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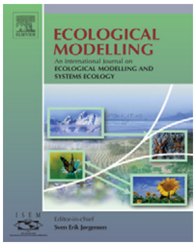

Clonal growth dynamics of the invasive *Carpobrotus affine acinaciformis* in Mediterranean coastal systems: A non-linear model

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ABSTRACT

Carpobrotus affine acinaciformis is one of the most harmful invasive plants in the Mediterranean basin. In this study, we built a numerical growth model containing simple, and essentially linear, growth rules that provided us a tool capable to analyse the complex non-linear behaviour observed in the dynamic growth of *Carpobrotus* spp. This model includes a set of ecologically relevant parameters such as: (1) the stolon elongation rate, setting the upper limit of the horizontal spreading of the clone, (2) the branching rate, closely related to the capacity of the plant to occupy the space forming a dense and complex network, (3) the branching angle, which is determinant in the efficiency of the space occupation during the growth process, (4) the node mortality, and (5) the node branching age. We found that young patches of *Carpobrotus* (<20 years old) are characterised by a biomass production and quantity and density of nodes that grow exponentially with an exponent that depends on the branching probability and the stolon elongation rate. The expansion in the diameter is initially produced from a very ramified morphology, characterised by a fractal dimension $D_f = 1.2$ (100 nodes; <5 years old; velocidad ≈ 0.3 m/year) that later turns into a more compact plant with less occupied space in its interior (20,000 nodes; >50 years old; speed keeps oscillating around 0.27 m/year further on) with a dimension equal to the euclidean one ($D_f = d = 2$). Regarding the implications for the management of *Carpobrotus*, it is remarkable that with few relevant parameters we have been able to reproduce the patch dynamics of this plant, which may indeed be quite useful to improve the yield prediction of *Carpobrotus* growth in coastal Mediterranean zones. Our modelling approach can further be extended to interdisciplinary problems in which dendritic patterns and branched structures are developed.

1. Introduction

In spite of genetic variability and intrinsic capacities, one of the characteristics which increase the probability of growth successful invasion is the ability of clonal growth (Heger and Ludwig, 2003). This type of asexual reproduction predominates in invasive perennial weeds (Boose and Holt, 1999 and references therein) and has been implicated as a greater liability to native flora than seed-producing species (Pyšek et al., 2003). There are several advantages associated

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with the reliance on clonal growth for population expansion (Lambrecht-McDowell and Radosevich, 2005 and references therein): (1) increases the potential to access unevenly distributed resources, such as light and water (Stuefer, 1996), (2) increases the capacity to recover from stresses such as defoliation, (3) rapidly captures and dominates an area, competitively excluding others species, and (4) changes the spatial and/or temporal distribution of ramets (Elberse et al., 2003).

A single initial clonal exotic plant introduction may act as exclusive founding population (Kowarik, 2003), like the highly invasive Japanese knotweed *Fallopia japonica* (Bailey and Conolly, 2000) or the green algae *Caulerpa taxifolia* (Meinesz, 1999). Within the Mediterranean area, we can find some examples of important invaders with asexual reproduction like *Oxalis pes-caprae* L., *Arundo donax* L., *Lemna minuta* Kunth, *Eichhornia crassipes* (Martius) Solms-Laubach, *Kalanchoe daigremontiana* R Hamet & H Perrier, *Opuntia* Miller spp., or *Agave* L. spp. However, one of the most dangerous invader clonal plant in coastal ecosystems is the South African *Carpobrotus affine acinaciformis*, particularly in the western coastal zones of the Mediterranean Basin. Both its fast clonal growth rate and its adaptability to extreme environmental conditions promote a great potential for spatial occupation, with subsequent negative consequence for the native flora (D'Antonio and Mahall, 1991; D'Antonio et al., 1993; Weber et al., 1998; Vilà et al., 2004; Suehs et al., 2004; Moragues and Traveset, 2005). The goal of the present study is to improve reliable estimates of the highly clonal *C. affine acinaciformis* growth and yield.

Numerical growth models are useful management planning tools. Moreover, the long-term impact of different harvesting strategies can be analysed and assessed for sustainability by simulating a variety of logging scenarios. To this end, we have developed a numerical model to simulate the growth dynamic of *Carpobrotus* spp. exhibit, as other typical stoloniferous plants, a highly organized clonal growth that can be described according to a set of simple rules (Bell, 1993). These rules are adequately represented by the stems growing along the substrate surface according to a regular structure of internodes between consecutive nodes, where *internodes* are the distances (or intervals of stem) between two nodes and a *node* is the point on the stem at which one or more leaves are inserted.

The possibility to describe the clonal growth from a few simple growth rules has been used to model space occupation in other species, mainly marine seagrasses (Routledge, 1990; Oborny and Cain, 1997; Marbà and Duarte, 1998; Sintes et al., 2005). These modelling exercises have allowed the description of network development (Bell, 1993; Brouns, 1987; Callaghan et al., 1990; Molenaar et al., 2000), the forecast of the spatial distribution of the clones in favourable and unfavourable environments in response to their foraging behaviour (e.g.,Sutherland and Stillman, 1990; Cain, 1994; Cain et al., 1996), and the test of the adaptive advantages of rigid or plastic growth in clonal plant populations (Oborny, 1994). While many of the works about horizontal growth are related to seagrasses, fewer examples are associated with terrestrial plants (Bell and Tomlinson, 1980; Callaghan et al., 1990). There has been also evidenced that clonal growth, either in seagrasses (Marbà and Duarte, 1998) or in terrestrial rhizomatous plants (Cain, 1990), involves non-linear processes resulting in faster space occupation rates than those predicted by simple radial growth models.

The formation of patterns reaching a high level of complexity from simple rules is also a subject of intense research in non-linear physics. Two basic models have become a paradigm of non-equilibrium growth models: the Eden model (Eden, 1961) and the diffusion limited aggregation (DLA) model (Witten and Sander, 1981). The Eden model was primarily developed to investigate the growth of biological cell colonies, and its main features are the following: initially, one site on a lattice is selected and filled representing a seed particle; the unoccupied nearest neighbour lattice sites to the seed defines its perimeter. In the simplest realization of the Eden model, a perimeter site is selected at random with equal probability and it is filled representing the growth process. This process can be repeated many times until a large circular and compact cluster with a rather rough surface is generated. In the DLA model, once the initial seed is placed, a new particle is released into the system, far away from the seed, and performs a random walk onto the lattice until eventually reaches a perimeter site. Then, this particle is incorporated to the growing cluster and the lattice site is filled. After repeating this process many times a branched structure is formed. The lack of penetration of the particles to the interior of the cluster is a consequence of the strong screening effect produced by the outer regions of the cluster. The two different cluster morphologies can be characterised by computing their fractal dimension D_f. A cluster containing N units is related to its typical linear size L (e.g., its radius) by $N \approx L^{Df}$. If the cluster is compact, $D_f = d$, where d is the Euclidean space dimension; whereas for a branched or porous object $D_f < d$. These models have been done on the basis of a wide range of applications in both physical and biological sciences, from the study of skin cancer (Williams and Bjerknes, 1972) to urban development (Batty, 1991).

In this paper we have studied the development of single clones of *C. affine acinaciformis* for which we have gathered extensive field data on its clonal growth rules. By using a growth model based on the formation of complex structures, we demonstrate the emergence of complex non-linear behaviour arising from simple growth rules. The parameters describing the clonal growth (Table 1) are all ecologically relevant, and the results have been analysed in the context of the two models described above (Eden and DLA models).

2. Methods

2.1. *Study species*

Our focal species is *C. affine acinaciformis* (L.) L. Bolus (Aizoaceae) (*Carpobrotus*, hereafter) was introduced in Europe since the end of the 17th century (Fournier, 1952) and it probably entered the Balearics about 30 years ago. It is quite likely of hybrid origin with *C. edulis* (L.) L. Bolus (Suehs et al., 2004). It is used a very common ornamental plant because of its fast growth rate and its low water requirements. It is a stoloniferous plant with an extensive plagiotropic monopodial system, with a radial patch growth, and with a basic structure of nodes and internodes (Wisura and Glen, 1993). The fruits are succulent and contain over a thousand seeds, which are commonly

Table 1 – *Carpobrotus* growth rules used in the numerical model (mean ± S.E.)

Parameter	Unit	Symbol	Value
Internode length (long shoots)	cm	ρ	4.59 ± 1.06
Stolon elongation rate	cm year^{-1} stolon node^{-1}	u	29.37 ± 9.35
Branching rate	Branches year^{-1} stolon node^{-1}	ν_b	1.54 ± 0.51
Branching angle	Degrees	ϕ	57 ± 19
Node mortality rate	ln units year^{-1}	μ_r	0.19 ± 0.03
Node branching age	Year	τ	>2.08
Radius of exclusion area[a]	cm	σ	4.5

[a] Parameter estimated with the model.

dispersed by rabbits and rats to short and long distances, which facilitates the expansion and spreading of the plant (D'Antonio, 1990; Bourgeois et al., 2005).

2.2. *Study site*

The study site was carried out in four coastal localities of Mallorca, the largest island of the Balearic Archipelago, located at the Western Mediterranean Basin. Three of the sites are located on rocky coast areas near the sea in the southern part of the island (Cala Figuera, Cap Enderrocat and Ses Salines) while the other is located in a dune ecosystem at the north (Son Serra de Marina). The predominant plant communities at Cala Figuera and Cap Enderrocat consist of the typical coastal xerophytic vegetation, characterised mainly by *Olea europaea* L. subsp. *sylvestris*, *Pistacia lentiscus* L., *Cistus monspeliensis* L. and *Anthyllis cytisoides* L. At Ses Salines, *Carpobrotus* is located within a shrubland sea-level community, where *Pistacia lentiscus* and *Juniperus phoenicea* L. subsp. *turbinata* (Guss.) Nyman are the most abundant species; lastly, Son Serra is characterised by the typical dune flora with predominance of *Ammophila arenaria* (L.) Link and shrubs like *Cistus salviifolius* L. and *Pistacia lentiscus* in the post strip of dunes.

2.3. *Measured traits in the Carpobrotus clones*

At each site, we sampled three clones of *Carpobrotus* of similar size and located under sunny conditions. We measured the number and the distance between nodes in two different kinds of shoots: long shoots and short shoots. Both of them are macroblasts, although they appear to have different functions. Long shoots contribute to 'explore' the environment extending the framework of the plant into new territory. In contrast, the short shoots are located along the long shoots and serve to 'explote' the occupied site; they contribute to plant volume increase, without or with little influence on horizontal plant growth (Traveset et al., in press). Apical meristem of short shoots eventually ceases vegetative growth or differentiates into a non-meristematic structure unable of continued extension, such as a flower. Also, a predictably short shoot bud may occasionally develop as a long shoot if its bearing axis is damaged. Both types of shoots, but especially short ones, often have a precise and consistent number of foliar components for each increment of growth (Bell, 1993). When building the model, we have considered only growth rate of long shoots. We monitored a total of 72 long shoots, three for each clone.

For a period of 2 years (2002–2003), we bimonthly measured growth rates in each type of shoot. Annual growth rate was obtained by averaging the growth during the 2-year periods (from August 2001 to June 2002 and from August 2002 to June 2003); every annual period is the sum of the node lengths every 4 months. Previously to pooling data from both years, we tested with a paired samples *t*-test that the two study years had similar growth rates.

2.4. *Numerical model*

We developed a numerical model to study the growth dynamics of *Carpobrotus* based in simple growth rules. This model uses a set of parameters (see Table 1) to simulate the development of complex networks including: stolon elongation (or internode length) ρ, stolon elongation rate u, long shoot branching rate ν_b, and its corresponding branching angle ϕ, node mortality rate μ_r, and node branching age τ (the average age beyond which a node is able to develop long branches). The estimated values for these set of parameters, as well as their standard deviation, have been derived from the field measurements obtained as described in Section 2.3 and the results are summarized in Table 1. In addition, the model accounts for the two following facts: it has been observed that 8.82% of the nodes do not branch, and we include an exclusion circular area of radius $\sigma < \rho$ (see Table 1) around the location of each node where no other node can settle to prevent the system from crowding. The value of the exclusion radius σ has been estimated by fitting this parameter to achieve the surface node density reported in natural stands of the species.

We examined the behaviour of relevant variables such as the dry biomass production, the internal density of nodes and the radial external apices of long shoots. These parameters are sufficient to develop a reliable growth model because vascular plants do exhibit the phenomenon of reiteration (Bell, 1993). The input parameters, given by their averaged and standard error values (see Table 1), derived from empirical field observations, were sampled at each time step by the numerical model from their corresponding Gaussian distributions characterised by their mean and standard deviation values, thereby accounting for the variability of these rules.

The simulation starts by placing a new individual from a rooted node at a coordinate $\mathbf{r}_i$. We assign to this node a randomly oriented stolon elongation velocity vector $\mathbf{u}_i$, setting the direction of the stolon extension, and a per capita distance between consecutive nodes ρ_i. The model iterates the growing process according to the following steps:

1. The stolon is proposed to grow from $\mathbf{r}_i$ to $\mathbf{r} = \mathbf{r}_i + \rho_i \mathbf{v}_i$, where $\mathbf{v}_i = \mathbf{u}_i/|\mathbf{u}_i|$ is a unitary vector director pointing in the direction of the stolon extension. The proposal will be accepted while the position of the proposed new node $\mathbf{r}$ does not fall into the exclusion area of any other node (i.e., the exclusion area principle is maintained) preserving stand density and avoiding the same position to be simultaneously occupied by more than one node. Then, a new potential branching node is added to the position $\mathbf{r}$ where a new long shoot will develop. A long shoot (monopodial axis) bears its own axillary shoots each with a fixed or flexible potential for development. In this process the direction of growth $\mathbf{v}_i$ does not change.

   Due to the apical dominance, step 1 is repeated, starting from the position of the last added node, until the branch contains potential branching nodes, that is, nodes older than the node branching age τ (Table 1). Extending growth at the distal ends is matched by death and disintegration at the proximal ends resulting in mobile organisms. Then we can proceed to step 2.
2. A potential branching node older than τ is selected at random (i.e., located at position $\mathbf{r}_b$) and a new long shoot (with a growing potential branching nodes) may develop at this point with probability ν_b per unit time (Table 1). Thus, the probability that a particular meristem will branch is given by the product $\nu_b \times \rho \times u^{-1}$, where u is the stolon elongation rate and ρ the internode length. A new long shoot will extend along a new vector $\mathbf{u}'$ forming an angle ϕ with $\mathbf{u}$, randomly oriented along the right or left side of $\mathbf{u}$. Only one long shoot is possible departing from $\mathbf{r}_b$. Additionally, the empirical fact that 8.82% of the long shoots does not branch is also incorporated in the model.
3. During step 1 or step 2, time is increased by an amount $\Delta t = \rho/(uN_a(t))$, being ρ is the distance between consecutive nodes (internode length) and $N_a(t)$ the number of potential branching nodes at time t.
4. Within this time step Δt, $\mu_r \Delta t$ nodes are selected at random, since the node mortality (μ_r) is assumed to be an age-independent, and are removed from the plant.

At regular time intervals (0.5 year) the total number of internodes, nodes and length of stolon produced are computed from which we can estimate the dry biomass production. The linear extension of the patch size is measured through the evaluation of the patch radius. The density of the patch is calculated through the measure of the average number of nodes in a square cell of size 20 cm × 20 cm and radial external apices of long shoots, comparable to the field estimation of node density.

We simulated the model over 100 years of plant growth and the computed data was averaged over 100 replicated runs to yield estimates of the average patch structure at each time step. In order to efficiently determine the available space for new nodes preserving the criteria of excluded area, we implemented a link cell method (Allen and Tildesley, 1987). The model was written in Fortran and was run on a parallel Beowulf computer.

3. Results

We analysed the change in time of the number of living nodes and potential branching nodes of long shoots and the overall stolon length production (Fig. 1). The dry biomass associated to the alive patch, as well as the overall necromass, was estimated from the measurement of the dry weight of the stem (0.17 ± 0.01 g/cm) and leaves (2.51 ± 0.19 g/leave) (Fig. 1a). The plot in semilog scale indicated a rapid exponential growth with time, shifting to a slower growth after approximately 20 years. A similar behaviour was observed in the change of the number of living nodes and potential branching nodes $N(t)$ (Fig. 1b). In both cases, the rapid initial increase was described by an exponential equation of the form:

$$N(t) \propto e^{(0.48\pm0.02)\mathrm{age(years)}} \tag{1}$$

In order to understand the above results we proposed a simple theoretical model. During the early stages of the plant growth, the outgrowing long shoots basically grow independently of each other, so that the process can be described by a time delay differential equation:

$$\frac{dN(t)}{dt} = \kappa N(t-\tau) \tag{2}$$

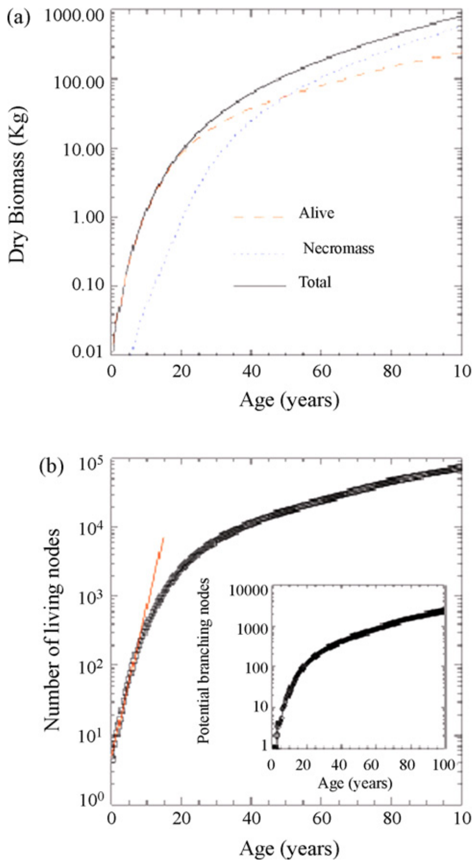

Fig. 1 – Non-linear time change in the (a) overall stolon length production (dry biomass) of *Carpobrotus affine acinaciformis* and (b) the number of living nodes and potential branching nodes of long shoots.

where κ is related to the branching and node mortality rates as $\kappa = (p\nu_{\mathrm{b}} - \mu_{\mathrm{r}})$, being p is the probability that a long shoot might produced lateral long shoots. From empirical observations it was found to be $p = 1 - 0.0882$. τ is the minimum estimated node age that could produce lateral long shoots (node branching age) (Table 1). In order to solve Eq. (2) we assumed $N(t)$ to grow exponentially with an effective exponent ω: $N(t) \propto e^{\omega t}$. Replacing this expression in Eq. (2) we obtained a transcendental equation for ω:

$$\omega = \kappa \exp(-\omega\tau) \qquad (3)$$

The solution of Eq. (3) got $\omega = 0.465$. This result was in agreement with our numerical findings 0.48 ± 0.02 (Eq. (1)).

The density of living nodes and of potential branching nodes was found to increase rapidly until an age of 20 years and then evolved towards a *plateau* value of about 170 living nodes/m^2 and 30 potential branching nodes/m^2 (Fig. 2).

In order to characterise the patch morphology we determined the fractal dimension of the growing patch D_{f}. As described above, a cluster containing $N(t)$ potential branching nodes was related to its characteristic linear size $L(t)$ by $L(t) \propto N(t)^{1/D_{\mathrm{f}}}$. In Fig. 3, we represented it in a double log plot, $L(t)$ versus $N(t)$. We identified two clear regimes. At the early stages of the plant growth, for patches containing less than 100 nodes (<5 years old), the best fit to the data leads to $1/D_{\mathrm{f}} = 0.83 \pm 0.08$. This slope continuously decreases with increasing patch size until a value of $1/D_{\mathrm{f}} = 0.50 \pm 0.01$ was reached. The latter value describes the pattern of large patches, above 20,000 nodes (>50 years old). In between, the transition zone was characterised by a low increase in the patch size despite the increasing number of shoots, indicative of the internal patch compactation. The evolution between both regimes is illustrated in Fig. 4 where different snapshots of the plant at different ages are presented. Initially (5 years), the clon was mainly elongated containing few long shoots (Fig. 4a). The number of directions of growth rapidly expanded, yielding after about 20 years, a rather circular shape (Fig. 4c). The compactation was progressively more notorious and in the final stage (50 years) the plant growth took place mainly along the perimeter line in a radial direction (Fig. 4d). The clon shape shifted from an almost linear weakly branched structure, with a characteristic fractal dimension $D_{\mathrm{f}} = 1.2 \pm 0.1$ (Fig. 4a) to a compact one where $D_{\mathrm{f}} = 2$ equal to the Euclidean space dimensionality (Fig. 4d).

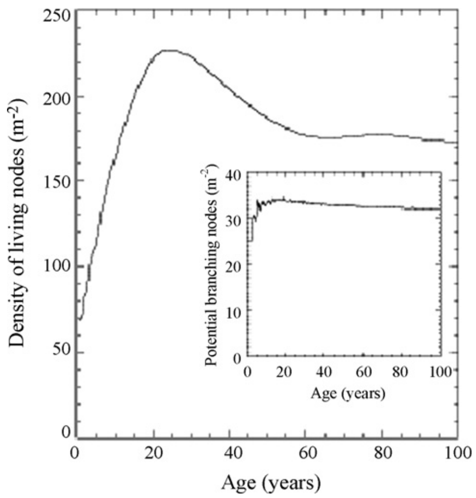

Fig. 2 – Change in density of living nodes (nodes/m^2) and potential branching nodes/m^2 of *C. affine acinaciformis* across time.

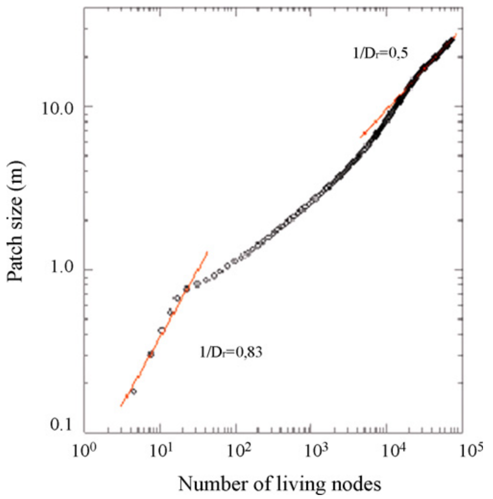

Fig. 3 – C. *affine acinaciformis* patch morphology determined by the fractal dimension of the growing patch Df.

The change in the characteristic linear patch size $L(t)$ given by the averaged diameter patch size, was also studied. At the early stages, an exponential growth was found:

$$L(t) \propto e^{(0.42\pm0.03)\mathrm{age(years)}} \qquad (4)$$

where the exponent could be directly related to the effective growing exponent ω and the fractal dimension of the plant D_{f}. Since $N(t) \propto e^{\omega t}$ and $L(t) \propto N(t)^{1/D\mathrm{f}}$ we expect $L(t)$ to grow exponentially with a characteristic exponent $\omega/D_{\mathrm{f}} = 0.39 \pm 0.04$. This result is in a reasonable agreement with our best fit to the data 0.42 ± 0.03 (Eq. (4)).

The patch growth rate was defined as the time derivative of the linear patch size dL/dt and provided information on the space colonization rate of the clone (Fig. 5). Young clones spread with growth rates below the stolon elongation rate $u \approx 0.3$ m/year (Table 1). This growth rate increased with the plant age until it reached a value close to the stolon elongation rate (≈50 years), keeping oscillating around 0.27 m/year further on. The age at which the plant reached its maximum value was rather circular in shape and compact (Fig. 4d), with a fractal dimension $D_{\mathrm{f}} = d = 2$ (Fig. 3). The subsequent oscillations could be identified with a radial spread followed by compacting processes. This result evidenced the non-linearities present in the growth dynamics of such plant.

Since the branching was controlled by the effective exponent ω (Eq. (3)) and the branching angle ϕ (Table 1) that could take place clockwise and counter-clockwise with equal probability, the time to the regime shift t_{R} could be estimated as $t_{\mathrm{R}} = 180^\circ/(\phi\omega/2) \approx 13 \pm 5$ years, comparable to the observed in our simulations (Fig. 2). That period was a qualitative estimation, according to empirical data, of the transition area from an exponential to a uniform growth.

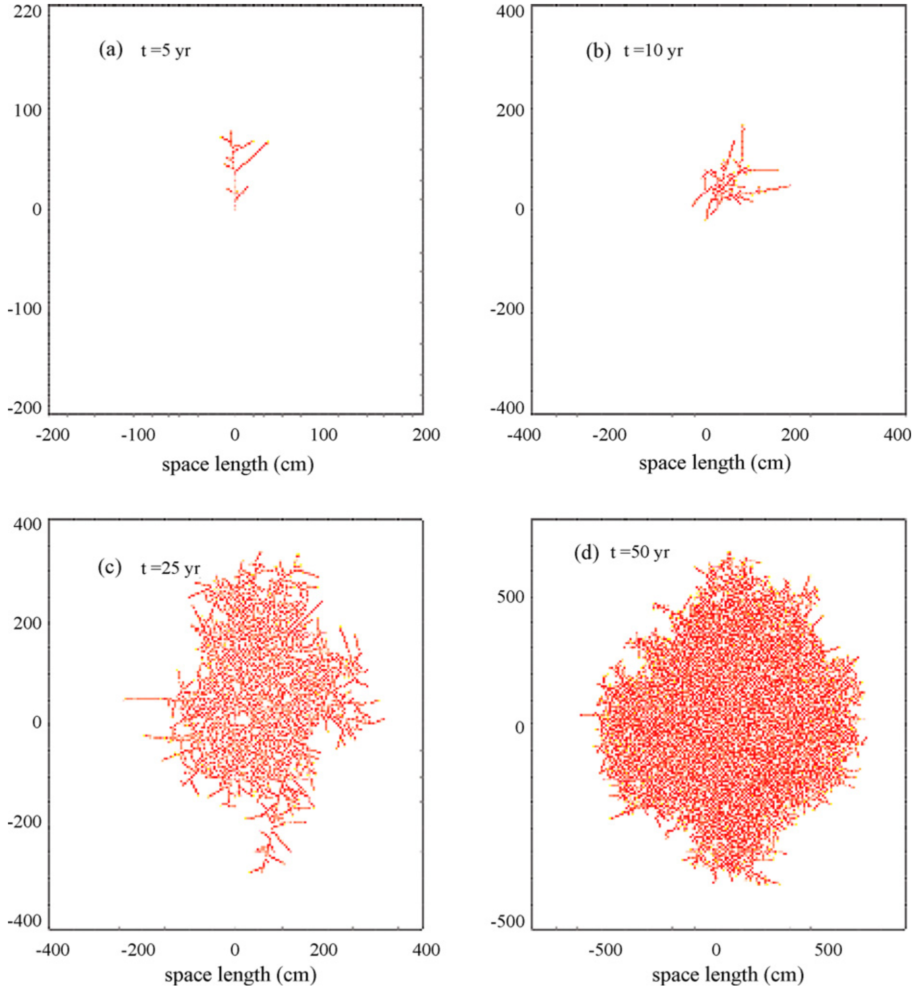

Fig. 4 – Morphology time transition of C. *affine acinaciformis*. From an opened clon (a) structure to an internal patch compactation (d).

4. Discussion

We found that young patches of *Carpobrotus* (<20 years old) are characterised by a biomass production that grows exponentially with an exponent that depends on the branching probability and the node branching age (apical dominance), which prevents a node – below 2 years old on average – to generate primary lateral branches. During this period of maximum growth, the values of alive biomass overcomes the values of necromass until *c*. Fifty years, time at which the volume of necromass is greater than that of alive biomass. This great increase in production values is due to the intrinsic characteristics of the plant as well as to the habitat traits where it lives, because the nitrophylous environments associated to coastal environments promote an increase of biomass and water assimilation (Ungar, 1991). In the model, we did not incorporate empirical data on decomposition rates, and thus, the high values of necromass are not completely realistic. This production rates reflect only the great amount of matter that a single *Carpobrotus* individual is able to generate in time and it is an indicator of the great effort handed for the transport and removal of vegetal material in eradication projects. For instance, in the island of Menorca (Balearic archipelago, Spain), a total of 900 tonnes of *Carpobrotus* plants have recently been eradicated from an extension of ca. 24 ha (Fraga et al., 2005).

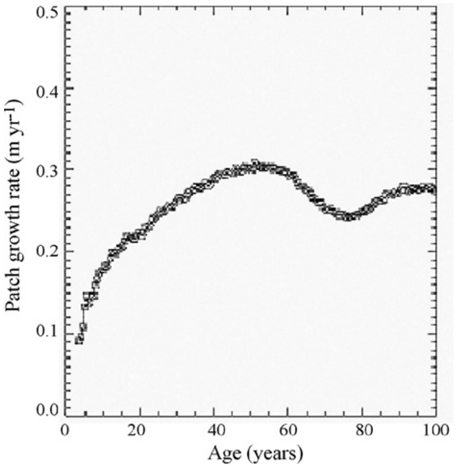

Fig. 5 – Space colonization rate of C. *affine acinaciformis* according to the linear patch size.

A similar non-linear growth behaviour as that found with biomass production has also been observed both with the quantity and density of nodes that a plant develops and which potentially can turn into new shoots of apical growth. This implies that it is during the first years of life when *Carpobrotus* invests much energy in its horizontal expansion and in the colonization of new areas, increasing its clone diameter. An exponential growth in volume occurs during the first 20 years, followed by a slight decrease that later becomes stabilized. The observed regime change during the growth of the clone around an age of 20 years can be attributed to crowding, where node space competition becomes relevant and, thus, a slow down of the growing rates takes place. This raise in volume is due to the growth of new branches over old ones, forming an inferior layer of necromass, of difficult and slow degradation (Vilà et al., 2006), and a superior layer of alive matter.

The expansion in the diameter of *Carpobrotus* is initially produced from a very ramified morphology, characterised by a fractal dimension $D_f = 1.2$ (100 nodes; <5 years old; patch growth rate <0.3 m/year) that later turns into a more compact plant with less occupied space in its interior (20,000 nodes; >50 years old; speed keeps oscillating around 0.27 m/year further on) with a dimension equal to the Euclidean one ($D_f = d = 2$). First, the interstices left behind during the early stages of clonal growth have been filled and the growth takes place mainly along the perimeter of the plant where most of the potential branching nodes are located. When the plant morphology looks rather compact, the density of nodes has reached a plateau value and the patch growth rate is close to the stolon elongation rate. We were able to estimate the time to the regime shift that depends on the stolon branching frequency, branching angle and the apical dominance, consistent with the simulation results. Such a compacting process of the clone is produced when it is ca. Fifty years old, and from then on the plant acquires a radial growth that will be maintained and developed through the rest of its life. As suggested in previous studies (Sintes et al., 2005), the critical event that accounts for the shift between the two growth modes requires the plant to progress from an initial random directional growth to a uniform centrifugal one. The latter can be achieved when enough branching events have taken place in order to allow a growth direction rotated 180° relative to the initial one.

Such a non-linear evolution both in biomass production and in the formation of alive nodes and potential branching nodes (Eq. (1)) converges, in its initial phase, to a theoretical exponential growth form that is governed by a time delay differential equation (Eq. (2)).

4.1. *Comparison with other models*

Several models have been developed in the past for clonal plant growth, mainly devoted to aquatic plants, that are typically classified into empirical and mechanistic models (Carr et al., 1997). Whereas mechanistic models calculate the plant growth from physiological processes, such us photosynthesis, disregarding the effects of clonal architecture, empirically designed models use specific growth rules involving a small set of parameters. Among them, typical ranges and standard deviations of rhizome lengths, branching frequency, branching angles, etc. are considered to generate simulations of growing patterns. A detailed classification of the different models used up to date can be found in the paper by Wolfer et al. (2006).

Since mechanistic models disregard clonal architecture, and spatial strategies for clonal plant propagation are missing. On the other hand, previous empirical models (Bell, 1979; Brouns, 1987) that simulated the growth of clonal plants on the basis of deterministic architectural parameters, did not incorporate their variability observed in the field, often failing to account for the interactions between neighbour nodes. More elaborated stochastic models (Callaghan et al., 1990) contain more than 12 parameters which makes it difficult to extract the key parameters responsible of clonal growth. More recent lattice models (Oborny, 1994) force the plant to grow on the lattice which constrains the value of the branching angle. In a recent paper, a simulation model for the *F. japonica,* using a 3D correlated random walk model has been presented (Smith et al., 2007). However, that study focuses mainly on the behaviour of the crown density and does not account for possible non-linear effects that are observed in the patch dynamics of clonal plants.

We have presented here an empirical model that allows us to study the effects and implications of simple but specific growth rules on the patch formation and growth on small and large scales. For example, how non-linear patch growth rates can emerge from a given uniform stolon elongation rate? Which are the key parameters controlling such non-linearities? Can we determine the age of the plant at which the transition between different regimes take place? We provide an answer to each of these questions. In contrast to other models, we here combine: (a) simulations performed in the contiuum space; (b) simplicity, since a small set of parameters taken from fieldwork is used; (c) variability and plasticity, since the parameters are characterised by their mean and standard deviation values helping to incorporate in the model any possible adjustment of the clonal architecture to external factors.

The results have been analysed in the physics base of two paradigmatic out of equilibrium, growth processes: the Eden model and the diffusion limited aggregation (DLA) model. Their connection to the world of fractal structures make possible the extension of our modeling approach to interdisciplinary problems in which dendritic patterns and branched structures are developed. Among them, and of particularly relevance, is the application of these models to urban development that, to a certain extent, might resemble a living system, not to mention any aquatic and terrestrial clonal plants.

In our study we have seen that the branching angle is a key parameter in determining the time to the regime shift from branched to compact structures. Thus, models developed in the continuum are needed to account for correct branching angle and its plasticity. A similar stochastic off-lattice model (Sintes et al., 2005) to the one presented here was developed to study the patch dynamics of seagrasses and succeeded in accounting for the non-linearities observed in the clone spread over time. However, such model did not incorporate the apical dominance ($\tau = 0$) and potential branching nodes were only located at the tips of the main branches.

Regarding the implications for the management of *Carpobrotus*, it is remarkable that with few relevant parameters we have been able to reproduce the patch dynamics of this plant, which may indeed be quite useful to improve the yield prediction of *Carpobrotus* growth in coastal Mediterranean zones. Moreover, the long-term impact of different harvesting strategies will be able to be analysed and assessed for sustainability by simulating a variety of logging scenarios improving our capacity to forecast their expansion rates. Such modelling approach is particularly important since time scales involved in clonal growth can be too long for direct observation.

Possible extensions of our model might incorporate the simultaneous development of two clonally growing and competing plant species, including reproduction modes and intra- and interspecific interactions. Such models have been typically described on a grid bases using random processes neglecting the clonal architecture on a local scale (Winkler and Klotz, 1997).

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