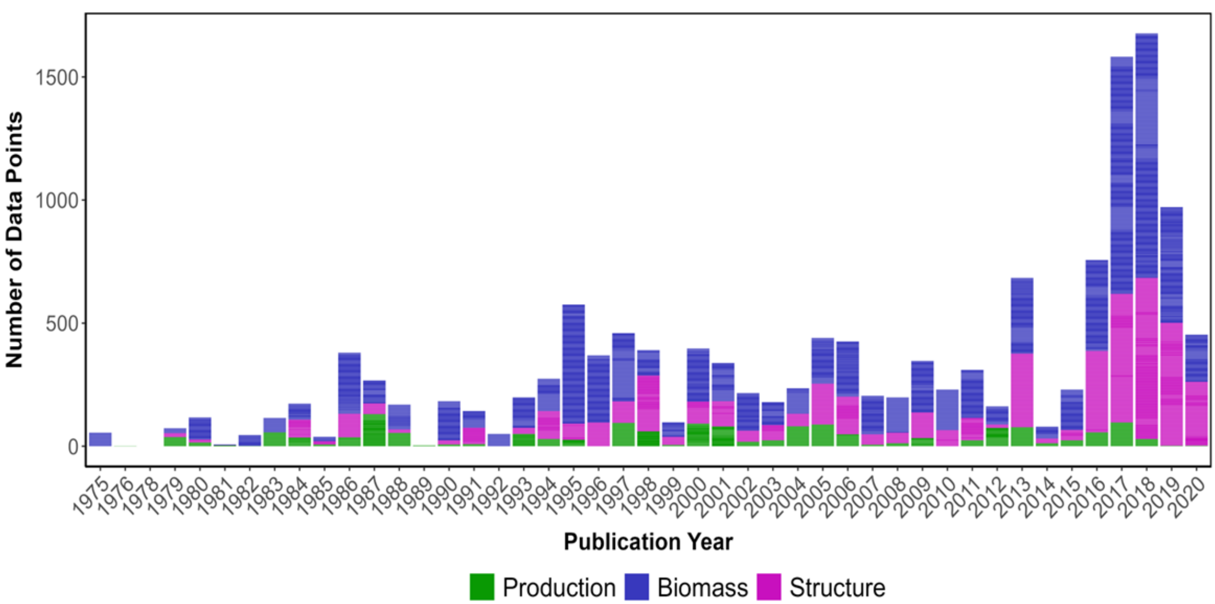

Figure 2. Number of publications that included seagrass data (coloured by type: biomass, structure and production) based on the year of data collection. Data from peer-reviewed publications that did not report the year of sampling, were not included in this figure.

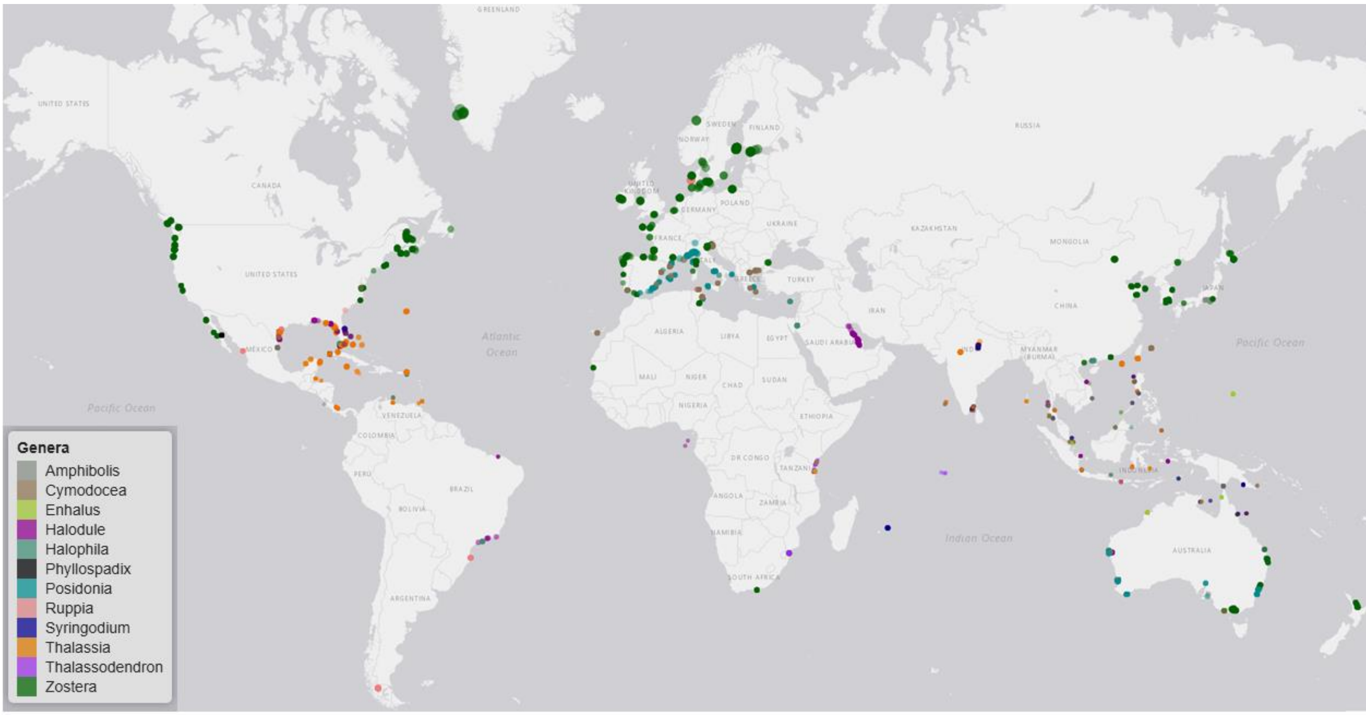

Figure 3. Global distribution map of data on seagrass structure, biomass and production coloured by genera. The coloured points indicate the genera of seagrass studied and where many studies overlap, the colour appears darker than key.

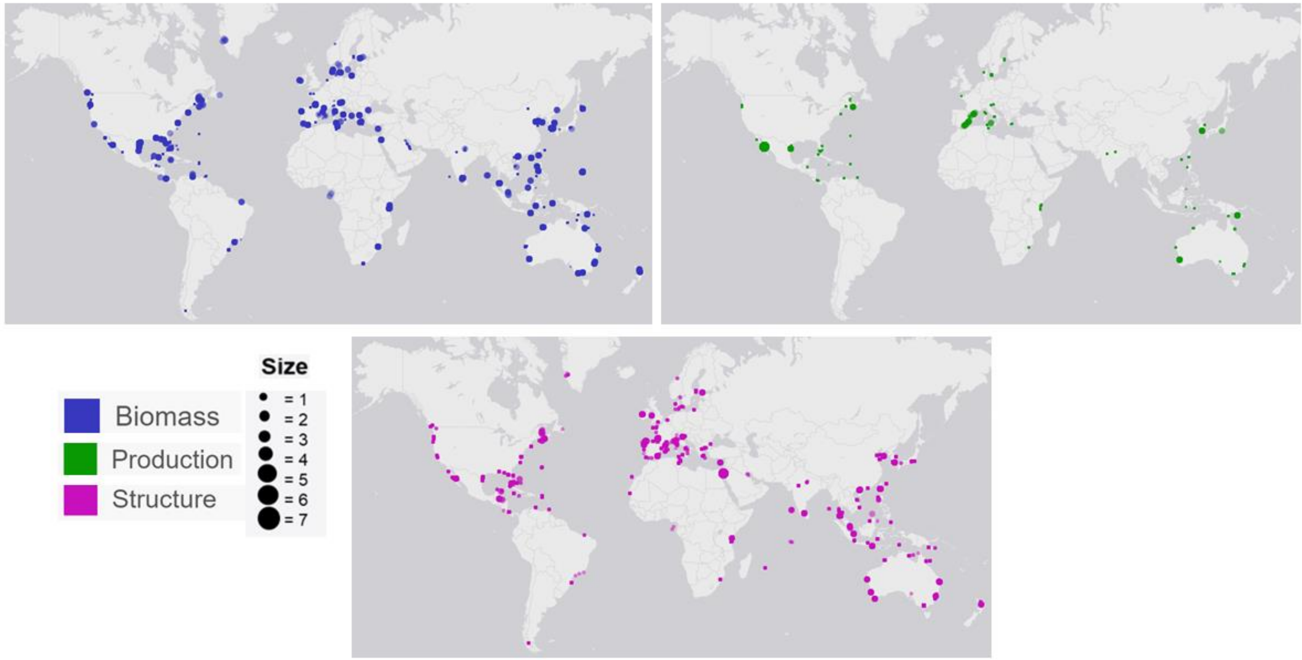

Figure 4. Global distribution map of seagrass study sites labelled as dots. The colours indicate the data type (biomass, production and structure), while the size of each dot illustrates the number of data points for each site.

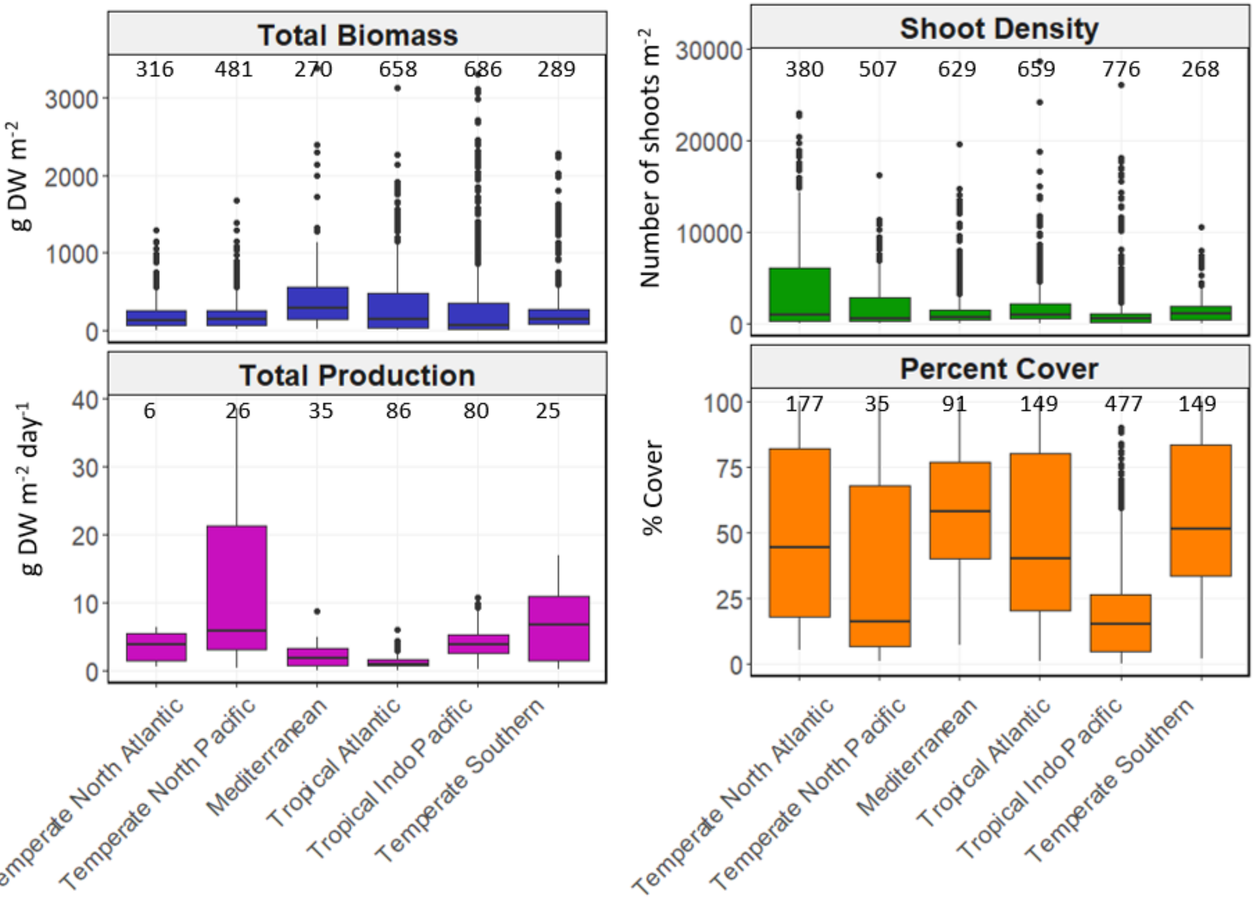

Figure 5. Box whisker plots depicting seagrass total biomass (including above-ground and below-ground biomass; g DW m^{-2}), shoot density (number of shoots m^{-2}), total production (g DW m^{-2} day^{-1}) and percent cover (%) values within each bioregion. The boxplots show the median value (black line within box), 75% and 25% percentiles create the top and bottom of the box and the tails are the maximum and minimum contributions within 1.5 interquartile range. Count of data (N) per bioregion is shown at the top of each whisker.

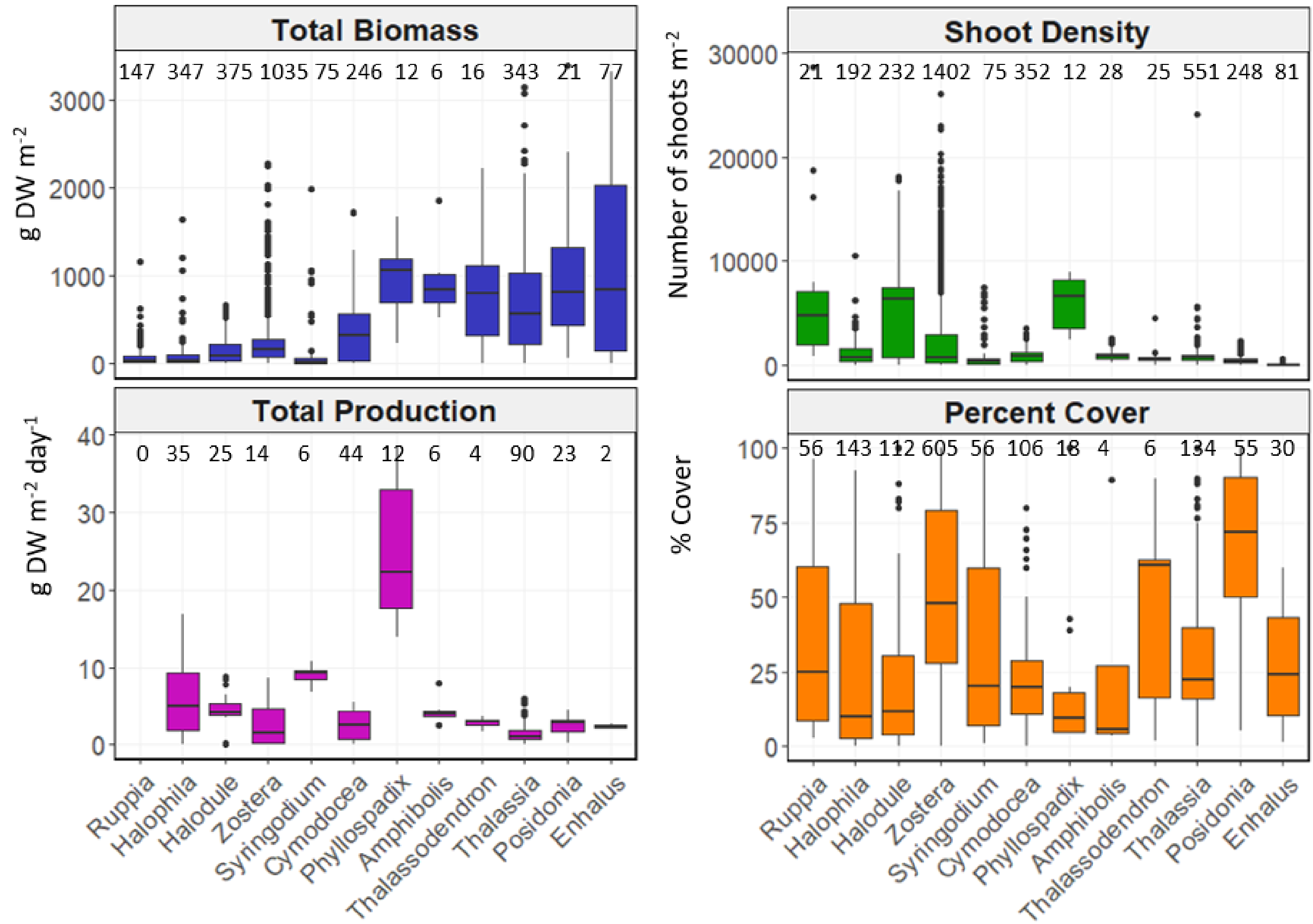

Figure 6. Box whisker plots depicting total biomass (g DW m^{-2}), shoot density (number of shoots m^{-2}), total net primary production (g DW m^{-2} day^{-1}) and percent cover (%) values per genera. The boxplots show the median value (black line within box), 75% and 25% percentiles create the top and bottom of the box and the tails are the maximum and minimum contributions within 1.5 interquartile range. Count of data (N) per bioregion is shown at the top of each whisker.

Table 1. Summary table outlining the count of data for each of the 15 seagrass variables based on bioregion, geotype and genera categorical variables. Above-ground biomass (AG), below-ground biomass (BG), total biomass (TB), shoot density (ShD), leaf density (LD), percent cover (Cov), above-ground production (AGP), below-ground production (BGP), total production (TP), shoot production (SP) and leaf production (LP).

Bioregion	**Geotype**	**Genera**	**AG**	**BG**	**TB**	**ShD**	**LD**	**Cov**	**AGP**	**BGP**	**TP**	**SP**	**LP**
Mediterranean	Coastal	*Cymodocea*	137	97	113	166	4	12	12	4	15		99
		Halophila	16	16	16	24	16	12					
		Posidonia	37	17	21	136	27	5	7	21	17	12	46
		Zostera	87	20	33	145	9	24			3		27
	Estuarine	*Cymodocea*	24	24	24	24			12				12
		Posidonia	6										
		Ruppia	10	1	3								
		Zostera	80	63	60	134	35						
Temperate North Atlantic	Coastal	*Halodule*					3						
		Thalassia	6	6	6	8							
		Zostera	91	51	63	83	42	6	24	23			29
	Estuarine	*Cymodocea*	5	5	5	5							
		Ruppia	26	26	26		7						
		Zostera	315	222	216	284	125	12	14	6	6	58	33
Temperate North Pacific	Coastal	*Halophila*	23	23	42	25			13	13	13		
		Phyllospadix	12	12	12	12	18		12	12	12	12	12
		Zostera	216	173	236	299	17	27		1	1		100
	Estuarine	*Ruppia*	6			5							
		Zostera	171	132	191	166		15	11				76
Temperate Southern	Coastal	*Amphibolis*	14		1	18		1	1				
		Cymodocea	2	2	2	2					2		

		Halodule	2	2	2	2					2		
		Halophila				3							
		Posidonia	125			59	24	8	9			1	11
		Zostera	2	2	2	2	19				2		
	Estuarine	*Halophila*	127	127	127		1		7	7	19		1
		Posidonia				40							37
		Ruppia	8	8	19	5							
		Zostera	186	93	136	137	322		55			2	2
Tropical Atlantic	Coastal	*Halodule*	90	90	86	45	16		18				1
		Halophila	12	9	47	21	1				3		
		Ruppia	42	42	42		19						
		Syringodium	14	3	22	12	2						1
		Thalassia	171	100	169	346	22		56	20	82	9	30
		Zostera	3	3	3		6					24	24
	Estuarine	*Halodule*	136	137	131	108	26						
		Halophila			3		2						
		Ruppia	58	52	57	11		14					
		Syringodium	11	13	8	5	25						5
		Thalassia	60	35	47	33	30				1		33
		Zostera	43	13	40	78						25	
Tropical Indo Pacific	Coastal	*Amphibolis*	16		5	10	4	5	5		6		
		Cymodocea	163	44	100	141	101		2	10	25	2	34
		Enhalus	119	61	66	78	28		1		2		18
		Halodule	95	46	129	65	55		1	1	18	1	23
		Halophila	139	74	88	96	100	1	3	1			
		Posidonia	6			13	4				6		
		Syringodium	52	17	43	55	29			6	6		7
		Thalassia	285	87	117	152	78		1		7	1	63
		Thalassodendron	29	13	14	23	6		1		4		11
		Zostera	68	10	13	6	20	4				1	
	Estuarine	*Cymodocea*	5	2	2	14					2		
		Enhalus	3		11	3	2						
		Halodule	17	17	27	11	11				2		

	Halophila	6	6	21	21	18						
	Syringodium	1			1							
	Thalassia	2	2	4	10	2						
	Thalassodendron	2	3	2	2						3	2
	Zostera	7	7	42	68	9				2		
Total # data		**3389**	**2008**	**2695**	**3212**	**1285**	**146**	**265**	**125**	**258**	**151**	**737**