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Which factors regulate seagrass growth and distribution?

The growth and distribution of seagrasses are controlled by the physical, chemical and biological properties of the environment they live in. Sufficient light, nutrients and inorganic carbon are basic needs for photosynthesis, but also a suitable substratum, moderate exposure, temperature and various biological factors affect the distribution of seagrasses. A complicated interaction between the factors makes it difficult to separate the effects of single factors as well as predict presence or distribution at a given time and place. Although complicated the most important factors determining seagrass growth and distribution can be identified.

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The basic physical requirements of seagrasses are sufficient light, a suitable substratum and moderate levels of wave exposure, but the presence and distribution of seagrasses around the world are also regulated by a number of other factors. The basic requirements for seagrass growth are similar to that of terrestrial plants. However, life in the aquatic environment differs considerably in many respects from the terrestrial environment, and some resources may be limited in accessibility or quantity. Besides basic physical and chemical requirements for growth, biological competition from other species may also influence the growth and distribution of the seagrasses. In this chapter the regulating factors of seagrass growth and distribution will be described along with a short description of the possible differences between the four European seagrass species that might exist.

Abiotic factors

Light

Light is one of the most important factors in the regulation of seagrass maximum depth distribution and seagrasses are therefore only growing in shallow coastal waters at depths receiving enough light for seagrass growth. Light is required to drive photosynthesis and hence growth, but in contrast to the terrestrial environment light is a limited resource in the aquatic environment. When light is passing through the water column it is absorbed or reflected by particles, such as phytoplankton,

suspended material and dissolved substances. Light therefore attenuates exponentially with increasing depth. In addition to varying between areas, light attenuation may also vary considerably within an area since water turbidity can be a result of local physical and biotic factors. Seagrasses have a minimum requirement for light: a rule of thumb of approximately 10 % of the surface irradiance (Fig 4.1). This value is however, an average and therefore not applicable for all seagrass species at all times, since the light compensation point of the plants differs among species and depends on other environmental factors such as temperature and sediment chemistry.

Within the range of irradiances that seagrasses can exist, special morphological acclimatisations in growth strategy are required. Decreasing light level causes the plants to prolong the leaves and thin the density of shoots. By this acclimatisation more light can be captured and converted into photosynthetic production. The growth acclimatisation to reduced irradiance is most pronounced in *Z. marina*, where leaf length varies from 15-20 cm in shallow water to more than 120 cm in deep water, but also *C. nodosa* and *P. oceanica* acclimatise to reduced irradiance, primarily by reducing shoot density in deep waters. *Zostera noltii* rarely shows this acclimatisation since it primarily grows in shallow intertidal waters with sufficient light. However, for most species light defines the lower limit of their depth distribution.

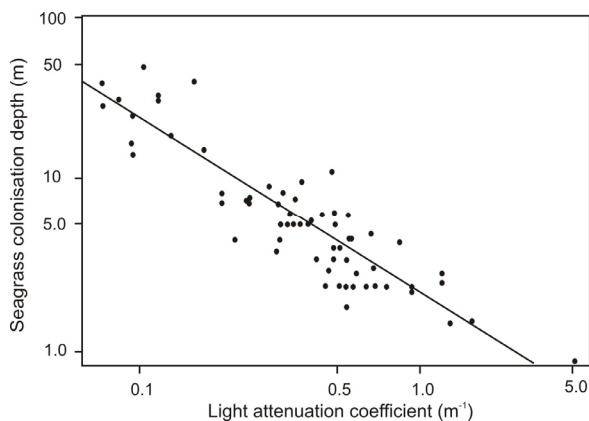


Figure 4.1. The relationship between seagrass colonisation depth and light availability expressed as the light attenuation coefficient (m^{-1}). The line is expressed by: $\log Z_c (\text{m}) = 0.26 - 1.07 \log K (\text{m}^{-1})$. Redrawn from Duarte 1991.

Physical exposure

Currents, wave action and tide are in contrast to light, the most important factors controlling the upper depth limit for seagrass distribution. In general it is estimated that seagrasses do not exist at flow velocities above 1.5 m per second or at very exposed shores. Currents and wave action prevent seagrass growth and distribution by causing resuspension and transport of the sediment. Besides affecting the general light climate of the water column, erosion can expose roots and rhizomes causing the seagrasses to detach from the sediment. Additionally, very strong currents or wave action may tear up entire plants or prevent new shoots from being established. As the sediment resettles other plants may be buried by sediment. High rates of resuspension or siltation can be crucial for seagrass populations although *Posidonia* or *Cymodocea* species with vertical shoots, might survive events of high sediment deposition by elongating vertical shoots.

Substratum

Another very important factor in the regulation of seagrass distribution is the presence of a suitable substratum. While macro algae are attached to stones and rocks on the seafloor, seagrasses mainly require a soft substrate of gravel, sand or mud, where rhizomes can elongate and roots can fasten. *Zostera marina*, *Z. noltii* and *C. nodosa* can be found on gravel as well as in mud rich in organic matter. In contrast, *P. oceanica* is usually found in more coarse sediments. There are exceptions and some seagrass beds can actually be found on rocky substrates. Some *C. nodosa*

populations near Albufeira on the Algarve coast of Portugal are growing on rocks with the roots and rhizomes inserted in cracks and crevices in the rock.

Carbon

In addition to light, seagrasses need inorganic carbon for photosynthesis. In water, inorganic carbon exists in three forms: CO_2 , HCO_3^- and CO_3^{2-} depending on the pH of the water, and both CO_2 and HCO_3^- are assimilated by seagrasses in the photosynthetic process. However, the leaves of seagrasses have a low capacity for extracting inorganic carbon and the photosynthesis seems, even under normal pH and salinity conditions, to be limited by the availability of inorganic carbon under high light conditions (Beer and Koch 1996). At high pH due to high rates of photosynthesis in shallow waters, carbon limitation is even more likely. Hence, seagrasses may profit from the ongoing increase in global atmospheric carbon dioxide caused by the profound use of fossil fuels (chapter 5). In estuaries supplied with freshwater of low inorganic carbon contents (e.g. the Baltic Sea), carbon limitation is more pronounced, and the increase in atmospheric CO_2 could have even greater impacts. It is, however, not known to what extent inorganic carbon can be supplied from the sediment via the roots and plant lacunae to seagrass leaves, and, therefore, the actual importance of carbon limitation to seagrass photosynthesis and growth needs to be examined further.

Nutrients

Seagrasses also require different kinds of inorganic nutrients, where nitrogen and phosphorous are the most quantitatively important. Nutrient requirements for seagrasses are lower than for other aquatic organisms such as macro algae and phytoplankton. It is estimated that seagrasses requires about 4 times less nitrogen and phosphorous per weight than phytoplankton cells. This gives the seagrasses an advantage for growth in nutrient-poor environments compared with other primary producers. In general, nutrient levels in the water column of seagrass beds are typically low, especially in warmer areas such as the Mediterranean, but in addition to uptake of nutrients from the water column seagrasses can take up nutrients from the sediment. Most sediments are rich in nutrients due to the mineralization of organic matter. Exceptions are carbonate sediments, which bind phosphorous and thereby induce phosphorous limitation to the

these plants. *Posidonia oceanica* and *C. nodosa* often grow in carbonate sediment with low nutrient content, and it has been documented that very low nutrient concentrations can reduce the growth of plants. *Zostera marina* and *Z. noltii* usually grow in organic sediments and are seldom limited by nutrients.

Temperature

Temperature affects all biological processes primarily by increasing reaction rates of the biochemical pathways. The most important processes, photosynthesis and respiration, are slow at very low temperatures but increase with increasing temperature. Respiration exceeds however, photosynthesis at high temperatures resulting in a negative energy balance within the plant. The temperature therefore defines the geographical limits for growth, although some adaptation to the local temperature regime is possible. The temperature tolerance differs between species. *Zostera marina* is in general adapted to relatively cold habitats with temperatures ranging between -1°C in winter and approximately 25°C in summer. *Zostera noltii* also thrives in cold habitats in the north but endures higher temperatures than *Z. marina*. The absence of *Z. noltii* in the northern/arctic part of Europe might be due to a higher temperature required for flowering than in *Z. marina* but this aspect needs further investigation. *Cymodocea nodosa* and *P. oceanica* grow in warmer environments with temperatures ranging from approximately 10°C up to about 30°C. The temperature is therefore considered the overall parameter controlling the geographical distribution of the species in Europe.

Salinity

Seagrasses grow at salinities ranging between 5 ‰ and 45 ‰. Salinity affects the osmotic pressure in the cells, but many seagrasses are well adapted to sudden changes in salinity. For example, seagrasses often grow in river outlets or estuarine habitats where salinity changes rapidly and varies considerably over time. Some species have, however, a higher tolerance to changes in salinity than others. *Zostera marina* and *Z. noltii* are frequently observed in estuaries and *Z. noltii* also occurs on intertidal flats where changes in salinity can change from only a few ‰ to more than 30 ‰ within a few hours. *C. nodosa* usually inhabits more saline areas with fluctuations from 26 - 44‰, whereas *P. oceanica* only inhabits marine waters with high salinities. Furthermore *P. oceanica* does not endure large variation in salinity like the three other species. In rare cases,

salinity increases significantly above the mean oceanic values of 33-36 ‰ because of desalination plants or profound water evaporation from shallow areas. Very high values of salinity (up to 60 ‰) are suspected to cause severe diebacks in shallow areas.

Oxygen

Seagrasses need oxygen to supply their metabolism of both above and below ground tissue. But, while leaves are usually situated in the oxygenated water column, roots and rhizomes are buried in anoxic sediments. Under normal circumstances, photosynthetically generated oxygen or water column oxygen is transported to roots and rhizomes by simple diffusion from the leaves to the roots in a well developed system of air tubes (lacunae) running through the plant. The below ground tissue may experience lack of oxygen if the water column becomes hypoxic or anoxic during periods of high degradation of organic matter in the sediment coupled with a stratified water column. Anoxic conditions influence the metabolism of the plants resulting in poor energy availability and production of toxic metabolites, both of which may negatively affect growth and survival of the plants. Anoxic conditions in the belowground tissue may also cause invasion of sulphide from the sediment.

Sulphide

High concentrations of sulphide in the sediment can harm seagrasses since sulphide is a plant toxin inhibiting respiration. Sulphide is present in sediment rich in organic matter and poor in iron. To be toxic, sulphide has to enter the plants, which is not possible under normal conditions when oxygen is present in the belowground tissue and in micro zones around the roots. Sulphide is oxidized in the root zone to the harmless compound sulphate before reaching the root surface. During oxygen deficiency in the water column, the supply of oxygen will be inadequate resulting in root anoxia and sulphide invasion. When the gaseous sulphide penetrates to the lacunae it will readily spread and can reach the meristem where it might be fatal to the plant. In the presence of iron in the sediment, iron reacts with the sediment sulphides, precipitating them as iron-sulphur minerals and thereby "buffer" the effects of toxic sulphides on the seagrasses.

Biotic factors

Growth and distribution of seagrasses are affected by other organisms primarily through competition or herbivory. High nutrient concentrations in the water column cause epiphytes and filamentous algae to develop in high densities, affecting the light climate in the water column and hence seagrass depth distribution. Furthermore, epiphytes expand the boundary layers around leaves limiting uptake of oxygen, inorganic carbon and nutrients. Filamentous algae can also form dense mats at the seafloor that will reduce water flow around the leaves and reduce the oxygen content in the water when they are degraded.

Competition

Competition between different species of seagrass will also set limits to growth and distribution. For example, *Z. noltii* often colonises the intertidal zone or the shallow waters where other species cannot establish populations. In deeper waters where *Z. marina* or *C. nodosa* can establish, they apparently have a competitive advantage and *Z. noltii* beds will disappear. Mussels (*Mytilus edulis*) may also compete with seagrass for the occupation of space. Mussels occasionally settle on the leaves of e.g. *Z. marina* in very high numbers. As they grow and become larger they eventually cover the bottom and suppress plant growth

Grazing

Grazing by waterfowls or invertebrates can also be important for the distribution of seagrasses in certain areas although it is not considered a major controlling factor. Birds usually graze on fresh leaves on very shallow water causing the leaves to disappear. Occasionally even rhizomes are consumed causing the seagrass population to disappear for a period. The effect of grazing by birds is highly variable in time and space since the population density of birds in a given area may vary considerably. Examples of grazing birds in European coastal water are mute swan (*Cygnus olor*), brent goose (*Branta bernicla*), pintail (*Anas acuta*), wigeon (*Anas penelope*) and mallard (*Anas platyrhynchos*), all of which graze on the *Zostera* species. Grazing from fish is probably not as profound as from birds and only a few fish species in the world feed exclusively on seagrasses. As an example of fish grazing on European seagrasses are the sparid fish (*Sarpa salpa* L.) which graze on *Posidonia oceanica* in the Mediterranean. The crustacean *Idotea*

chelipes and the purple sea urchin *Paracentrotus lividus* have also been found to graze on *Z. marina* and *P. oceanica*, respectively. The importance of grazing for the distribution of seagrasses is in general considered relatively low in European waters, but investigations suggest that grazing on fresh leaves is more important in the fast growing species *Z. marina*, *Z. noltii* and *C. nodosa* than in *P. oceanica* probably because the content of indigestible lignin-cellulose compounds is considerably larger in *P. oceanica*.

Conclusion

Seagrasses can grow in the shallow coastal zone of marine habitats, but several factors regulate growth and distribution of the plants in these areas. Light is the most important factor regulating the lower depth distribution, whereas exposure is the most important factor regulating the upper depth distribution. Seagrasses might be nutrient limited even though they assimilate nutrients from the sediment. In local areas biological factors such as grazing may also affect the distribution of seagrasses, but the overall effect of grazing in European waters are considered small.

References:

- Beer S, Koch E (1996) Photosynthesis of marine macroalgae and seagrasses in globally changing CO₂ environments. Marine Ecology Progress Series 141: 199-204
- Bester K (2000) Effects of pesticides on seagrass beds. Helgoland Marine Research 54: 95-98
- Borum J, Sand-Jensen K, Binzer T, Pedersen O, Greve TM. Chapter 10 – Oxygen movements in seagrasses. In Biology of seagrasses. Eds Larkum, Orth & Duarte. In press
- Dennison WC (1987) Effects of light on seagrass photosynthesis, growth and depth distribution. Aquatic Botany 27: 15-26
- Duarte CM (1991) Seagrass depth limits. Aquatic Botany 40: 363-377
- Greve TM, Krause-Jensen D. Predictive modelling of eelgrass (*Zostera marina* L.) depth limits. Marine Biology accepted
- Hemminga MA, Duarte CM (2000) Seagrass Ecology. Cambridge University Press
- Krause-Jensen D, Pedersen MF, Jensen C (2003) Regulation of eelgrass (*Zostera marina*)

cover along depth gradients in Danish coastal waters. *Estuaries* 26(4A): 866-877

Marba N, Duarte CM (1995) Coupling of seagrass (*Cymodocea nodosa*) patch dynamics to subaqueous dune migration. *Journal of Ecology* 83(3): 381-389

Nielsen SL, Sand-Jensen K, Borum J, Geertz-Hansen O (2002) Phytoplankton, nutrients, and transparency in Danish coastal waters. *Estuaries* 25(5): 930-937

Valentine JF, Heck Jr. KL (1999) Seagrass herbivory: evidence for the continued grazing of marine grasses. *Marine Ecology Progress Series* 176: 291-302

Via JD, Sturmbauer C, Schönweger G, Sötz E, Mathekwitsch S, Stifter M, Rieger R (1998) Light gradients and meadow structure in *Posidonia oceanica*: ecomorphological and functional correlates. *Marine Ecology Progress Series* 163: 267-278