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How do seagrasses grow and spread?

Seagrass colonisation and meadow maintenance proceeds by patch stabilishment, from seed germination and plant fragments, and clonal growth. Knowledge on seagrass growth rates and success of reproductive effort is crucial to manage seagrass ecosystems, particularly to derive expectations on the recolonisation times required to recover seagrass meadows.

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Seagrasses are clonal plants sharing a similar architecture and presenting a highly organised growth. Seagrass growth relies on the reiteration of ramets, which are composed of modules (i.e. leaves, piece of rhizome, roots, flowers or inflorescences). The understanding of the design of seagrasses provides insight on their growth patterns. Despite the similar architecture of seagrasses, plant size and growth rate vary some orders of magnitude across species. To a large extent, variability in rates between seagrass species reflects differences in plant size, with smaller species growing faster than larger ones. In addition, seagrass growth is able to adapt to environmental change, and it exhibits substantial plasticity. Knowledge on seagrass growth rates allows assessment of meadow productivity and seagrass health, as well as forecasting their capacity to survive disturbances. In addition, seagrass rhizome growth responses to disturbances remain imprinted on the plant allowing reconstruction of past disturbance dynamics.

Vegetative proliferation is the main mechanism of seagrasses to occupy habitat space, and thus it is a critical process for seagrass meadows to spread and persist. Most ramets in seagrass populations are produced as rhizomes elongate. Rhizome growth is the process that regulates the rate of formation and the spatial distribution of ramets (and, thus, modules) within seagrass meadows, and, thus, it constrains the development of their populations. The spread, and maintenance, of seagrass meadows also depend on sexual reproduction since it is the main mechanism regulating patch formation. Hence, information about the effort and success of seagrass reproduction and rhizome growth patterns are

essential to predict the time scales of seagrass colonisation and, thus, recovery.

In this chapter we aim to provide an understanding of seagrass growth processes and their rates, as well as mechanisms of seagrasses to spread. We do so by describing seagrass architectural features and the wide repertoire of module addition and growth rates, and discussing the mechanisms and rates of seagrass colonisation. Four sections of this chapter are dedicated to the growth pattern and spreading mechanisms of those seagrass species present along European coasts. At the end we discuss the implications of European seagrass growth and spread for management.

Seagrass achitecture

Seagrasses share a common architecture, all species being clonal, rhizomatous plants. Rhizomes are stems extending horizontally below the sediment surface or vertically, raising the leaves towards, or above, the sediment surface. Seagrasses are modular plants composed of units repeated during clonal growth. Each unit is composed of a set of modules: a piece of rhizome, which can be either horizontal or vertical; a bundle of leaves attached to the rhizome; and a root system (see chapter 1). In addition, the units may hold flowers or fruits, depending on the timing of observation. The morphology of seagrasses does not present any peculiar deviations relative to those of other terrestrial monocotyledons.

The rhizome is responsible for the extension of the clone in space, as well as for connecting neighbouring ramets, thereby maintaining

integration within the clone (see below). The rhizomes of most seagrass species are flexible, whereas those of *Posidonia oceanica* are highly lignified and explain the persistence of dead tissues in the sediments, which extends for millenia in *Posidonia oceanica*. Seagrass rhizomes are composed of internodes, the rhizome fragments in between two nodes, which are the insertion points of leaves. The distinct lines identifying the nodes after leaf abscission are also referred to as “leaf scars”. Rhizome internodes range widely in size among seagrass species (Table 3.1).

Cymodocea nodosa and *Posidonia oceanica* have both horizontal and vertical rhizomes, whereas *Zostera* species have only horizontal rhizomes. Horizontal rhizomes can revert into vertical rhizomes, which leads to the cessation of their horizontal growth. In turn, vertical rhizomes can branch to produce horizontal rhizomes when the apical meristem of the original horizontal rhizome dies, thereby resuming the capacity for horizontal growth. *Zostera* species bear a leaf on each horizontal rhizome node, and *Posidonia oceanica* and *Cymodocea nodosa* bear leaves on the nodes of both horizontal and vertical rhizomes.

European seagrasses have long and relatively narrow strap-like leaves, ranging in size, from the small leaf areas of *Zostera noltii* to the large leaf areas of *Posidonia oceanica* (Table 3.1). The leaves are often present in bundles on shoots, with up to 8 leaves per shoot in *Posidonia oceanica* and 2 to 5 leaves in the other species. Seagrass roots provide the necessary anchoring and nutrient acquisition, and vary greatly in size across the European species (Table 3.1). Seagrass flowers are often inconspicuous and very simple, for they do not rely on animals for pollination. Seagrass flowers, seeds and fruits range greatly in size from the minute flowers of *Zostera noltii*, which contain multiple ovaries and seeds to the large inflorescences of *Posidonia*, which yield large fruits known as sea olives. *Cymodocea nodosa* has separate male and female clones, unlike the other European seagrasses, which are hermaphrodites. *Cymodocea nodosa* shoots produce two seeds, attached to the base of the shoot, *Posidonia oceanica* produces half a dozen seeds per shoot, and flowering shoots of *Zostera noltii* and *Z. marina* produce hundreds of seeds.

Formation of leaves, rhizomes and roots: clonal growth

The rate of formation of seagrass leaves, rhizomes and roots, and, therefore, the spread of the clone, depends on the activity of meristems, which are the areas where active cell division, and therefore, growth takes place. The division of the meristems is a rather continuous process, responsible for the maintenance and expansion of seagrass clones. Small seagrass species, such as *Zostera noltii*, produce new leaves much faster (13.71 days) than species with large leaves, such as *Posidonia oceanica* (50.68 days). Roots are typically formed in the internodes of rhizomes, both horizontal and vertical. The death of the meristems results in the discontinuity of the production of new modules (leaves, internodes, etc.). The production of new rhizome material, which leads to the development of new shoots and roots, as well as new branches, is the basis of the growth of seagrass clones. Clonal growth is, therefore, a fundamental component of the production and space occupation of seagrasses, particularly during the colonization of new habitats or their recovery from disturbance.

Meristematic death is also associated to sexual reproduction in *Zostera spp*, which have terminal inflorescences. Meristematic death is followed by the loss of functionality of the modules, which may be subsequently shed, thereby avoiding respiratory losses by non-functional organs. The life span of seagrass shoots, leaves and roots, which reflects the life span of their associated meristems, differs greatly among species, and is scaled to their size, with small species having short leaf life spans and larger species having longer leaf life spans. Leaf life span ranges from a few days in *Zostera noltii* to almost a year in *Posidonia oceanica* (Table 3.1). Available information suggests that roots are longer-lived than leaves, remaining attached to the plants longer than leaves do. The life span of the shoots of European seagrasses ranges from weeks (*Zostera noltii*) to decades for *Posidonia oceanica* (Table 3.1). The life span of the meristems of horizontal rhizomes is presently unknown, except for species, such as *Zostera spp*, for which sexual reproduction is a terminal event.

Seagrass growth rate

Leaf growth rates

New leaves are produced centrally in the leaf bundles by the meristems. Once the leaf has

Table 3.1 Average architectural features and growth rates of European seagrass species. nd: no data. Range of values are indicated within brackets when available. Data from Duarte 1991, Marbà et al 1996, Duarte et al 1998, Marbà and Duarte 1998, and Hemminga et al 1999.

	<i>Cymodocea nodosa</i>	<i>Posidonia oceanica</i>	<i>Zostera marina</i>	<i>Zostera noltii</i>
Leaf surface (cm ²)	9	82.8	34.6	1.15
Shoot mass (mgDW)	82.8	731	272.5	6.5
Fruit size (mm ³)	48	523.6	18	2.8
Horizontal internodal length (mm)	25 (6-53)	3 (1-4)	11 (9-12)	12 (3-20)
Vertical internodal length (mm)	1.4 (0.1-2.5)	1 (0.4-2)	nd	nd
Root length (cm)	21.3	43.1	nd	3.2
Shoot elongation rate (cm shoot ⁻¹ d ⁻¹)	1.3	0.8	3.2	0.7
Horizontal rhizome elongation rate (cm apex ⁻¹ yr ⁻¹)	40 (7-204)	2 (1-6)	26 (22-31)	68 (10-127)
Vertical rhizome elongation rate (cm apex ⁻¹ yr ⁻¹)	1.4 (0.1-16)	1 (0.1-4)	nd	nd
Leaf life span (days)	79 (50-155)	295 (256-345)	88 (33-164)	86 (46-125)
Shoot life span (days)	876	4373	554.8	nd

been produced, it elongates from its basal part, where the leaf meristem is located, until it attains the length characteristic of the species and enforced by the habitat conditions. Seagrass shoots produce new leaves while the standing ones are still growing. When summed over the leaves present on any given shoot, the total daily leaf elongation rate per shoot tends to be on the order of one or a few centimetres

Horizontal and vertical growth rates

The growth rates of seagrass rhizomes vary greatly, from a few centimetres per year in *Posidonia oceanica* to more than 2 m yr⁻¹ in *Cymodocea nodosa* (Table 3.1). The vertical rhizomes of *P. oceanica* and *C. nodosa* also extend, but at slow rates of a few centimetres per year. Seagrass horizontal rhizomes branch, accelerating the occupation of space. Horizontal branching is more profuse in small species (e.g. *Zostera noltii* may branch at every node), than in large seagrass species (e.g. *P. oceanica* rhizomes produce, on average, a branch every 30 years). In addition, the horizontal branching angle varies across species, small seagrasses (e.g. *Zostera noltii*) branching with angles close to 90° and large ones (e.g. *P. oceanica*) branching with angles about 40°. Small seagrass species elongate and branch their rhizomes at much faster rates than large ones. Hence, small seagrass spread in two dimensions at a greater rate than large seagrass species do, so that small seagrass species play a pioneer role and are better able to recover from disturbance.

Environmental and internal controls on growth rates

Seagrass growth rates, to large extend, are species-specific and scaled to plant size. The negative relationship between seagrass growth and size derives from the increasing construction costs of seagrass modules the larger they are. In addition, seagrasses modulate their growth in response to environmental (e.g. climate, nutrients, sediment quality) and population (shoot density) conditions. Leaf and rhizome growth of European seagrasses, except horizontal rhizome growth of *P. oceanica*, exhibits wide seasonal fluctuations in response to changes in temperature and/or irradiance. Growth of European seagrasses is maximal during summer and minimal during winter, when in most species (*C. nodosa*, *Z. marina*, *Z. noltii*) it almost ceases. Seagrass response to seasonality remains imprinted on the length of rhizome internodes, allowing retrospective quantification of rhizome growth over the time scale equal to rhizome longevity (i.e. from few months in *Z. noltii* to decades in *P. oceanica*). Seagrass growth requires light conditions being at least 11 % of surface irradiance. During periods of fast seagrass growth, ambient nutrient availability may constrain seagrass growth. Seagrasses with leaf nitrogen and phosphorous concentrations below 1.8 % plant dry weight and 0.2 % plant dry weight, respectively, are susceptible to encounter growth limitations, and they often respond to nutrient sediment additions by increasing leaf growth (e.g. *C. nodosa* and *P. oceanica*). Seagrass

rhizospheres tend to be denser, with more branched root networks when they grow in more nutrient-poor surroundings. On the contrary, excess of ambient ammonia has been demonstrated to be detrimental for seagrass (*Zostera marina*) survival. Deterioration of sediment quality, reflected by strongly reducing sediment conditions and high concentrations of toxic compounds (e.g. sulphide), has been shown to suppress seagrass growth. Sediment dynamics also alters seagrass growth. Sand erosion and deposition on seagrass beds decrease shoot survival. However, seagrass species with vertical rhizomes are able to cope with sand deposition because the growth of vertical rhizomes, and leaves, of surviving shoots is enhanced with moderate sand burial, increasing at proportional rates as the height of sand accreted. Similarly, they reduce vertical rhizome and leaf growth to minimum rates when sand is eroded. The response of seagrasses to sand burial is triggered by darkness around vertical rhizome meristems. The seagrass response to sediment deposition remains imprinted on the vertical rhizomes as long internodes, allowing retrospective identification of burial/erosional events. Seagrass clonal growth is also dependent on the density of neighbouring shoots. Horizontal rhizome elongation and branching rate of at least *C. nodosa* and *Z. marina* decrease with increasing shoot density around the growing rhizome apex. Because rhizome growth regulates shoot proliferation in seagrass beds, regulation of clonal growth rate in response to neighbouring shoot density is an important mechanism to avoid shoot density-mortality under crowding conditions, and, thus, intra-specific competition.

The response of seagrass growth to environmental and population changes is species-specific as a consequence of differences in sensitivity to environmental forcing and capacity to uncouple plant growth from ambient conditions among species. For instance, seasonality in *C. nodosa* growth is highly dependent on temperature, whereas that in *Z. marina* growth is mainly forced by light conditions. The high sensitivity of *C. nodosa* to temperature conditions has been attributed to the tropical origin of this seagrass genus. Seagrasses store resources (carbon and nutrients) in their belowground organs that they use during periods when ambient resource availability does not suffice to fulfil resource demand. Resource storage capacity largely depends on plant size and plant longevity, both features being strongly species dependent. In addition, the architecture of seagrasses allows the ramets of a clone to remain physiologically

integrated over time scales ranging from, at least, less than one month in small species (*Z. noltii*) and several years in large ones (*P. oceanica*). The greater capacity of large seagrasses to store and mobilize resources in their clones than small ones allows them to uncouple their growth more from ambient resource heterogeneity, and, thereby, buffer their growth responses.

Seagrass spreading

Vegetative vs. sexual spreading

The reproductive biology of seagrass species has interested naturalists for about two centuries. Flowering of seagrasses is often controlled by temperature and often occurs simultaneously across large spatial scales. European seagrass species flower in late spring, and some of them (*Zostera spp*) throughout the summer as well, when irradiance improves and water temperature increases, except for the Mediterranean species *Posidonia oceanica*, which flowers in the fall (October). Flowering is a rare event for most seagrass species, where typically < 10 % of the shoots flower each year. Yet, flowering is profuse in annual *Z. marina* populations developing at the intertidal zone. The reproductive effort of seagrasses can be highly variable between years and among populations, and episodic mass flowering can occur in connection to climatic extremes, such as the massive flowering of *Posidonia oceanica* in connection to extreme summer temperatures in 2003. Disturbances, such as burial derived from the migration of sand waves may also enhance seagrass flowering. Because of the low probability of flowering, sexual reproduction is a negligible component of the carbon allocation of seagrasses, involving < 10 % of the annual production for most species. All European seagrass species have hydrophilous pollination, in which pollen grains are released in the water column to fertilise the female flower. Seed production can reach thousands of seed m⁻² for *Zostera* species, whereas it is in the order of, at most, tens of seeds m⁻² for *Cymodocea nodosa* and *Posidonia oceanica*. A significant percent of the seeds seagrass produce are lost before being released due to predation by invertebrates and fish.

Seagrasses can disperse through sexual propagules as well as through detached or drifting rhizome fragments. Dispersal by fragments was considered to be rare, but new evidence suggests that the importance of this mechanism may have been underestimated. Dispersal can also occur

through a combination of both processes, as flowering shoots may detach and disperse, subsequently releasing the seeds. The mature seeds of *Cymodocea nodosa* are produced at the base of the shoots, and are often positioned at, or just below, the sediment surface. These seeds are, therefore, not likely to disperse far. *Zostera* seeds disperse with currents, and have been shown to have a relatively short dispersal range restricted to tens of meters. In contrast, the seeds of *Posidonia oceanica* remain buoyant for hours and can be potentially dispersed across distances of tens or even hundreds of kilometres, although there are no direct observations to confirm whether such potential is realised.

Patch formation

Once in the sediments, the seeds of some seagrass species can remain dormant for some time before germinating, with a documented dormancy period of about half a year for *Zostera marina* and 7-9 months for *Cymodocea nodosa*, thereby building a rather ephemeral seed bank. Seedling density is comparatively low (one or two orders of magnitude) relative to seed production, due to multiple aggregated losses. These losses are due to many factors, including lack of viability, physical damage, export to unsuitable areas, burial, and predation. Initiation of clonal growth (i.e. rhizome extension) will lead to the formation of patches by the seedlings. Yet, most seedlings die without ever initiating clonal growth, because these require the accumulation of important amounts of resources, such as nutrients.

Patch growth

The basic components of the clonal spreading of seagrasses, which leads to the formation of patches or the maintenance of closed meadows, are the rate of horizontal extension, and the probability and angle of branching of the rhizomes. The clonal growth of seagrasses can, therefore, be simulated from knowledge of this basic set of rules, an approach that has proved most useful in the examination of space occupation by clonal plants. The simulation of the space occupation by seagrass clones confirms the prediction that small seagrass species have a less efficient, but more compact occupation of space, which has been referred to as the "phalanx" strategy, whereas large, slow growing species have a more efficient, but looser occupation of the space, the "guerrilla strategy". Indeed, if large species did have broader branching angles, the time required to occupy the space would be so long that they would not be

able to develop meadows despite the long life span of their modules. A simulation analysis of seagrass clonal growth also showed that the branching process continuously accelerates the occupation of space, such that the space occupied by a seagrass clone increases as the third power of time for all seagrass species simulated. Thus, branching rates and branching angles are even more important determinants of the rate of space occupation than the linear extension rate of the rhizomes, the parameter that has received most attention to date.

The growth rates of patches of European seagrass species are constrained by the growth rate of their rhizomes, with *Posidonia oceanica* patches showing the slowest growth (2 cm year⁻¹) and *Cymodocea nodosa* showing the fastest growth (200 cm year⁻¹).

Posidonia oceanica

P. oceanica is a long-living and very slow-growing seagrass species. *P. oceanica* leaves may live for a bit less than 1 year, vertical rhizomes for several decades, and clones probably for centuries. The slow horizontal rhizome elongation and branching rate (Table 3.1) of this species explains the extremely slow spread of its clones. Simulation models based on rhizome growth and branching patterns indicate that *P. oceanica* should spend 350 yr to develop a 15 m diameter clone. *P. oceanica* vertical rhizomes elongate at rates that may be of similar order of magnitude as horizontal rhizomes do, which is unusual for seagrass species with differentiated rhizomes. Because of the relatively fast vertical growth of *P. oceanica* as compared to horizontal growth, the long life span of the meadows and the slow decomposition of its rhizomes, *P. oceanica* is able to develop reefs up to 3 m high and meadows with complex topography, particularly when *P. oceanica* colonises shallow coastal areas. *P. oceanica* growth is particularly sensitive to deterioration of sediment quality and, at meadow depth limit, water quality.

P. oceanica flowers between August and November. The number of flowering shoots in *P. oceanica* meadows is usually very low, generally lower than 3 % per year. However, flowering intensity widely fluctuates between years. Massive flowering events (when more than 10% shoots flower) have been observed associated to extremely warm summers. Flowering intensity also varies with water depth, decreasing the number of flowering shoots with increasing water depth, and it depends on local conditions. Many

P. oceanica female flowers do not succeed to develop viable fruits as a consequence of fruit abortion and, to less extent, predation. Actual seed production is less than 1% of potential seed production provided the amount of ovaries produced during flowering. Very little information is available on seedling survival and clone initiation rate, but it should be extremely slow.

The little investment and low success of sexual reproduction, combined with the extremely slow clonal spread of *P. oceanica* explains the extremely slow colonisation rate of this species. Numerical models simulating the occupation of space by a *P. oceanica* meadow indicate that it would need 600 years to cover 66 % of the space available. Similar colonisation time scales have been retrospectively calculated based on patch size and patch growth rate in patchy *P. oceanica* meadows. The very long time scales for colonisation of this species indicate that recovery of disturbed *P. oceanica* meadows, where important plant losses have occurred, would involve several centuries.

Zostera marina

Zostera marina has intermediate rates of growth and spread compared to other European seagrasses. Besides the potential for spread derived from the horizontal growth rates of the rhizomes, *Zostera marina* is able to release large numbers of seeds. At the time of reproduction, eelgrass shoots produce inflorescences which can each develop large numbers of seeds. Reproductive shoots die off following seed set, so that flowering represents a terminal event for eelgrass shoots. Seed production rates in *Zostera marina* beds reach several thousand per square meter. However, they do not travel far – a few meters at best - from the mother plant after being released, as they are negatively buoyant and sink to the bottom. However, flowering shoots may detach, because of disturbance, and float away, releasing the seeds at considerable distances from the stand where they were produced, which is the mechanism for long-term dispersal available to this species. In addition, swans and geese may ingest seeds and transport them, although this potential mechanism has not yet been investigated. A significant fraction of the seeds released are lost due to the activity of grazers, such as crabs, which have been shown to significantly reduce the seed pool produced by eelgrass.

The germination of eelgrass seeds leads to the initiation of patches, which are subject to intense

dynamics. Most of the new patches formed disappear within one year and only a few grow to effectively increase the cover of eelgrass in coastal zones. The time scales required for the recolonisation of eelgrass meadows has been estimated, provided favourable environmental conditions, to be in the order of a decade. *Z. marina* clones, however, may persist over centuries in areas where sexual reproduction is scarce (e.g. Baltic Sea).

Zostera noltii

The fast rate of rhizome elongation (68 cm year⁻¹) and profuse great branching rate lead to a compact space occupation. The species has a high leaf turnover rate, i.e. as new leaves are formed, the older are shed in a rapid process during the shoot lifetime. Besides, the leaf growth rate is also high, as well as the shoot production, which represent much of the production of the species. As a small species, the modules of *Z. noltii* have a short life span, with high mortality and recruitment rates, which is typical of colonizing seagrass species. The high rates of growth and production of *Z. noltii* allow this species to sustain even under considerable disturbance.

Beside vegetative development, these plants can reproduce sexually by producing flowering shoots (Photographs 3-4) and seeds (Photograph 5). Seed production and other events related to this process (flowering, seed release, dispersal, and germination) are valuable to maintain genetic diversity and may be the only significant mechanism for seagrass colonization of bare sediment areas. Coupling both vegetative and reproductive patterns may therefore constitute an excellent survival strategy in adverse and disturbed environments or in the establishment of new areas.

Flowering of *Z. noltii* can extend from March to November but the flowering season may vary from place to place, since factors such as water temperature, day length, tidal amplitude and fluctuating salinity regimes control the flowering event. The flowering shoots flourish from the rhizome as the vegetative ones and consist of several inflorescences, each containing the male and female flowers. The female flowers are pollinated by males from different inflorescences, to avoid self-pollination. The females that were fertilized develop a fruit inside, which originates a seed. Seeds are not likely to disperse far since they are negatively buoyant. However, detached flowering shoots containing seeds may be

transported by water currents over long distances. Observation of *Z. noltii* seedlings in the field is a rare event, for less than 5% of the plants originate from seeds. In spite of the investment in sexual reproduction, flowering represents less than 10% of the shoots, which suggests that this is not the main way of reproduction.

Cymodocea nodosa

C. nodosa growth ranks amongst the fastest ones across European seagrasses. The fast clonal growth of this species allows the clones to spread across 300 m² after 7 years. The life span of *C. nodosa* modules and ramets is intermediate, average shoot population life-span varying between 4-22 months, and average leaf life-span ranging from 2 to 5 months. *C. nodosa* clones, however, may live for at least 1 decade. *C. nodosa* growth almost exclusively occurs during spring and summer. *C. nodosa* growth exhibits substantial plasticity, which allows this species to survive disturbances. For instance, vertical and horizontal rhizome growth of *C. nodosa* is plastic enough for this species to colonise areas with intense sediment dynamics, such as bedforms with subaqueous dunes, with an average amplitude of 20 cm (range 7-65 cm) and wave length of 21 m (7-29 m), that migrate at average velocities of 13 m yr⁻¹. The close coupling between *C. nodosa* vertical rhizome growth and sediment accretion has been used to quantify shallow coastal sediment dynamics impossible to be measured with conventional sedimentary techniques. *C. nodosa* also exhibits substantial plasticity in response to ambient nutrient availability.

Only *C. nodosa* shoots older than 1 year flower, and they do so between March and June. Fruit development takes 2-3 months, although maximum density of shoots bearing fruits is observed in July-August. Afterwards, fruits detach from the mother shoot and, because they have negative-buoyancy, they are rapidly buried into the sediment nearby the mother plant. During events of intense sediment dynamics (e.g. strong storms), however, seeds may be transported across long distances, since there are meadows separated from the closest one by more than 300 km, and seeds of *C. nodosa* can be observed, although not very often, washed on the beaches. From April til June of the following year seeds germinate. *C. nodosa* clone formation rate has been estimated to be about 0.009 clones m⁻² yr⁻¹ in an area with intense sexual reproduction. However, clone mortality rate is about 50-70 % during the first year of life, hence, decreasing

substantially the success of sexual reproduction. Reproductive effort and success in *C. nodosa* exhibits temporal and spatial heterogeneity. Flowering intensity, for instance, has been observed to increase in response to sand burial, like in other seagrasses. In addition, seed production in *C. nodosa* should be constrained by the spatial distribution and abundance of male and female clones. The consequences of clone sex composition on reproductive success are evident when examining *C. nodosa* meadow genetic diversity. For instance, there is almost no genetic diversity in a *C. nodosa* meadow at the Algarve (S Portugal), where no female flowers have been observed.

The fast growth of *C. nodosa* clones and the relatively high patch formation rate of this species, when compared with the other European seagrasses, indicate that *C. nodosa* should be able to develop a meadow within a decade, if the colonisation process were initiated, on bare sediments. The time scales for meadow recovery if not all *C. nodosa* vegetation were lost should be even shorter. The rapid occupation of space by *C. nodosa* resulting from fast clonal growth, and the relatively high patch formation rate of this species explains the pioneering role that *C. nodosa* play during succession process in the Mediterranean.

Conclusion

European seagrass flora encompasses species with slow-growing rhizomes (*Posidonia oceanica*), and intermediate rhizomes expansion rates (*Cymodocea nodosa*, *Zostera marina*, *Z. noltii*), when compared with the range of clonal growth rates displayed by seagrasses. The slow horizontal rhizome elongation and branching rates observed in *P. oceanica* forecast slow (from centuries to millenia) recovery time scales for this species. Conversely, the rates of horizontal rhizome extension and branching frequency quantified for the other European seagrasses should allow recovery time scales of decades. In addition to the differences in clonal growth rules observed between European seagrass species, their growth is able to adapt to environmental change. Seagrass plasticity, however, differs among species, *C. nodosa* being amongst the most plastic species, and *P. oceanica* growth being the least plastic.

Knowledge on seagrass growth rates and success of reproductive effort is crucial to manage seagrass ecosystems, particularly to derive expectations on the recolonisation times required to recover seagrass meadows. Because of the

low survival rate of seedlings and young patches, they should be particularly protected. The time scale in which patches are most vulnerable ranges from a few months for *Zostera noltii* to half a century for *Posidonia oceanica*.

The time required for the patches to develop meadows ranges, across the European seagrass flora, from months to a year for *Zostera noltii*, to less than a decade for *Zostera marina* and *Cymodocea nodosa*, and several centuries for *Posidonia oceanica*. The acceleration of the colonisation process along these, sometimes too extended, time scales can be promoted through the maintenance of adequate habitat conditions, including, improved light penetration and reduced organic and nutrient inputs to the waters.

The recovery of *Zostera noltii* is relatively fast, whereas that of the other species is slow, and *Posidonia oceanica*, in particular, does not have the capacity to recover in operational time scales. Hence, the management approach to the slow-recovering species should emphasize the conservation and protection of the area they cover as to avoid losses.

References

- Duarte CM (1991) Allometric scaling of seagrass form and productivity. *Marine Ecology Progress Series* 77: 289-300.
- Duarte CM, Merino M, Agawin NSR, Uri J, Fortes MD, Gallegos ME, Marbà N, Hemminga MA (1998) Root production and belowground seagrass biomass. *Marine Ecology Progress Series* 171: 97-108
- Hemminga MA, Duarte CM (2000) *Seagrass Ecology*. Cambridge University Press
- Hemminga MA, Marbà N, Stapel J. (1999). Leaf nutrient resorption, leaf life span and the retention of nutrients in seagrass systems. *Aquatic Botany* 65: 141-158
- Marbà N, Duarte CM (1998) Rhizome elongation and seagrass clonal growth. *Marine Ecology Progress Series* 174: 269-280
- Marbà N, Duarte CM, Cebrián J, Enríquez S, Gallegos ME, Olesen B, Sand-Jensen K (1996) Growth and population dynamics of *Posidonia oceanica* in the Spanish Mediterranean coast: elucidating seagrass decline. *Marine Ecology Progress Series* 137: 203-213.