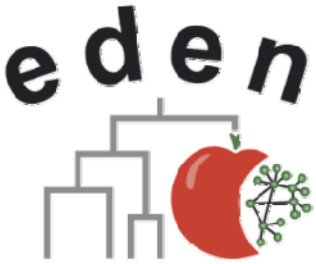

Project no. 043251

EDEN

ECOLOGICAL DIVERSITY AND EVOLUTIONARY NETWORKS

Instrument: Specific Targeted Project (STREP)

Thematic Priority: Integrating and strengthening the European Research Area

NEST Pathfinder initiative Tackling Complexity in Science

D3.1 (D6)**: Report on population network structure obtained from computer simulations**

Due date of deliverable: Month 18

Actual submission date: Month 18

Start date of project: 1 January 2007 Duration: 36 months

Organisation name of lead contractor for this deliverable: **Bioinf Leipzig**

Other contributors: **IMEDEA-UIB**, **CCMAR**

Project co-funded by the European Commission within the Sixth Framework Programme (2002-2006)		
Dissemination Level		
PU	Public	**X**
PP	Restricted to other programme participants (including the Commission Services)	
RE	Restricted to a group specified by the consortium (including the Commission Services)	
CO	Confidential, only for members of the consortium (including the Commission Services)	

TABLE OF CONTENTS

Population network structure obtained from computer simulations

Summary

A new two-dimensional off-lattice numerical model, based on known non-equilibrium growth processes in the context of condensed matter physics, is introduced in order to simulate the space colonization of clonal plants. The growth is controlled by a reduced set of key parameters, such as, the rhizome elongation rate, the average distance between consecutive units, the lateral branching probability and its characteristic branching angle and, finally, the shoot mortality rate. On addition, a clonal diversity probability factor is introduced in the model to study the genetic variability and the spatial distribution of genets. This probability will act as an effetive quantity that resumes the sexual and asexual reproduction ratios as well as the mutation processes that take place during the meristematic cell division.

The purpose of this deliverable is twofold: *i)* Develope a numerical model to study the space occupation and growth of clonal plants (i.e. seagrasses) and the spatial distribution of genets with the plant size and age, and *ii)* Compare with observed field measurements of the clonal diversity in P oceanica and Z marina species analysing the effect of the different sampling procedures and a limited sampling size.

Introduction

Theoretical modeling and, more recently, advances in computation techniques (Meakin, 1997) give researchers powerful tools to understand the mechanisms and paths of spatial and genetic pattern formation. Recent studies of the development of marine phanerogams (Posidonia, Cymodocea, …) (Vidondo et al., 1998, Barbà and Duarte, 1998) have observed nonlinearities in growth rates and colonization rhythms, difficult to understand in terms of the usually considered variables. Recently, adaptation of numerical models known in the context of condensed matter physics and of general pattern formation studies (DLE, Eden, …) to the growth of clonal plants has been successful in explaining the variability in occupation rates and morphologies (Sintes et al., 2005; Sintes et al., 2006). One of the aspects not considered yet is the understanding the degree of polymorphism (or endogamy) observed in the meadows (Billingham et al., 2003; Arnaud-Haond et al., 2007). This observation is relevant for the adaptability to physico-chemical environmental changes and species competition.

One of the objectives proposed in this WP is to advance in the comprehension of these phenomena by integrating in the same study the modelling of genetic variability and spatial distribution of the genotypes.

In a previously developed model of clonal plant growth (Sintes et al., 2005; Sintes et al., 2006) the probability of generation of a new genet has been implemented. This probability will act effectively in such a way that resumes the behavior of species that are able to reproduce both sexually and asexually as well as the mutation probability in the process of meristemic cell division. The generation of different genotypes will be considered together with the size and age of the plant.

Model Description

The simulation starts by placing a seed (a shoot holding an apical meristem) at an origin coordinate $\mathbf{r}_0$, and assigning to it a unitary, randomly-oriented, vector director $\mathbf{u}$, setting the direction of the rhizome extension. We assign to each shoot a per capita area of radius ρ (i.e. distance between consecutive shoots), and an exclusion area of radius $\sigma < \rho$ defined whereby any invading shoot will be strongly penalised, thereby preserving stand density and avoiding the same position to be simultaneously occupied by more than one shoot. The exclusion area was estimated by fitting this parameter to achieve the shoot density reported in natural stands of the species. The robustness of the empirically fitted exclusion area is supported by the observation that the resulting density of rhizome apices, which is independent of the fitting procedure, also matches field observations. The model iterates the clonal growth process according to the following steps:

1. A rhizome, that originates in the apex, is proposed to grow from $\mathbf{r}_0$ to $\mathbf{r} = \mathbf{r}_0+\rho\mathbf{u}$. The proposal will be accepted while the exclusion area principle is preserved. Then, the apex is relocated to the new position $\mathbf{r}$ where a new shoot will develop holding the genetic information contained in the apex. In this process the direction of growth $\mathbf{u}$ does not change.

2. A new branch (with a growing apex) may develop at **r** with probability ν per unit time. Thus, the probability that a particular meristem will branch at any one iteration is given by the factor $\nu\rho/v$, where v is the rhizome elongation rate (cm apex^{-1} yr^{-1}). A new branch will extend along a new vector director **u'** forming a characteristic angle ϕ with **u**, randomly selected along the right or left side of **u.** Only one branch is possible, as defined by the probability ν evaluated only at the time the rhizome apex occupies a particular position.
3. During this process, time is increased as $\Delta t=\rho/(v\ N(t))$, being ρ the distance between consecutive shoots, and N(t) the number of apices at time t.
4. Within this time step $\mu\Delta t$ shoots are selected at random, being μ the seagrass shoot mortality rate, and are removed from the patch.
5. At the end of steps 1 and 2 a new genotype is assign with probability γ to the new apices that may eventually develop.

This process is iterated until the stand achives a given age.

At regular time intervals, the total number of apices, shoots and their corresponding surface density are computed as descriptors of the clonal growth. The density of the patch is calculated through the evaluation of the average number of shoots and apices in a square cell of size 20x20 cm^2, comparable to the field estimation of shoot density.

In addition to the previous quantities, the total number of genotypes is evaluated in order to obtain a measure of the clonal diversity defined as the ratio between the number of genotypes and the number of living shoots. At the same time, the clonal diversity is determined through two independent procedures that resemble how field measurements are done: *i*) from a fixed number of samples, randomly selected along the whole stand, and *ii*) selecting shoots regularly spaced and distributed along a linear transect. The first procedure is characteristic of small patches (< 300 m^2), whereas the second one is typical in larger sites.

All measurements are finally averaged over 50 different computer runs.

Results and Conclusions

The model has been tested over two different seagrass species from which genotype data is available in the literature: Zostera marina (Billingham et al., 2003) and Posidonia oceanica (Arnaud-Haond et al., 2007). Interestingly, in the case of Z marina the clon diversity has been analysed in patches located in the same geographical area (Ria Formosa, Portugal) and with different sizes, providing information on how the genetic diversity changes with the plant age. This result will be determinant in setting up the effective probability γ ruling the genetic change in our model.

The rest of the model parameters are summarized in the following table.

Z marina	P oceanica
$\rho = 5.1 \pm 0.3$ cm	$\rho = 2.87 \pm 0.20$ cm
$v = 26 \pm 5$ cm yr^{-1}	$v = 6{,}1 \pm 1.0$ cm yr^{-1}
$\nu = 1.6 \pm 0.03$ branches yr^{-1} $apex^{-1}$	$\nu = 0{,}06 \pm 0.01$ branches yr^{-1} $apex^{-1}$
$\phi = 67 \pm 30$ degrees	$\phi = 39 \pm 20$ degrees
$\mu = 1.27 \pm 0.20$ units yr^{-1}	$\mu = 0.16 \pm 0.04$ units yr^{-1}

The growth of Z marina has been simulated over 20 years. At this age the plant covers, on average, a surface of 120 m^2 that is comparable to the data collected from the site of Viveiro da Culatra (Billingham et al., 2003). In the case of P oceanica, the simulation extends over 400 years where typically the plant extends over 1600 m^2. The latter being the typical surface area analyzed for P oceanica (Arnaud-Haond et al., 2007).

A. Clonal growth

Results of the clonal growth for Z marina are shown in Figure 1. Two different regimes can be easily identified. At small ages (< 7 years) the number of nodes (and apices as well) grow exponentially with an exponent that corresponds to the frequency of horizontal branching (ν), as expected. This period is characterized by low density stands with little competition among shoots for resources (nutrients or light). At ages above 10 years the density of nodes increases considerably, the space becomes tightly occupied and competition among nodes is important enough to modify the plant growth.

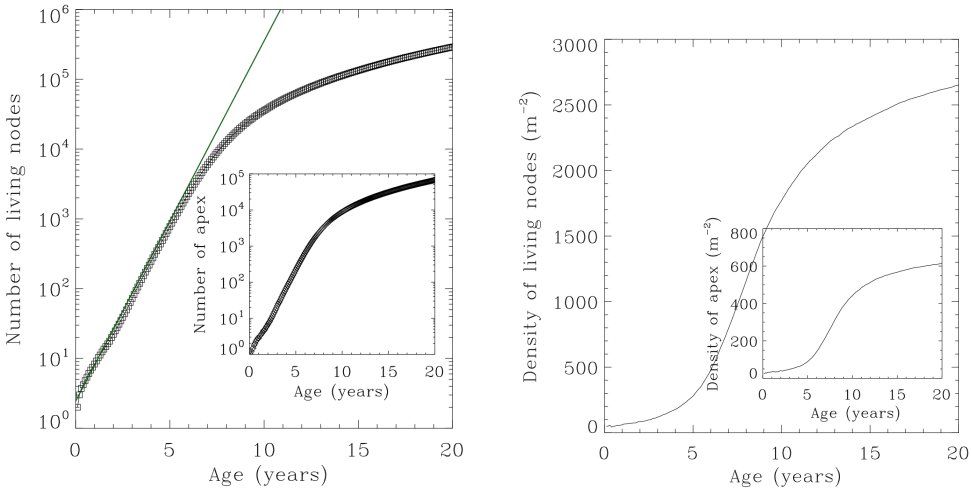

Fig.1 (left) change in the number of nodes and apices –inset- for Z marina. (right) change of the patch density with plant age.

Similar results are found for P oceanica (Figure 2)

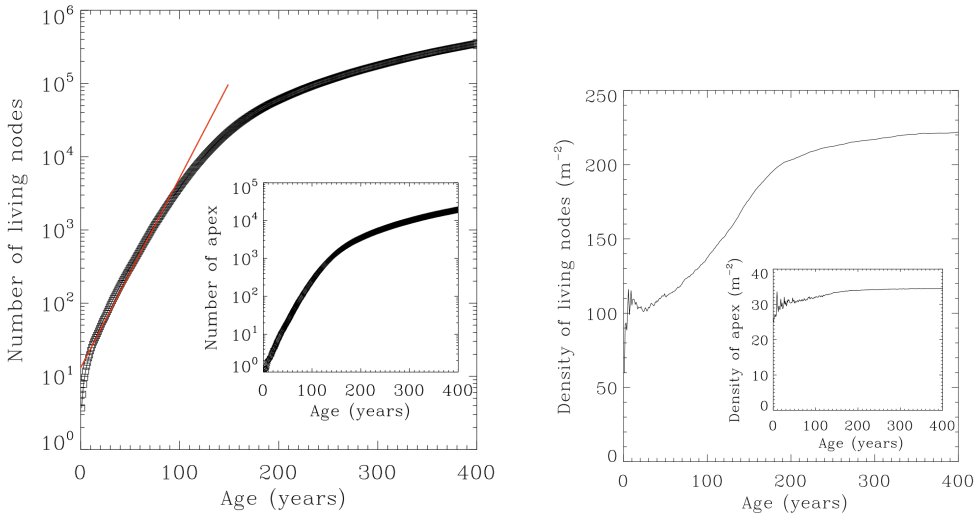

Fig.2 (left) change in the number of nodes and apices –inset- for P oceanica. (right) change of the patch density with plant age.

B. Genetic diversity

The genetic diversity, defined as the ratio between the number of distinct genets and the number of nodes analysed, has been evaluated in the following ways:

i) Number of distinct genets found in a sample of a fixed number of nodes randomly selected.
   - Z marina: 30 nodes (typical sampling size in patches of size > 100 m^2)
   - P oceanica: 40 nodes (typical sampling size in patches covering 1600 m^2)

ii) Number of genets found along a linear transect crossing the seagrass stand selecting shoots regularly spaced. The selected separation enables us to perform an average sampling comparable to the experimental ones.
   - Z marina: separation distance between nodes: 40 cm. For instance, 5 nodes are selected on average in a patch extended over 10 m^2, and 26 nodes in a patch size of 120 m^2. These quantities are comparable to those performed at Viveiro da Culatra (Billingham et al., 2003).
   - P oceanica: a separation of 80 cm is used to ensure an average sampling size of 35 nodes, comparable to the experimental values (35-40) (Arnaud-Haond et al., 2007).

iii) Taking the ratio between the overall number of distinc genets in the model sample and the total number of nodes.

The effective probability of genetic change has been set for both species to:
$\gamma = 0{,}0015$ apex^{-1}yr^{-1}

This value of γ best fits the experimental findings of a clonal diversity following the analysis depicted in sections: *i*) and *ii*). It is close to 0,20 for Z marina (see Viveiro de Culatra in Billingham et al., 2003); and close to 0,60 in P oceanica (several sites along the Mediterraneal coast in Arnaud-Haond et al., 2007).

Two different snapshots of Z marina and P oceanica are presented in Figure 3.

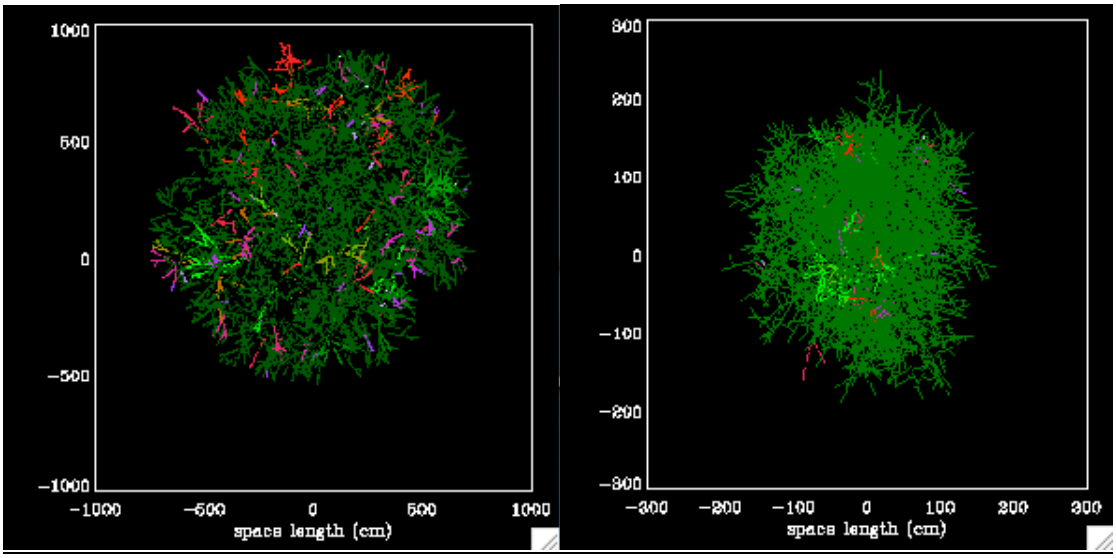

Fig. 3 (left) Snapshot of P oceanica after 150 years. The plant extends over 125 m^2, contains 22275 nodes and 135 distinct genets - identified with different colours- . (right) Snapshot of Z marina after 7,5 years. Area covered: 10m^2 and contains 10300 nodes and 29 distinct genets.

The change of the clonal diversity with the patch size is summarized in Figure 4. The red line corresponds to a samping along the linear transects. The blue line provide the results for a fixed randomly selected number of samples. The black line correspond to the true clonal diversity considering the whole stand.

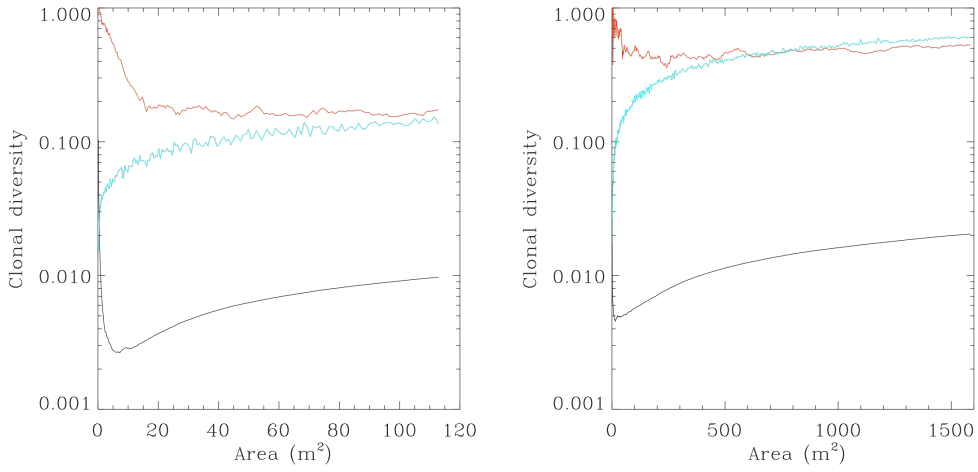

Fig. 4. (left) Change in the genetic diversity in Z marina. (right) same a before for P oceanica.

In both cases, we can observe an overstimated clonal diversity of more than one order of magnitud when it has been measured within a reduced sampling size. The sampling method, either selecting nodes randomly either along a linear transect does not provide significant differences for large seagrass meadows and both converge to the same value. The initial differences found at small patch sizes is simply due to the fact that there is a small (even a single) genotype, whereas the sampling size is larger where a fixed number of samples is considered (30 for Z marina and 40 for P oceanica).

The dependence of the measure of the clonal diversity with the sampling size is analysed in Figure 5. We can observe a monotonically decrease in the clonal diversity with increasing number of units genotyped. The clonal diversity can be fitted assuming a power-law behavior and two regimes can be identified. For a sampling size below the real number of distict genets the clonal diversity decays with an exponent -0,18, whereas for a larger sampling size it decays with an exponent -0,60. This result can be explained in the sense that considering a large number of sampling units (above the total number of genets) all distinct genotypes can be identified, and this quantity is kept constant, whereas the sampling size keeps increasing, thus reducing the ratio, until the real value is achived.

Our results indicate that, no matter the sampling methodology, the sampling size becomes crucial in determining the real genetic diversity in seagrasses populations.

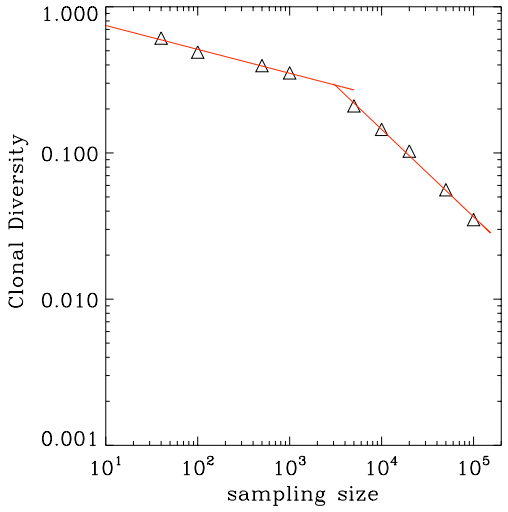

Fig. 5. Dependence of the genetic diversity with the sampling size. Data corresponds to P oceanica meadows at an age of 400 years. Assuming a powe-law behavior, two distinct regimes can be identified with slopes -0,18 and -0,60 for small and large sampling sizes, respectively.

References

- S. Arnaud-Haond, M. Migliaccio, E. Díaz-Almela, S. Texeira, M. Susanne van de Vliet, F. Alberto, G. Procaccini, C. M. Duarte and E. A. Serrão (2007), *Vicariance patterns in the Mediterranean Sea: east-west cleavage and low dispersal in the endemic seagrass Posidonia oceanica*, J. Biogeography **34**, 963-976.
- M.R. Billingham, T.B.H. Reusch, F. Alberto and E.A. Serrão (2003), *Is asexual reproduction more important at geographical limits? A genetic study of the seagrass Zostera marina in the Ria Formosa, Portugal,* Marine Ecology Progress Series **265**, 77-83.
- N. Marbà and C.M. Duarte (1998), *Rhizome elongation and seagrass clonal growth*, Marine Ecology Progress Series **174**, 269-280.
- P. Meakin (1997), *Fractals, scaling and growth far from equilibrium*. Cambridge: Cambridge University Press.
- T. Sintes, N. Marbà, C.M. Duarte and G. Kendrick (2005), *Non-linear processes in Seagrass Colonisation Explained by Simple Clonal Growth Rules*, Oikos **108**, 165-175.
- T. Sintes, N. Marbà and C.M. Duarte (2006), *Modeling non-linear seagrass clonal growth: Assessing the efficiency of space occupation across the seagrass flora*, Estuaries, **29**, 72-80.
- B. Vidondo, A. Middleboe, K. Stefansen, T. Lützen, S.L. Nielsen and C.M. Duarte (1997), *Dynamics of a patchy seagrass (Cymodocea nodosa) landscape. Size and age distributions, growth and demography of seagrass patches*, Marine Ecology Progress Series **158**, 131-138.