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Herbicide Impact on Seagrass Communities

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Additional information is available at the end of the chapter

<http://dx.doi.org/10.5772/55973>

1. Introduction

Anthropogenic chemical contamination is of concern due to the continuous decline of ecosystems. Pesticide use impacts whole environmental matrices, especially aquatic ones, because of collecting watershed pollution in streams, rivers, and finally coastal areas. The coastal environment is one of the most vulnerable: global changes (current sea level rising, ocean acidification, global warming) add to land use disruption (soil erosion, chemical uses, urban sprawl) in coastline areas. Moreover, population growth mainly affects this endangered environment because of rural flight and city growth –75% of billions of human beings will live in 100km-large belt around global seas in 2035 [1] imposing urban lifestyle demands. Environmental stress due to such a heterogeneous population repartition will be acute (1) on freshwater, in order to provide it for drinking, industrial and agricultural needs, and (2) on coastal ecosystems because of waste waters and coastline management. Such environmental concerns are critical for tropical countries because of some that are being discovered to be biodiversity hot spots [2].

Human impact is partly due to pesticide use [3-5]. In order to feed a growing population and to manage urban areas, herbicides are often used profusely [6]. These herbicides affect wild fauna and flora through improper use, inefficient (even lack of) wastewater treatment plant effluents or the direct input of herbicide contained by sewage sludge into aquatic environments [7]. For hydrophobic pesticides, contaminated solid phases transfer downstream, in an erosive context due to deforestation and agricultural intensification is involved [8].

Thus, herbicides will contaminate coastal environments [9-10]. In shallow water, such residues will expose remarkable biocoenosis, especially in tropical contexts, because of conserved biodiversity compared to temperate ones, i.e. exposed for decades to aquatic pollution from developed countries' activities.

Considering such shallow waters, herbicides could influence seagrasses. Such tracheophyte flowering plants are the result of terrestrial grass adaptation to marine environments. These monocotyledons colonize shallow water bottoms, especially in silty-sandy substrata because of roots, unlike bryophytes and algae. Thus, in opposition to those non-tracheophyte ones, seagrass meadows could limit sediment erosion and stabilise navigation channels.

2. Seagrasses: Unique origin, physiology and performances

Seagrass is a taxonomic group of about 60 species worldwide likely evolving from a single monocotyledonous flowering plant ancestor (70-100 million years ago), divided into three independent lineages: Hydrocharitaceae, Cymodoceaceae and Zosteraceae [11]. Seagrass species have strong physiological similitude and low interspecies diversity.

As flowering plants, they are anchored in sediments by their roots –what non-tracheophyte marine plant species don't have. Notwithstanding, seagrass only live in submarine environments, even for pollination or other critical steps, unlike other aquatic flowering plants who should use an emerged organ or pass by a terrestrial stage [12]. Seagrasses have some of the highest light requirements (25% of incident radiation when 1% is the average requirement of angiosperm species [13]) even if epidermal chloroplast and internal gas transport systems have been developed, in order to maintain oxidative conditions, despite highly reducing sediment, including toxic sulphide levels, for large amounts of non-photosynthetic tissues [14]. Seagrasses are especially vulnerable to lack of light, mainly due to erosion or eutrophication.

While algae, whose growth is proportioned to the eutrophication level and thus could lead to a dystrophic crisis due to algal necromass decomposition, seagrass growth biomass is sustainable. Seagrass bed increase due to nutrient input makes seagrass meadows, for carbon trapping and storing [15], like corn or sugar cane, among the most efficient trapping plants [16]. Seagrass meadows are a more efficient carbon sink than trees: with an equivalent carbon sequestration per year (about 27 million tons [17]), carbon sequestered in meadows will be buried and therefore partly avoid decomposition in the mat [18]; Pergent et al. [19] estimated this stored amount about a third of the primary production. Living seagrass biomass actually reaches 19.9 billion tons [17].

Moreover, to this biomass should be added suspended matters that seagrass leaves could efficiently sequester because of the blade effect on suspended matter, i.e. acting like a mat, trapping suspended matter and inherent organic matter, and because seagrass decomposition is too long for inducing dead zones [12]. Seagrass blades could drift to the abyss where they are an indispensable carbon contribution for poor-carbon deep sea biocoenosis [20].

Seagrass could be susceptible to exondation because of tides. Such events could be fatal depending on shore temperature. Temperatures of 35°C and greater, not found in the marine environment but possible in pools or during extreme low tide coefficient, could kill seagrass [21, 22] because of photosynthesis interruption; irreparable structural alterations to the PhotoSystem II (PSII) reaction centres induce chloroplast dysfunction, leading the plants to insufficiently jugulate of the reductive conditions in roots.

As marine species, seagrasses are vulnerable to low salinity events and cannot colonize upstream estuaries and freshwater shallows. A 5‰ salinity is the smallest salinity amount compatible with seagrass development (Iversen, 1931 cited by Vermaat et al. [23];[24-26]), whereas seagrass communities can stand waters which are more salty than the global ocean salinity (35‰): Depending on species, seagrasses could stand a salty environment up to 42‰ [27]. Euryhaline seagrass species, i.e. large scale salinity ones, colonize all the climatic areas except polar ones. But, in all of them, these remarkable adaptations are balanced by severe seagrass meadow regression.

3. Seagrass meadows repartition and involved landscape

Seagrasses are present in all the marine ecotones, except polar ones ([28]; Figures 1 and 2).

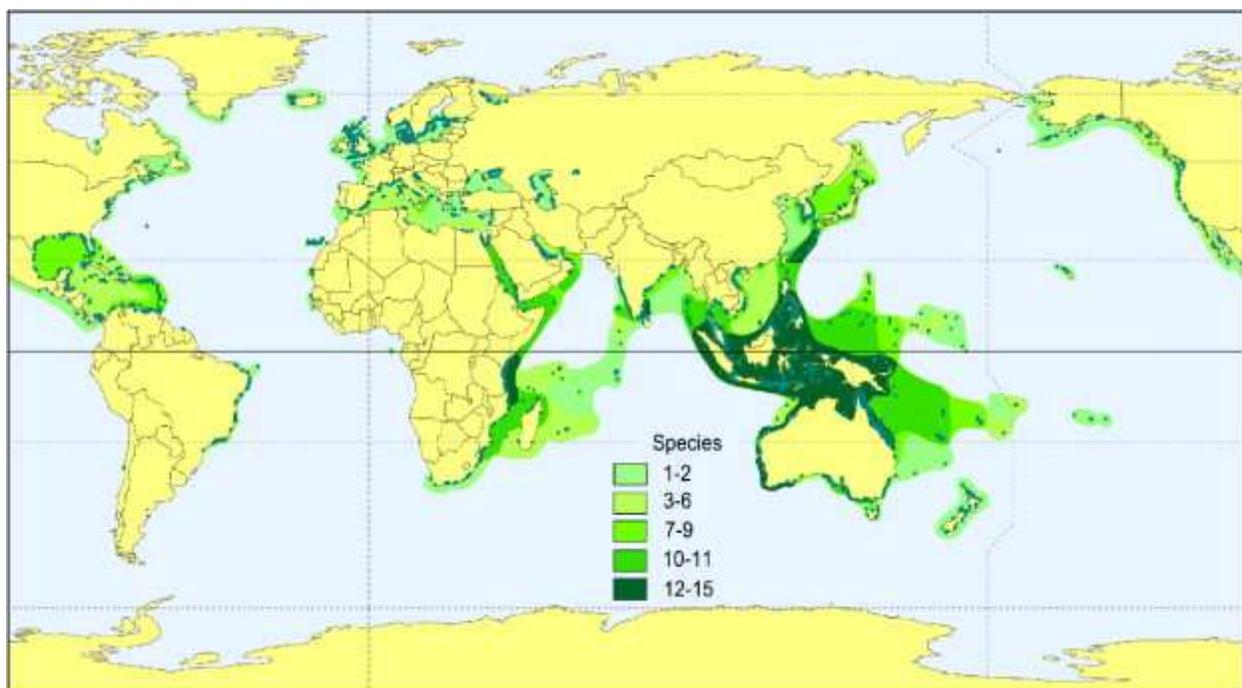


Figure 1. Global seagrass diversity and distribution. Shades of green indicate numbers of species reported for an area; blue points and polygons indicate documented reports of seagrass occurrence (from 2005 UNEP-WCMC).

Temperate areas are marked by seasons with different temperatures, light and precipitation regimes. Land and sea weathers provide extreme wind and flow conditions. Nutrient inputs occur by pulses which seagrass meadows must cope with [29]. Seagrass meadows will consume nutrients in perennial vegetative growth, limiting eutrophication conditions [30].

Ecosystems including seagrasses are listed in Figure 3. In temperate marine water, seagrasses are associated with marshes and kelp beds, and have been providing for centuries ecosystem services to coastal lands [31]. Human use of kelp began as picking fodder, fertilizer –even organic matter- and food on shore. During the late modern time period, dried kelp was used

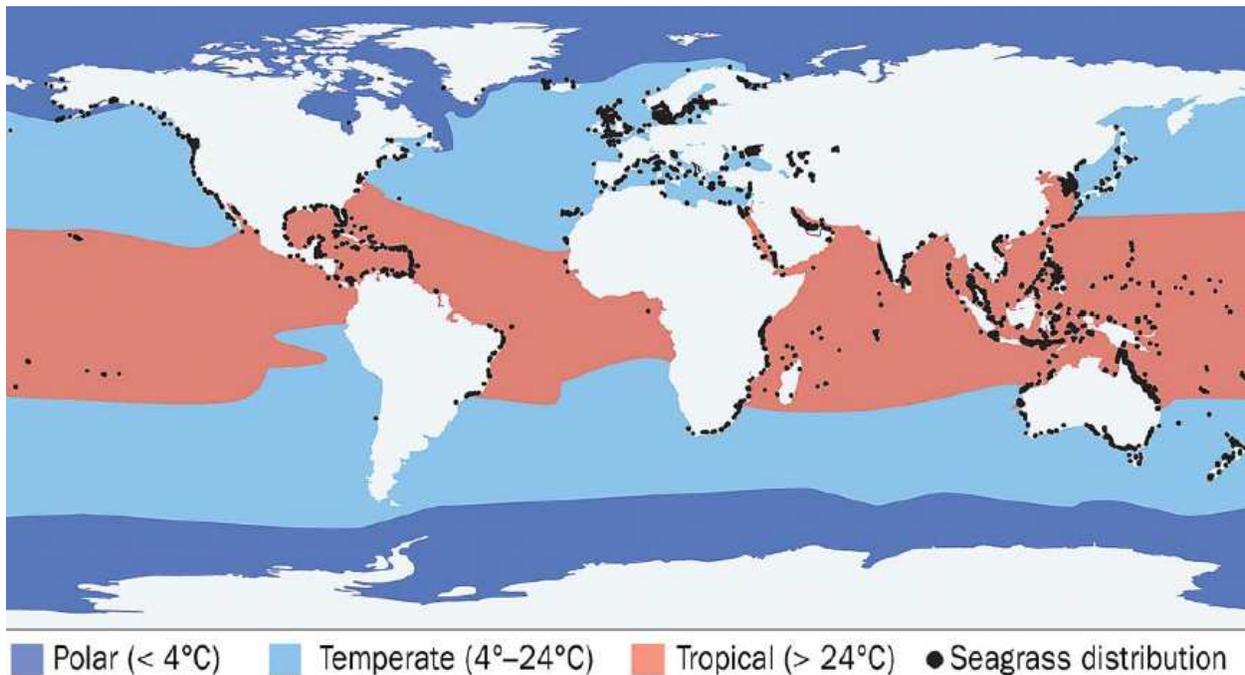


Figure 2. Current global distribution of seagrass in relation to mean ocean temperature. Regional divisions are based on polar (<4 degrees Celsius [°C]), temperate (4°C–24°C), and tropical (>24°C) climate [52].

in order to provide “non-caustic” or “commercial” soda (in fact, sodium carbonate Na_2CO_3) for early industries (glass, photograph, soap, etc.). Seagrass meadows are colonizing near-shore environment mixing or not with seaweeds, i.e. seagrasses mainly settle on movable substrata where their roots could anchor them and seaweeds only settle on hard substrata (rocks or shingles) needed by their basal adhesive organ. Seaweeds are sessile, macroscopic, benthic and multi-cellular algae [32] constituting a polyphyletic community. Seagrass meadows and seaweeds live in adjacent environments and could marginally be in competition. However, the relationship between them does not present the same cooperative side as in tropical areas.

In tropical areas, marine seagrasses are associated with preserved triptych mangrove-meadows-corals [33]: (1) Mangrove stabilises and protects the coastline, limits sediment input in marine environments and holds tidal biodiversity [34]; (2) seagrass meadows, because of blades and roots, limits current movements, enhances suspended particular matter deposition, provides food for endangered species like sea turtles and manatees [35]; (3) coral reefs protect the shore from waves, acting like living breakwater, an especially acute property in tropical areas subjected to typhoons and tsunamis [36]. Triptych partners have a mutual service relationship, i.e. corals are vulnerable to sedimentation limited by mangroves, which are vulnerable to large waves buffered by coral reefs. Moreover, each partner has a nursing role for marine species [37, 38]: for example, considering the eastern area of the Caribbean Sea, 80% of fisheries are located in mangrove, meadow or coral areas for juvenile stages [39]. However, significant landscapes of corresponding environments are limited to some French West Indies bays, exposed to land speculation. Thus, because each triptych partner has its own vulnera-

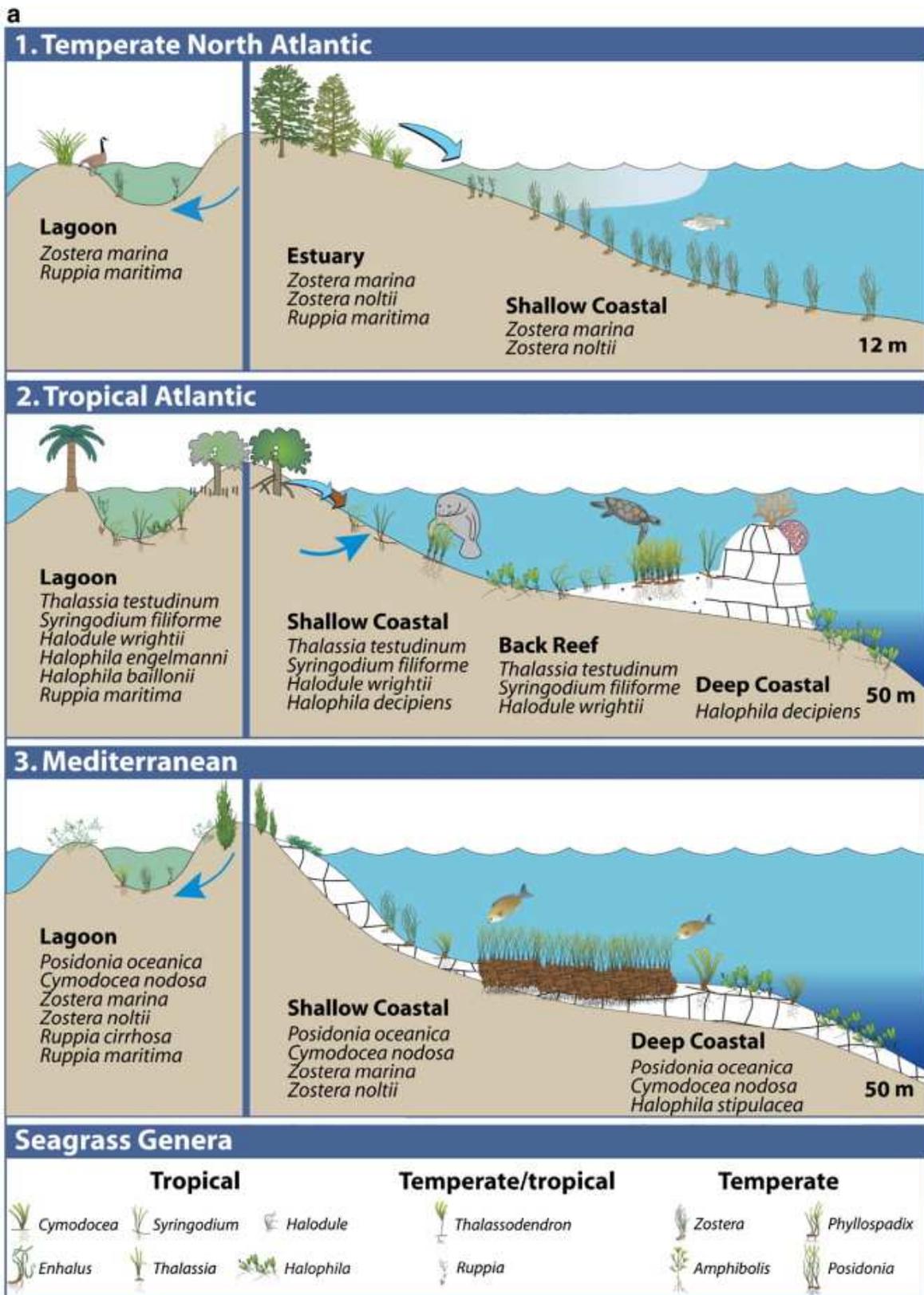


Figure 3. Seagrass habitat diagrams for (a) Bioregions 1–3 and (b) Bioregions 4–6. Major species for each bioregion listed according to dominance within habitats. Maximum reported depths [113].

bilities, this ecosystemic symbiosis is acutely vulnerable; if mangroves are largely unaffected by water quality [40], seagrass meadows are highly susceptible to chemical inputs [12] when corals are mainly sensitive to herbicides because of endosymbiosis [41], i.e. corals include algal symbionts which are highly vulnerable to PSII herbicides, in a few minutes and for ng/L contamination range [42]. The Achilles' heel of each ecological partner endangers the whole ecosystem equilibrium.

Notwithstanding ecological and fishery services, rendered in tropical and temperate zones, seagrass meadows support the detrital food web, perpetuates navigation supports, and have a key position considering carbon and nutrient cycles. Each seagrass annual services have been estimated between \$9,000 and \$28,000 per acre [43] –globally \$1.9 trillion per year by Watson et al. [44] describing seagrass meadows as constituting an endangered capital.

4. Seagrass: The silent fall

Indeed, because of local triptych disruption due to anthropogenic needs or airiness in tropical areas or due to the global environmental decline, seagrass meadows are threatened (Figure 4). All over the world, this unique biocoenosis is regressing; during the last decade, between 20 and 100% in the Gulf of Mexico, depending on the coastal zone, 85% in Florida, 40% in the bay of Arcachon [45], an accelerating loss process [28] leading to an evaluated total loss since 1980 of about 30% of global seagrass meadows, i.e. at the same scale as mangrove regression ($-1.8\% \text{ yr}^{-1}$ [46]). Thus, seagrass meadows are more endangered than the tropical rain forest (-0.5 yr^{-1} [47]) and as precious as it for carbon storage (cf. *supra*). Mangrove and seagrass regression undermine coral reefs, more sensitive to the seagrass meadows' regression and sensitive to another threats (-0.72 to $-9\% \text{ yr}^{-1}$ [48-50]). Each year, about 177,000 km² of seagrass meadows, i.e. 1.5% of global seagrass meadows (Ibid.), are lost –about 299 million tonnes of carbon trapped [12].

Worldwide seagrass meadow loss is not balanced by seeding or planting campaigns. First, restoration scales are largely smaller than the seagrass meadows loss; most of them are <1 ha because of costs –even if restoration cost is still less expensive than seagrass loss consequences themselves. Secondly, restoration success rate is low: about 30% [51] or more [52] –but some seagrass species are not transplantable [51] leading them to a more acute endangered situation in lineage, vulnerable because of poor genetic diversity [53]. But restoration initiatives are induced by information about seagrass loss and its consequences. Actually, information lacks in order to know the impact of seagrass meadow fragmentation; such interconnectivity loss is due to human activity because of the declining chemical quality of seawater as well as to building or coastline management [54].

Notwithstanding the alarming situation and issues, the publication rate about seagrass meadow loss remains low; the actual increase of publication numbers and quality about this concern should be proportioned to the global ocean crisis. Mangrove, salt marsh, and coral reefs, in particular, have are three- to one hundred-fold more publications than seagrass

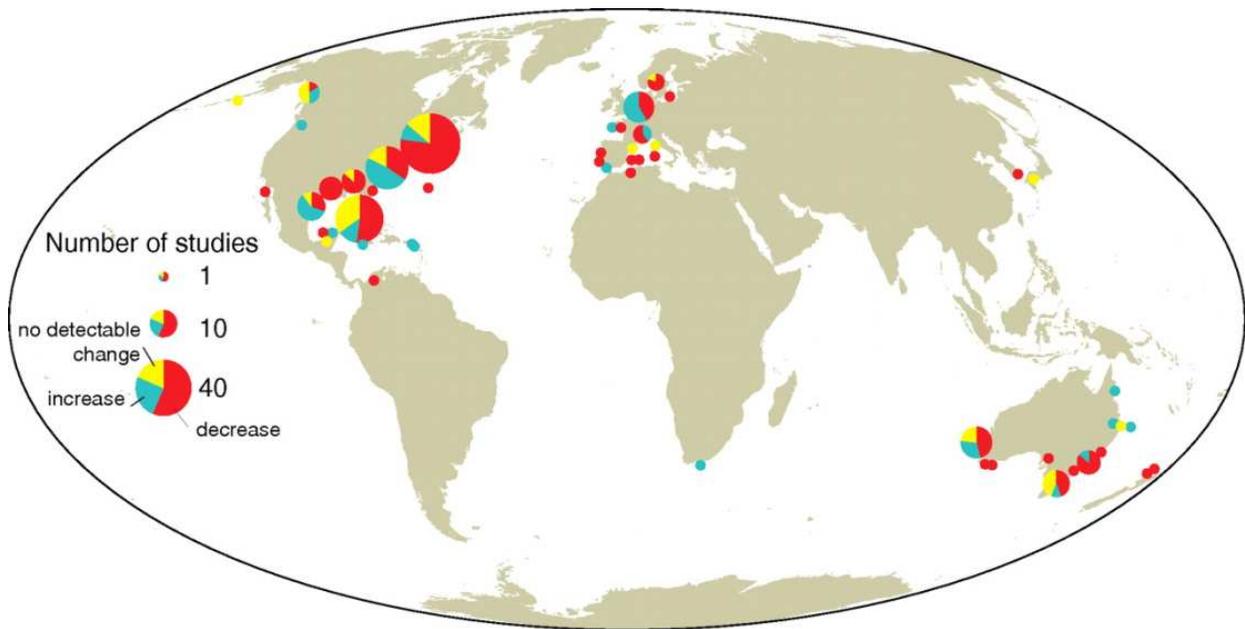


Figure 4. Global map indicating changes in seagrass area plotted by coastline regions. Changes in seagrass areal extent at each site are defined as declining (red) or increasing (green) when areal extent changed by >10%, or no detectable change (yellow) when final area was within $\pm 10\%$ of the initial area. There were 131 sites in North America, 34 sites in Europe, and 40 sites in Australia [28].

meadows [12] even though estimated monetary value of seagrass meadows is more than two-fold more important than mangrove or marshes, and four-fold more than coral reefs [43].

The seagrass loss origin is actually unknown. First of all because, due to perennial growth of seagrass meadows, environmental disease impact is more obviously observed than for other marine plants, and particularly unicellular organisms. Moreover, because of the macroscopic size of seagrass specimens and their eminent services for the environment and for human activity, seagrass meadow loss critically alters coastal activities [51]. Lastly, seagrass meadow loss reveals a long-term impact on the environment when planktonic or fugacious species providing short-term environmental status; such outcomes need high-frequency monitoring for a valuable putting into perspective. Orth et al. [12] defined seagrass as “coastal canaries”.

5. Predominant pesticide effects applied to seagrass physiology

Chemical content in seawater is directly, but locally, altered by port uses, i.e. antifouling coatings and urban pesticide uses, and indirectly, but globally, altered by agricultural and urban chemical input due to landscape runoff and subsequent river pollution [55] and when groundwater tables well up through the soil directly at the sea (phenomenon known as Submarine Groundwater Discharge [56]). Their terrestrial impact is well known, as on soils, then on groundwater, surface water [3], sediments [57], biota [4] and human health [58].

Vulnerability of aquatic environments to organic chemicals, and especially pesticides, has been asserted for decades. In many countries, pesticide monitoring is performed for groundwater,

often in order to ensure drinking water, as well as for surface water. Incidentally, it is possible to determine the most frequently used herbicides. According to Gilliom [3] for the U.S.A. and to Schäfer et al. [4] in the European Union, 21 herbicides could be identified as being the most frequently used in developed countries, leading them to probably being significantly used in developing ones (Table 1). Haynes et al. [59-61] consider diuron as the most threatening herbicide, even pesticide, for seagrass meadows, partnering the corals of the Great Barrier Reef. However, aquatic plant toxicology is not well-known: BCPC [62] only informs us about two aquatic plant toxicological tests: EC50 (120h) for diuron on *Selenastrum capricornutum* (0.002mg/L) and atrazine EC50 (96h) for *S. capricornutum* (0.01mg/L). Lewis & Devereux [55] provided the first review on non-nutrient anthropogenic chemicals in seagrass ecosystems, summarizing all publications on seagrass –and finding only ten on herbicide impact on seagrass.

	Solubility	Koc	Kow	Application	Effects/metabolic target	Notes
glyphosate	10500		-3.2 (1)	2	block EPSPS-catabolic crossroad for proteins	Very easily complexed
diuron	37.4	400	2.85	6-30 (10-30 total)	PSII, especially on dichotyledons	DT50: 50-180d depending to humidity Hill et al., 1955
atrazine	33		2.5	1,5	PSII, especially on dichotyledons	
simazine	6.2 (1)	103-277: 160	2,1	1,5 (3 tropical)	PSII	
prometon	750		2.69	10-20	PSII	
amitrole	26000 pH7-c; "/>1384000 d		-0.969 (2)	1-3	triazole	DT90: 15d without anoxia
isoproturon	65		2.5 (1)	1.15	PSII	DT50: 1560d
linuron	63.8 (1)	500-600	3		PSII	DT50: "/>1000d for all pH
metolachlor	488	121-309		1-2,5	PSII	DT50 hydrolysis: "/>200d
S- metolachlor	480	61-369		0.6-1.6	PSII	non hydrolyzable
cyanazine	171			1-3	selectif	
acetochlor	282			3	No definitively known	
metribuzin	1050			0.07-1.45	species-specific; PSII	
bentazone	570 (1)	13.3-176 142	0.77 (a); -0.46; -0.55 (b)	1-2,2	species-specific; PSII	winter herbicide; low hydrolysis but high photolysis
EPTC	375		3.2	4.5-6.7	Inhibit lipid synthesis	

	Solubility	Koc	Kow	Application	Effects/metabolic target	Notes
trifluraline	0.221 (calc) 0.395 (field)	4400-4000 0	483 (1)	0.5-1	microtubule polymerisation inhibition in roots	not hydrolyzable
molinatate	1100	121-252	2.86 (pH7.85-7.94 (2))	2.5-5	lipid synthesis disruption: inhibition germination	Photosensible; no degradation after 2 years); not hydrolyzable
norflurazon	34	218-635	2.45 (pH6,5)	0,5-2		photosensible; high volatilizable; shelf-life: 4 years and more
tebuthiuron	2500 (1)		1,82 (1)	0,6-6,87	PSII	
2,4D	311	60 (calc)	-0.75(sp)	0.28-2.3	synthetic auxin	turns crystal in hard water
bromacil	807a; 700; 1287b		1,88a	1.5-8; 5-15 total	PSII	

Table 1. Summary of properties of the predominant herbicides in Europe [4] and in U.S.A.[3]. Solubility is expressed in mg/L, Koc in mL/g, application in kg/ha. Experimental temperature is 25°C without complementary information: (1): 20°C; (2): 23°C; (3): Experimental pH is 7 without complementary information: a: pH 5; b: pH 9; c: pH 10; d: pH 4. EPSPS: 5-enolpyruvylshikimate-3-phosphate synthase, an enzyme involved in aromatic amino acids phenylalanine, tyrosine and tryptophan biosynthesis. PSII: inhibition of Hill reaction in photosynthetic electron transport. Triazole: probable interference with carotenoid biosynthesis leading to photooxidation of chlorophyll. Sp: 2,4-D Kow: 2.58-2.83 (pH 1); 0.04-0.33 (pH 5); -0.75 (pH 7) Calc: Value obtained by calculation. Total: total weed killing –in order to obtain a bare soil.

Herbicide effects have been summarized by Jurado et al. [63]. The biochemical target of many herbicides is PhotoSystem II (P680), acting in photosynthesis as a photon-electron converting disruptor. More precisely, the inhibition of Hill reaction (photosynthetic electron transport) is performed in A site by triazines, uraciles pyridazines, in B site by ureas. Acylanilides, diphenyl ethers and nitriles inhibit the Hill reaction too. In the 21 predominant herbicides compilation list [3, 4], 11 herbicides uncouple the biochemical cascade in PSII leading to plastoquinone terminal electron acceptor. Instead of this outcome, formation of unmanaged singlet oxygen provokes lesions proportioned to photosynthesis. Biosynthesis of carotenoids, used to manage singlet oxygen, could be a collateral damage facilitating herbicide effects (pyridazines).

On a plant scale, PSII herbicides lead to a more marked leaf yellowing in new leaves than in old ones, i.e. leafs where photosynthesis has been active, and in places of intense photosynthesis i.e. between leaf veins. Such symptomology should impact on shallow water depth seagrass communities and even save seagrass communities in turbid water. However, light provides food for seagrasses [64] like for the other photosynthetic taxa, but it is a way of detoxifying too. Over time, depending on contamination by such herbicides, light conditions favourable to seagrass communities could be limited by (1) minimal photosynthesis needs, especially high for seagrasses in order to confront sediment anaerobic conditions, and (2) lethal photosynthetic induction, due to poisonous singlet oxygen produced by incident radiation. Indeed, seagrasses reach a 25% requirement of incident radiation [65], due to their submarine

adaptation and because of anoxia containment in buried non-photosynthetic tissues [66]. Seagrass incident radiation requirement is to compare with 1% or less of the requirements for other angiosperm species [65]. Seagrasses will physiologically enhance their incident radiation: chloroplast efficiency is modulated for better light capture: adaptation at biochemical level [67] and at organelle scale by conditioning its position in the cell and orientation relatively to the light source [68]. Acting for maximizing photon capture, seagrasses could maximize the risk of lesions due to electron transport alteration by herbicides especially if PSII disruptors mimic a lacks of light because of induced low photosynthetic yield.

The photosynthetic stress hypothesis is strengthened by ten publications (Table 2) observing oxygen production alteration [69-71] and especially oxygen production stimulation for low atrazine concentration (75µg/L) for EC50 at 320µg/L [69]. In the same way (and at same scale, leading to suggest that it is the same phenomenon but with a different descriptor), photosynthesis alteration [72] reaches 120µg/L for immediate (2h) IC50 [42] when pigments, chlorophyll and fluorescence are altered from 10µg/L [73, 74].

Test species	Response parameters	Test duration	Effect concentration (µg/L)	References
<i>Thalassia testudinum</i>	Oxygen production	40h, 88h	320 (EC50)	[71]
<i>Zostera marina</i>	Oxygen production	24h	100i, 1000ti	[70]
<i>Zostera marina</i>	Oxygen production	21-42d	75e, 650i	[69]
<i>Zostera marina</i>	Adenine nucleotides	6h, 21d	10, 100	[76]
	Growth			
	Mortality			
<i>Zostera marina</i>	Growth	10-40d	1900 (first effect, whole plant)	[114]
	Mortality			
	Chlorophyll			
<i>Zostera capricorni</i>	Chlorophyll	10h, 4d (rec)	10, 100	[74]
	Fluorescence			
	Pigments			
<i>Halophila ovalis</i>	Chlorophyll	4d	10	[73]
	Fluorescence			
	Pigments			
<i>Ruppia maritima</i>	Photosynthesis	2h	120 (IC50)	[42]
<i>Ruppia maritima</i>	Growth	35d	2,500, 44,700 (EC50)	[72]
	Photosynthesis			
<i>Halodule wrightii</i>	Growth	22d	10e, 40e, 120e, 420i	[75]

Table 2. Example of toxic effect concentrations reported for atrazine and seagrasses. EC50, IC50 –concentration reducing effect parameter 50% relative to control. rec: recovery; i: inhibition; ti: total inhibition; e: enhancement;

However, some remarks are necessary: (1) like for many environmental monitoring, metrology improvement since decades enhances phenomena perception: concentrations reached 30 years ago could be regarded as overestimated, (2) interspecies heterogeneity could be important: *Halodule wrightii* growth is enhanced at 120µg/L [75] when, at the same concentration *Ruppia maritima* photosynthesis IC50 is reached [42] and *Zostera marina* presents mortalities [76] (3) *Zostera marina* mortalities [76] are noted for concentrations considered as stimulating [69], but in the second case after much more exposition time, (5) the effect is less and recovery is greater *in situ* [74].

Seagrasses are mainly regarded as shadow plants [77]. Indeed, the situation is critical during summer low tides when photoinhibition is a threat. Photoinhibition is defined by Touchette & Burkholder [78] as a reduction in the photosynthetic rate due to other processes such as the toxicological impact of herbicides [79]. Photoinhibition is primarily a photoprotective tool, avoiding PSII excessive photophosphorylation, and dissipating energy as heat [80, 81]. Photoinhibition is obtained by PSII centres rarefaction [81] or inactivation because of D1 protein photolysis surpassing D1 synthesis [80-84] and the increase of xanthophylls cycle's violaxanthin de-epoxidation agent leading to energy dissipation: zeaxanthin. Protein D1 is known to be influenced by ATP in thylakoid lumen; in the case of a lack of ATP production, for example as herbicide impact occurs, seagrass could maintain a high photosynthetic level, initiating a vicious circle leading to the herbicide effect. Such an herbicide trajectory could lead first to photosuppression with excessive UV radiations [85].

The second critical target for seagrass, i.e. especially critical due to aquatic life, is a photorespiration process which is, like for several topics, innovative in the case of seagrasses [78]. Indeed, respiration provides to seagrasses oxidative conditions propitious to life in their partially reductive environment. In order to maintain a redox potential suitable for whole enzymatic activity even in tissues buried into the sediment, seagrasses will actively manage inner gas exchanges. A large part of tissue volume will be due to lacunae or *aerarium*, empty spaces allowing to preserve terrestrial-like conditions for cells, providing oxidative conditions and leaving the leaf erect. Respiration will produce CO₂ for the plant –which will mainly consume its own CO₂ production in order to limit exchanges with external marine environments. Such C3-C4 intermediate plants present, moreover, concentrating carbon systems strengthening ribulose 1,5-bisphosphate carboxylase (Rubisco) in carbon acquisition. 2,4-D photosynthetic pathways are negatively impacted [86], even in micromolar concentrations, by auxin like 2,4-D, leading to up-regulating growth. Because of gas flows to the external environment are more strictly controlled by seagrasses' stomata, which are less numerous than terrestrial plants' ones, auxin-like activity of 2,4-D causes an up - regulation in oxygen production and a subsequent oxygen-inhibition of a key enzyme Rubisco. Lack of carbon-sequestering photosynthetic processes leads to carbon and energy deficits aggravated by messy leaf creation induced by 2,4-D, exhausting the plant, drawing on belowground stocks, and limiting photosynthesis efficiency.

Photorespiration leads to consume O₂ and is considered as protective for photosynthetic electron transport, limiting damage to the photosynthetic apparatus to photo-inactivation during periods of low CO₂ availability and high light intensity [87]. Rates of photorespiration

activity are considerably lower in most submersed aquatic plants than in terrestrial ones [78]; if O₂ depletion is too great, anaerobic conditions rule: Krebs cycle's NAD⁺ reduction, leading to energy storage in mitochondria by NADH production driving ATP synthesis, is interrupted. NADH accumulates and NAD⁺ lacks for critical metabolic processes [88]. Parenthetically, pyruvate is metabolized, leading to fermentation (Davies, 1980) and alcohol content increases, altering whole tissues and thus removing the main obstacle to reductive conditions which are unfit for seagrass life.

Unlike photosynthesis which increases with temperature up to 5–10°C above ambient, respiration rates continue to increase with increasing temperatures in excess of 40°C [78, 89-91]. Light, then depth [92] can also significantly influence respiration; water-column nitrate enrichment tissue NR activity enhances respiration rates in *Z. marina* [93].

6. *In situ*: Chemical cocktail, interaction with metals and temperature increase

If Lewis & Devereux [55] rightly indicated that seagrass are quite non-sensitive to herbicides, based on scientific literature showing the high herbicide concentration reached in order to observe seagrass alteration *in vitro* (Table 2), such results *ex situ* should be weighted by monitoring results, showing everywhere a variegated contamination in space, in time and, moreover, in impact. In the same way, limited impact of herbicides and organic chemicals is mentioned by Waycott et al. [94].

Seagrass meadow contamination by herbicides is well known, as from rivers, as from anti-fouling coatings [55, 95 and therein]. The impact of herbicides on seagrass is more scarcely noted [60, 96, 97], even on a limited scale (3% inhibition of photosynthetic biomaterial assay [98]). But seagrass vulnerability to short but intense contamination has been highlighted [99] and such events could be difficult to monitor. Moreover, short term contamination could be integrated by passive samplers, deployed for weeks, and weighted by the mean concentration in the aquatic environment: depending to monitoring protocol, fugacious pollution could be neglected. Then, seagrass could be resistant to long-term herbicide contamination with severe concentration [61] but vulnerable to toxic pulses [99].

Seagrass physiology is temperature dependant. Seagrass growth is enhanced by temperature increases; the optimal temperature for temperate species is between 11.5°C and 26°C when tropical ones' *preferenda* is between 23°C and 32°C (Lee et al., 2007). Temperature conditions:

- Respiration (see supra); temperature is the predominant factor for respiration control [66, 100],
- Rubisco oxygenase fonction (increased by increasing temperature [88]),
- Sucrose synthase (SS) activity, enhanced in belowground tissues with O₂ decrease and temperature increase [78],

–Sucrose-P synthase (SPS), in the opposite way of terrestrial plants: increasing temperature leads to the increase of SPS activity, which is also influenced by salinity, photosynthesis, CO₂ availability, NH₄⁺ and grazing [93, 101, 102].

–C metabolism, i.e. C-sink or C-source depending on temperature [103],

–Stomata function: stomata will be closed in high temperatures, in order to avoid dehydration.

Thus, temperature impacts seagrass growth independently to insulation [104].

Without herbicide impact, 40-45°C is considered as the threshold temperature [22]: for higher ones, irreversible effects are observed, especially at PSII scale. The herbicide presence, even at limited concentrations, could lower such threshold temperature, considering the complex physiologic equilibrium that herbicides could disrupt; such temperature sensibility leads to an enhanced impact of herbicides in warm conditions [105]. Metal accumulation is enhanced by temperature increases [106]. Metals are toxic for seagrasses and especially for PSII [107]. Cu, used in this way as an antifouling alternative, early impacts PSII complex [108-111] in a few days after contamination. The cocktail effect is highlighted [74] for Cu and Irgarol 1051. Gamain [112] shows that herbicide impact is increased in presence of Cu and following temperature: at a temperature for which *Z. noltii* when free of herbicide alteration, even on a biochemical scale, seagrass presents damages in presence of this cocktail. However, these cocktail and summer temperatures are more close to field conditions, especially in tropical waters, than cold conditions and isolate herbicides.

7. Conclusion

Seagrass decline is actually misunderstood. If nutrients increase, it leads to epiphyte proliferation which limits seagrass photosynthesis [104]. Erosion, burying meadows and inducing turbidity limiting photosynthesis, are evoked as the main threat on the seagrass community, chemical interactions could be regarded as underestimated. Even if seagrasses seem to be resilient to herbicide pollution, and even if seagrass recovery has been shown to be better *in situ* than *in vitro*, the cocktail impact seems to be a promising study field. Data concerning seagrass contamination are dramatically scarce despite the precious services that the seagrass community provides, as for economical activity as for environmental concerns like biodiversity preservation and carbon fixation. In the field, seagrass meadows are regressing, and their resilience seem to be altered. Impacts of herbicides on the minimal requirement and on the adaptation to high irradiances are not sufficiently studied leading to observe regression without understanding underlying phenomenology [45]. Seagrass originality involves more largely trans-disciplinarily in order preventing the meadows' decline –but if such a consistent *pièce de résistance* will need appropriate research efforts, the seagrass crisis, taken into account by environmental monitoring like Water Framework, allows, after all, hope for a remediation.

Acknowledgements

Authors wish to thank William and Diana R. Corby for their contributions to their English improvement.

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