



The role of reproductive plant traits and biotic interactions in the dynamics of semi-arid plant communities

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ARTICLE INFO

Article history:

Received 27 April 2010

Available online 25 September 2010

Keywords:

Competition

Facilitation

Seed dispersal

Vegetative propagation

Self-organization

Scale-dependent feedback

ABSTRACT

The dynamics of semi-arid plant communities are determined by the interplay between competition and facilitation among plants. The sign and strength of these biotic interactions depend on plant traits. However, the relationships between plant traits and biotic interactions, and the consequences for plant communities are still poorly understood. Our objective here was to investigate, with a modelling approach, the role of plant reproductive traits on biotic interactions, and the consequences for processes such as plant succession and invasion. The dynamics of two plant types were modelled with a spatially-explicit integrodifferential model: (1) a plant with seed dispersal (colonizer of bare soil) and (2) a plant with local vegetative propagation (local competitor). Both plant types were involved in facilitation due to a local positive feedback between vegetation biomass and soil water availability, which promoted establishment and growth. Plants in the system also competed for limited water. The efficiency in water acquisition (dependent on reproductive and growth plant traits) determined which plant type dominated the community at the steady state. Facilitative interactions between plant types also played an important role in the community dynamics, promoting establishment in the driest conditions and recovery from low biomass. Plants with vegetative propagation took advantage of the ability of seed dispersers to establish on bare soil from a low initial biomass. Seed dispersers were good invaders, maintained high biomass at intermediate and high rainfall and showed a high ability in taking profit from the positive feedback originated by plants with vegetative propagation under the driest conditions. However, seed dispersers lost competitiveness with an increasing investment in fecundity. All together, our results showed that reproductive plant traits can affect the balance between facilitative and competitive interactions. Understanding this effect of plant traits on biotic interactions provides insights in processes such as plant succession and shrub encroachment.

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1. Introduction

Biotic interactions between plants influence the dynamics of plant communities (Armas and Pugnaire, 2005; Callaway, 2007). Although facilitative interactions are relevant in areas with abiotic stress, such as arid and semi-arid ecosystems (Bertness and Callaway, 1994; Callaway and Walker, 1997), competitive interactions also take place in those ecosystems (Fowler, 1986). Competitive and facilitative interactions frequently act simultaneously (Díaz-Sierra et al., 2010; Holmgren et al., 1997;

Holzapfel and Mahall, 1999), usually affecting plant communities at different spatial scales. While facilitation is a local process, competition for limiting resources (mainly water in arid and semi-arid environments) can occur at a larger spatial scale. This “scale-dependent feedback” between plants and water availability, positive locally and negative farther away, has been shown to be responsible for many regular spatial patterns frequently observed in semi-arid environments (Gilad et al., 2004; Lejeune et al., 2002; Rietkerk et al., 2004; Rietkerk and Van de Koppel, 2008).

From a temporal point of view, facilitation at the establishment stage often shifts to competition at later stages, as the seedlings grow and start competing with the nurse plant for the limiting resources (Miriti, 2006; Schiffrers and Tielborger, 2006). This nurse effect occurring at the establishment stage, although limited in time, is a key process in maintaining the productivity and the biodiversity in arid and semi-arid ecosystems (Aguar and Sala, 1994; Armas and Pugnaire, 2005; Flores and Jurado, 2003).

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The sign and intensity of the biotic interactions between plants is known to be species-specific (Callaway, 1998). Usually nurse plant species have distinctive traits. In arid and semiarid environments, they are typically plants with deep roots, that provide shade, and form fertile soil mounds with improved infiltration (Callaway, 1998) and, at the same time, do not compete for water in the upper layers with seedlings and shallow-rooted plants (Sala et al., 1989). Also, nurse plants are usually stress-tolerant with good colonization ability, being able to establish on bare soil, and to create patches with ameliorated environmental conditions for the establishment of stress-intolerant plants (Soriano et al., 1994). In general, the net outcome of biotic interactions depends on the balance between the stress tolerance and the competitive ability of both the nurse and the facilitated plant (Chen et al., 2009; Choler et al., 2001; Liancourt et al., 2005). Life-history traits that lead to stress tolerance typically reduce competitive ability and vice versa (Grime, 1979). Because of this trade-off, stress tolerant nurse plants often facilitate stress intolerant and more competitive plants, which compete efficiently for resources with the nurse plant (Armas and Pugnaire, 2005; Valiente-Banuet et al., 1991). Thus, plant traits define the plant's strategy to survive in plant communities under limited resources and strongly influence the net biotic interaction between plants (Suding et al., 2003). However, the relationship between plant traits and biotic interactions is still poorly understood.

Here, we wanted to investigate the relationship between plant reproductive traits and biotic interactions in arid and semi-arid environments. We focused on plant reproductive traits for two reasons. First, plant reproductive traits strongly influence establishment which is a key stage in these ecosystems. Second, plant reproductive traits enabling the colonization of bare areas are involved in the trade-off between stress tolerance at colonization and local competitive ability. This trade-off could play an important role for understanding the biotic interactions between plants, especially in spatially-heterogeneous environments like arid and semi-arid environments.

We chose a modelling approach where two plant types were modelled, (1) a plant type with seed dispersal and (2) a plant type with local vegetative propagation. We assumed that the plants with local vegetative propagation invest most of their biomass in growing around the patch that they occupy, and thus, they would be efficient competitors. Plants dispersing by seeds can reach long distances and establish on bare soil, and thus they are, depending on water availability, able to create new patches. Nevertheless, colonization and competition abilities would depend in the last term on plant biological traits such as the investment in fecundity, the seedling establishment ability and the efficiency in water acquisition. In the model, facilitation occurred through a local positive feedback between vegetation biomass and soil water, the main limiting resource. Competition for water occurred at a larger spatial scale than facilitation, as water concentration in vegetation patches led to its depletion farther away (Rietkerk et al., 2002).

2. The model

We modified a spatially-explicit integrodifferential model developed for arid ecosystems (Pueyo et al., 2008; Rietkerk et al., 2002) to describe: (i) plant growth as a saturation function of water uptake, (ii) water flow, infiltration and runoff in unsaturated soil layers and surface, and (iii) plant reproduction, either as vegetative growth or by seed dispersal. Seed dispersal was modelled through an integrodifferential equation (Eq. (1)) that captured non-local dynamics (Andersen, 1991). The biomass invested in seeds, subtracted from the vegetative biomass (the term $-f \cdot S$ in Eq. (1)), was proportional to the plant's biomass by means of the fecundity

value, f , which represented the grams of seeds produced per gram of biomass. Vegetative propagation (Eq. (2)) was modelled with a diffusion term (HilleRisLambers et al., 2001). The clones and seedling establishment depended on water availability.

A detailed description of the model can be found in Rietkerk et al. (2002) and Pueyo et al. (2008). The model reads:

Seed disperser density, S (g m^{-2})

$$\frac{\partial S}{\partial t} = c_S \cdot g_{S \max} \frac{W}{W + k_1} S - (d_S + f) \cdot S + Rc \cdot \frac{W}{W + k_1} \cdot g_S \cdot \int_{\Omega} f S(x', t) \left(\frac{2}{\pi L^2} \right) e^{-\frac{2|x-x'|}{L}} dx'. \quad (1)$$

Density of plants with vegetative propagation, V (g m^{-2})

$$\frac{\partial V}{\partial t} = c_V \cdot g_{V \max} \frac{W}{W + k_2} V - d_V \cdot V + D_V \Delta V. \quad (2)$$

Surface water, O (mm)

$$\frac{\partial O}{\partial t} = R - \alpha \cdot O \frac{(V + S) + k_3 \cdot W_0}{(V + S) + k_3} + D_O \Delta O. \quad (3)$$

Soil water, W (mm)

$$\frac{\partial W}{\partial t} = \alpha \cdot O \frac{(V + S) + k_3 \cdot W_0}{(V + S) + k_3} - g_{V \max} \frac{W}{W + k_2} V - g_{S \max} \frac{W}{W + k_1} S - r_W W + D_W \Delta W \quad (4)$$

where c_S is the conversion of water uptake to the seed disperser's growth, $g_{S \max}$ is the maximum specific water uptake of the seed disperser, k_1 is the half-saturation constant of specific growth and water uptake for the seed disperser, d_S is the seed disperser's mortality, f is the fecundity of seed dispersers, Rc is the maximum specific seed recruitment, g_S is the specific conversion rate of seeds in seedlings, L is the mean dispersal distance, c_V is the conversion of water uptake to growth of the plants with vegetative propagation, $g_{V \max}$ is the maximum specific water uptake of the plant with vegetative propagation, k_2 is the half-saturation constant of specific growth and water uptake of the plant with vegetative propagation, d_V is the mortality of the plant with vegetative propagation, R is the rainfall, α is the maximum infiltration rate, k_3 is the saturation constant of water infiltration, W_0 is the water infiltration rate in the absence of plants, r_W is the water loss due to drainage and evaporation, D_V is the diffusion coefficient for plant vegetative growth, D_O is the diffusion coefficient for surface water, and D_W is the diffusion coefficient for soil water. ΔV , ΔO and ΔW are Laplacian operators for vegetative plant growth, surface and soil water diffusion respectively (HilleRisLambers et al., 2001; Rietkerk et al., 2002). The parameters, their interpretations, units and values are displayed in Table 1.

For simplicity, we assumed that facilitative effects of the plant-water feedback were the same for both plant types (note that the parameter regulating the strength of the plant water-feedback, k_3 , is the same for both plant types in Eqs. (3) and (4)).

We derived a non-spatial version of the model by turning the diffusion terms to zero and the seed dispersal term to $f \cdot S$. We compared the results between the non-spatial model and the spatial model for different reproductive strategies to identify the effect of plant traits on biotic interactions (i.e. competition for water acquisition and facilitation at the establishment stage) taking place in a spatial context. The equilibrium points of the non-spatial model were analytically calculated (Appendix A). The spatial model was solved numerically, performing two-dimensional simulations in a rectangular grid of 128×128 cells with periodic boundary conditions until the steady state was reached. Cell size was 2×2 square meters, and the time step was

Table 1

Abbreviation, description, units and values of the model's parameters.

Parameter	Description	Units	Value(s)
c_s	Conversion of water uptake by the seed disperser to plant growth	$\text{g mm}^{-1} \text{m}^{-2}$	10
$g_{s \max}$	Maximum specific water uptake of the seed disperser	$\text{mm g}^{-1} \text{m}^2 \text{d}^{-1}$	0.05
k_1	Half-saturation constant of specific growth and water uptake by the seed disperser	mm	5
d_s	Seed disperser mortality rate	d^{-1}	0.2–0.4
f	Fecundity	$\text{g seeds g plant}^{-1} \text{day}^{-1}$	$1 \cdot 10^{-4}$ –0.02
R_c	Maximum specific recruitment probability	–	0.01–1
g_s	Specific conversion rate of seeds in seedling	$\text{g plant g seeds}^{-1}$	1–35
L	Mean distance travelled by dispersing seeds	m	10
c_v	Conversion of water uptake by the vegetative plant to plant growth	$\text{g mm}^{-1} \text{m}^{-2}$	10
$g_{v \max}$	Maximum specific water uptake of the vegetative plant	$\text{mm g}^{-1} \text{m}^2 \text{d}^{-1}$	0.05
k_2	Half-saturation constant of specific growth and water uptake by the vegetative plant	mm	5
d_v	Vegetative plant mortality rate	d^{-1}	0.2–0.4
D_v	Diffusion coefficient for vegetative propagation	$\text{m}^2 \text{d}^{-1}$	0.1
R	Precipitation	mm d^{-1}	0.5–1.8
α	Maximum infiltration rate	d^{-1}	0.2
k_3	Saturation constant of water infiltration	g m^{-2}	5
W_0	Water infiltration rate in the absence of plants	–	0.2
D_0	Diffusion coefficient for surface water	$\text{m}^2 \text{d}^{-1}$	100
r_w	Water loss due to drainage and evaporation	d^{-1}	0.2
D_w	Diffusion coefficient for soil water	$\text{m}^2 \text{d}^{-1}$	0.1

Table 2

Research objectives, simulations performed, initial conditions of the simulations, details about parameter values adopted and corresponding figures showing the results for each research objective.

Objective	Simulations	Initial conditions	Parameters ^a	Figures
To investigate the role of plant traits along environmental gradients	Monospecific community along a rainfall (R) gradient	Random vegetation peaks of 0.1 and 90 g m^{-2}	$R = 0.5$ – 1.8 mm d^{-1} ; For the seed disperser $f = 0.005 \text{ g seeds g plant}^{-1} \text{day}^{-1}$; $R_c \cdot g_s = 0.6$ and 6 $\text{g plant g seed}^{-1}$	2(a)
To study facilitative and competitive interactions between plant types along environmental gradients	Two plant types along a rainfall (R) gradient	Random vegetation peaks of 0.1 and 90 g m^{-2}	$R = 0.5$ – 1.8 mm d^{-1} ; For the seed disperser $f = 0.005 \text{ g seeds g plant}^{-1} \text{day}^{-1}$; $R_c \cdot g_s = 0.6$ (in Fig. 2(b) and (c)) and 6 (in Fig. 2(b) and (d)) $\text{g plant g seed}^{-1}$	2(b)–(d)
To understand the role of reproductive effort on competition for water	Two plant types along a gradient of fecundity (f) of the seed disperser	Random vegetation peaks of 0.1 and 90 g m^{-2}	$f = 10^{-4}$ – $0.02 \text{ g seeds g plant}^{-1} \text{day}^{-1}$	3
To understand the role of reproductive traits in invasion processes along different environmental conditions	One plant type invading a monospecific plant community of the other plant type under dry and wet conditions	Monospecific mature community of one plant type and random vegetation peaks (0.1 g m^{-2}) of the invader	$R = 0.7$ and 1.2 mm d^{-1} ; $W_v = W_s = 5$ in Fig. 4; $W_v = 5$ and $W_s = 6.2875$ in Fig. 5	4 and 5

^a The rest of the parameter values are specified in the corresponding figure legends.

set as one day. Simulations started with random plant biomass peaks in 1% of the grid elements for each plant type, and setting homogeneous surface and soil water conditions ($W = R/r_w$, $O = R/(\alpha W_0)$). The simulations performed with their related research objectives and model specifications are detailed in Table 2.

3. Results

3.1. Analysis of the non-spatial model

In the non-spatial model, the spatial terms have been eliminated, that is: $D_v = D_0 = D_w = 0$ and the seed dispersal term is $f \cdot S$.

\bar{W}_ϕ , the amount of water in the soil at the steady state, reflects the plants' efficiency in water acquisition. When two plant types compete for one resource, the one able to decrease the level of the resource outcompetes the other (Tilman, 1982). This means that the plant type that has the lowest value of soil water at the steady state, \bar{W}_ϕ , will persist while the other will go extinct. Consequently, the two plant types are competitive equivalent in the non-spatial model if $\bar{W}_v = \bar{W}_s$, that is

$$\frac{k_2 \cdot d_v}{c_v \cdot g_{v \max} - d_v} = \frac{k_1(d_s + f)}{c_s \cdot g_{s \max} - d_s - f + R_c \cdot g_s \cdot f} \quad (5)$$

using Eqs. (A.2) and (A.3) as given in Box I in Appendix A. Under this situation the two plant types could theoretically coexist.

All the combinations of parameters that make \bar{W}_v smaller than \bar{W}_s give the advantage to the plants with vegetative propagation which then outcompete the seed dispersers at the steady state in the non-spatial model, while the reverse is true for all parameter combinations for which \bar{W}_s is smaller than \bar{W}_v . Note that the outcome of competition does not depend on the amount of rainfall, R , or on the soil type, W_0 : the vegetated final state (in terms of type composition) is not dependent on environmental conditions, but only on the biological parameters. The plant type dominating at the steady state must be more efficient in water acquisition, meaning that it lives longer (small d), it grows faster (large c), it is more efficient in converting water uptake into biomass (small k_2) or, in the case of the seed dispersers, it establishes better (large R_c and g_s ; Table 1), all of which leads to a lower \bar{W}_ϕ . Thus, the competitiveness in water acquisition is determined by local processes, such as growth and mortality, and the ability in seed establishment, which depends on two parameters of the model, the maximum specific seed recruitment, R_c , and the specific conversion rate of seeds in seedlings, g_s .

The relationship between competitiveness in water acquisition of the seed disperser, \bar{W}_s , and fecundity, f , was derived as follows. Using Eqs. (A.2) and (A.3) as given in Box I in Appendix A, we found

$$\bar{W}_v = 5$$

$$\bar{W}_s = \frac{1.25 + 5f}{0.25 - f + R_c \cdot g_s \cdot f} \quad (6)$$

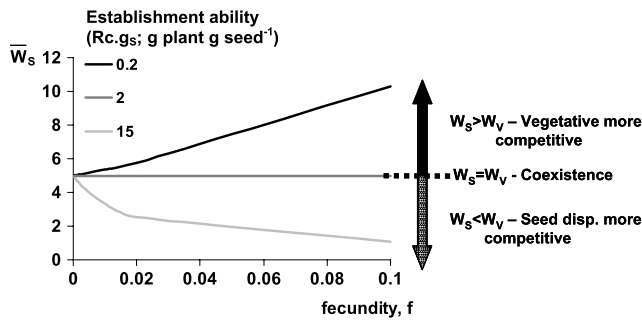


Fig. 1. Relationship between fecundity and \bar{W}_s for different values in the establishment ability, $Rc \cdot g_s$. $\bar{W}_v = 5$ for the given parameters. $R = 1$; $W_0 = 0.2$; $\alpha = 0.2$; $r_w = 0.2$; $c_v = 10$; $c_s = 10$; $g_{s \max} = 0.05$; $g_{v \max} = 0.05$; $d_s = 0.25$; $d_v = 0.2507$; $k_1 = 5$; $k_2 = 5$; $k_3 = 5$; $D_v = 0.1$; $D_w = 0.1$; $D_0 = 100$; $D = 10$.

for $W_0 = 0.2$; $\alpha = 0.2$; $r_w = 0.2$; $c_v = 10$; $c_s = 10$; $g_{s \max} = 0.05$; $g_{v \max} = 0.05$; $d_s = 0.25$; $d_v = 0.25$; $k_1 = 5$; $k_2 = 5$ and $k_3 = 5$.

And thus,

- (i) for $f = 0$, $\bar{W}_s = \bar{W}_v = 5$;
- (ii) for $Rc \cdot g_s = 2$, $\bar{W}_s = \bar{W}_v = 5$, for all values of f ;
- (iii) for $Rc \cdot g_s < 2$, $\bar{W}_s > \bar{W}_v$ always, and the difference is larger when fecundity increases;
- (iv) for $Rc \cdot g_s > 2$, $\bar{W}_s < \bar{W}_v$ always, and the difference is larger when fecundity increases (Fig. 1).

Thus, the non-spatial model predicted that both plants had the same competitiveness at $Rc \cdot g_s = 2$, and thus, that they coexist. Plants with seed dispersal outcompeted plants with vegetative propagation when establishment was high (i.e. $Rc \cdot g_s > 2$), and the contrary when establishment was low (i.e. $Rc \cdot g_s < 2$). Moreover, the investment in fecundity increased the competitive advantage of seed dispersers only when the establishment ability, $Rc \cdot g_s$, was high (Fig. 1).

3.2. The role of the reproductive traits along environmental gradients

In the spatial model, we first compared the plants' biomass at a steady state of monospecific plant communities along a rainfall gradient for three plant reproductive strategies: a seed disperser with low competitiveness in water acquisition ($\bar{W}_s = 5.141$) due to low ability in the establishment ($Rc \cdot g_s = 0.6$), a seed disperser with high competitiveness in water acquisition ($\bar{W}_s = 4.636$) due to high ability in the establishment ($Rc \cdot g_s = 6$), and a plant with vegetative propagation with intermediate competitiveness ($\bar{W}_v = 5$). Vegetative propagation allowed surviving better under low rainfall even having larger \bar{W}_ϕ than one of the seed dispersers, while seed dispersal helped maintaining more biomass when rainfall was larger (Fig. 2(a)). So, in initially monospecific simulations, a smaller \bar{W}_ϕ was not directly related to vegetation performance in the spatial model along a rainfall gradient.

Comparing the performance of the two seed dispersers at low rainfall, a high ability in the establishment allowed a larger plant biomass (Fig. 2(a)). Interestingly, seed dispersers with low ability in the establishment could sustain more biomass than the two other vegetation types at intermediate rainfall (between rainfall 0.9 and 1.3 mm d⁻¹), even having the worst efficiency in water acquisition, namely the largest \bar{W}_ϕ . At larger rainfall, when the vegetation cover was homogeneous (no patchy spatial pattern), the plant biomass at the steady state was inversely related to \bar{W}_ϕ (Fig. 2(a)), as predicted in the non-spatial model. Both plant types showed a hysteresis loop, meaning that the final state of the ecosystem depends on the previous trajectory, and a region of bistability (vegetated and non-vegetated stable states were

possible for the same rainfall, depending on the initial conditions). The hysteresis loop was shorter with regeneration by seeds than with vegetative propagation (Fig. 2(a), dotted lines), meaning that seed dispersal helped recovering from a low initial biomass at intermediate rainfall.

3.3. Facilitation and competition between plant types

Next, we investigated the dynamics of plant communities initially composed of the two plant types, plants with vegetative propagation and plants with seed dispersal, along a rainfall gradient. We investigated two cases: one where plants with vegetative propagation were more efficient in water acquisition ($\bar{W}_v < \bar{W}_s$) and one where seed dispersers were more efficient in water acquisition ($\bar{W}_v > \bar{W}_s$). The two plant types had the same initial biomass. In all the simulations, the plant type with the lower \bar{W}_ϕ took over and the simulation ended in monospecific communities at the steady state (Fig. 2(b); black line: biomass of a plant with vegetative propagation at the steady state when $\bar{W}_v < \bar{W}_s$; grey line: biomass of a seed disperser at the steady state when $\bar{W}_v > \bar{W}_s$).

Comparing the vegetative plant biomass at the steady state in the monospecific simulations (Fig. 2(a), solid and dotted black lines) with the vegetative plant biomass at the steady state with the initial presence of the seed disperser (Fig. 2(b), solid and dotted black lines), we observed that the hysteresis loop (dotted black line in Fig. 2(a) and (b)) was shorter when the seed disperser was initially present in the system (Fig. 2(b), dotted black line). Indeed, in a monospecific plant community, plants with vegetative propagation could not establish from a low initial biomass until $R = 1.1$ (Fig. 2(a), dotted black line), whereas seed dispersers could establish from a low initial biomass at a lower rainfall ($R = 1$, Fig. 2(a), dotted grey lines). When both grew together at $R = 1$, in a simulation where plants with vegetative propagation had a lower \bar{W}_ϕ than the seed dispersers, the initial establishment of the seed dispersers at $R = 1$ facilitated the colonization of plants with vegetative reproduction from a low biomass (Fig. 2(b), dotted black line and Fig. 2(c)).

Furthermore, we observed that seed dispersers could only sustain a very low biomass at low rainfall in monospecific plant communities (Fig. 2(a), solid grey lines). In initially mixed plant communities where seed dispersers were more competitive in water acquisition than plants with vegetative propagation ($\bar{W}_s < \bar{W}_v$), there was a facilitative effect of the latter at low rainfall (Fig. 2(b), solid grey line and Fig. 2(d)). In this situation, the vegetative propagation was more efficient in creating vegetation patches which then were taken over by the more competitive seed disperser in a later stage (Fig. 2(d)).

Summarizing, when the two plant types grew together initially, the plant type that would eventually remain at the steady state as a monospecific stand could benefit from the advantages of the other plant type. Plants with vegetative propagation could benefit from the ability of seed dispersers to recover from a very low biomass because of their bare soil colonization capacities. In turn, seed dispersers benefited from the ability of plants with vegetative reproduction to form patches and activate the plant-water positive feedback in the driest part of the aridity gradient.

3.4. The role of plant reproductive traits in affecting the efficiency in water acquisition

In the spatial model, the investment in fecundity modified the expected outcome predicted by the difference between \bar{W}_s and \bar{W}_v in the mean field model. Seed dispersers dominated at the steady state if the investment in fecundity, f , was small, even when $\bar{W}_s > \bar{W}_v$ (but not when $\bar{W}_s \gg \bar{W}_v$; Fig. 3). On the contrary,

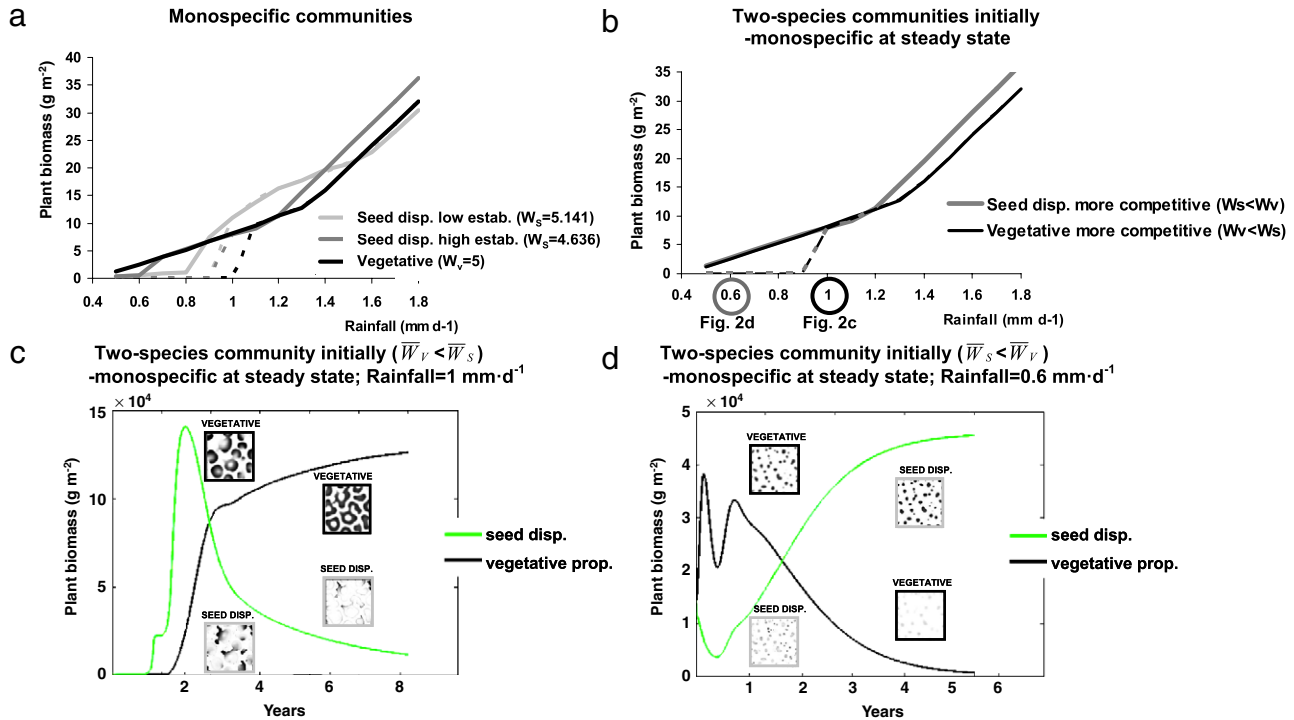


Fig. 2. (a) Plant biomass in monospecific populations along a rainfall gradient at the steady state. Light grey line: plants with seed dispersal and low ability in the establishment ($Rc \cdot g_s = 0.6$, $\bar{W}_s = 5.1411$); dark grey line: plants with seed dispersal and high ability in the establishment ($Rc \cdot g_s = 6$, $\bar{W}_s = 4.6364$); black line: plants with vegetative propagation ($\bar{W}_v = 5$). Solid lines, with initial biomass: 90 g m⁻². Dotted lines represent the recovery from low biomass (0.1 g m⁻²). (b) Plants with seed dispersal and plants with vegetative propagation in a mixed community. Black line: biomass of the plant with vegetative propagation when it is more efficient in water acquisition than the seed disperser ($\bar{W}_v < \bar{W}_s$) due to the low ability in the establishment of the seed disperser ($Rc \cdot g_s = 0.6$, $\bar{W}_s = 5.1411$, $\bar{W}_v = 5$); Grey line: biomass of the plant with seed dispersal when it is more efficient in water acquisition than the plant with vegetative propagation ($\bar{W}_s < \bar{W}_v$) due to the high ability in the establishment ($Rc \cdot g_s = 6$, $\bar{W}_s = 4.6364$, $\bar{W}_v = 5$). (c) Spatial patterns and biomass along time of a seed disperser and a plant with vegetative propagation growing together, illustrating the role of the seed disperser facilitating the establishment of the plant with vegetative propagation. (d) Spatial patterns and biomass along time of a seed disperser and a plant with vegetative propagation growing together, illustrating the role of the plant with vegetative propagation facilitating the establishment of the seed disperser with low rainfall ($R = 0.6$). $W_0 = 0.2$; $\alpha = 0.2$; $r_w = 0.2$; $c_v = 10$; $c_s = 10$; $g_{s \max} = 0.05$; $g_{v \max} = 0.05$; $d_s = 0.25$; $d_v = 0.25$; $k_1 = 5$; $k_2 = 5$; $k_3 = 5$; $D_v = 0.1$; $D_w = 0.1$; $D_0 = 100$; $D = 10$; $f = 0.005$, $R = 1$, Initial biomass = 0.1 g m⁻², $Rc \cdot g_s = 0.6$, $\bar{W}_v = 5$, $\bar{W}_s = 5.1411$ in (c) and $R = 0.6$, Initial biomass = 90 g m⁻², $Rc \cdot g_s = 6$, $\bar{W}_v = 5$, $\bar{W}_s = 4.6364$ in (d). Note that the value of a biological parameter ($Rc \cdot g_s$) is different between the seed disperser being facilitated by the plant with vegetative propagation in (c) and the seed disperser facilitating the plant with vegetative propagation in (d).

when the investment in fecundity was high ($f \geq 0.007$), the seed disperser was less efficient in water acquisition and the plant with vegetative propagation won at the steady state even when $\bar{W}_s < \bar{W}_v$ (Fig. 3). These results suggest that, in a heterogeneous environment with suitable and unsuitable sites for establishment, dispersal has a cost in terms of local competition.

3.5. Plant reproductive traits in invasion processes

We then looked at cases where one of the two plant types was initially rare in a population dominated by the other plant type. We first investigated the invasion of an initially rare seed disperser in a community dominated by plants with vegetative propagation when $\bar{W}_s = \bar{W}_v$. A small quantity of biomass dispersed by seeds was able to profit from the water available around the vegetative patches, and the seeds established around the vegetative patches when fecundity, f was low ($f = 0.001$; Fig. 4(a)). There was an intermediate state when the vegetative patches were surrounded by a ring of seedlings (Fig. 4(a) and (b)). Then, the vegetative patches were slowly replaced by seed dispersers coming from outside the patch. Interestingly, when rainfall was high ($R = 1.2$) plants with vegetative propagation occupied almost all the space, and the invasion of seed dispersers was hampered (Fig. 4(c) and (d)).

Plants with vegetative propagation were worse invaders. When $\bar{W}_v = \bar{W}_s$, plants with vegetative propagation could never invade a developed seed disperser population, even when the fecundity of the seed disperser was very high ($f = 0.02$; not shown). When

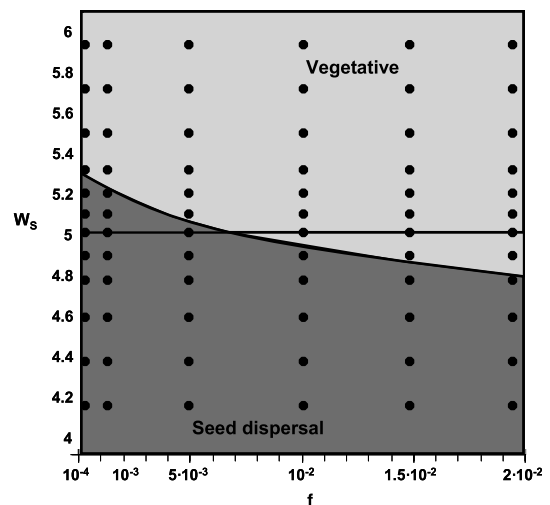


Fig. 3. The effect of plant fecundity on efficiency in water acquisition. Final steady state in simulations of a mixed community (plant with vegetative propagation and seed disperser) for different values (black dots) of W_s and f . The horizontal line represents the limit between the seed dispersal and the vegetative dominance in the non spatial model, when $\bar{W}_s = \bar{W}_v = 5$. In the spatial model, the low fecundity gives advantage to the seed disperser even when $\bar{W}_s > \bar{W}_v$. On the contrary, the high fecundity of the seed disperser gives advantage to the plant with vegetative reproduction even when $\bar{W}_s < \bar{W}_v$. $R = 1$; $W_0 = 0.2$; $\alpha = 0.2$; $r_w = 0.2$; $c_v = 10$; $c_s = 10$; $g_{s \max} = 0.05$; $g_{v \max} = 0.05$; $d_s = 0.25$; $d_v = 0.2507$; $k_1 = 5$; $k_2 = 5$; $k_3 = 5$; $D_v = 0.1$; $D_w = 0.1$; $D_0 = 100$; $g_s = 2$; $Rc = 1$; $D = 10$.

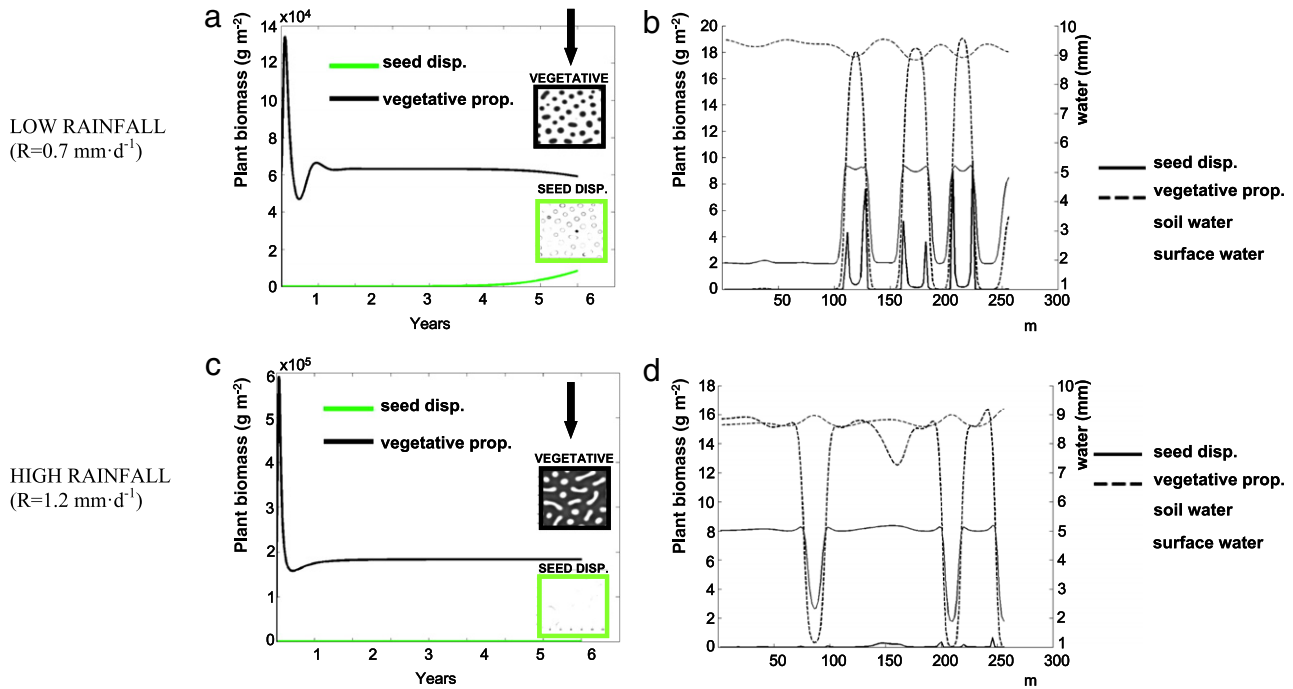


Fig. 4. Seed disperser as an invader of an established plant population with vegetative propagation with low and high rainfall. (a) Plant biomass along with time and spatial patterns of the two plant types with low rainfall ($R = 0.7$); (b) profile showing the invasion process with low rainfall ($R = 0.7$). (c) Plant biomass along with time and spatial patterns of the two plant types with high rainfall ($R = 1.2$); (d) profile showing the invasion process with high rainfall. Arrows indicate the time step of the spatial patterns and profiles shown. $W_0 = 0.2$; $\alpha = 0.2$; $r_w = 0.2$; $c_V = 10$; $c_S = 10$; $g_{S \max} = 0.05$; $g_{V \max} = 0.05$; $d_S = 0.25$; $d_V = 0.25$; $k_1 = 5$; $k_2 = 5$; $k_3 = 5$; $D_V = 0.1$; $D_W = 0.1$; $D_0 = 100$; $g_S = 2$; $Rc = 1$; $D = 10$; $g_S = 2$; $f = 0.001$. $\bar{W}_V = \bar{W}_S = 5$. Initial biomass of the invader: 0.1 g m^{-2} .

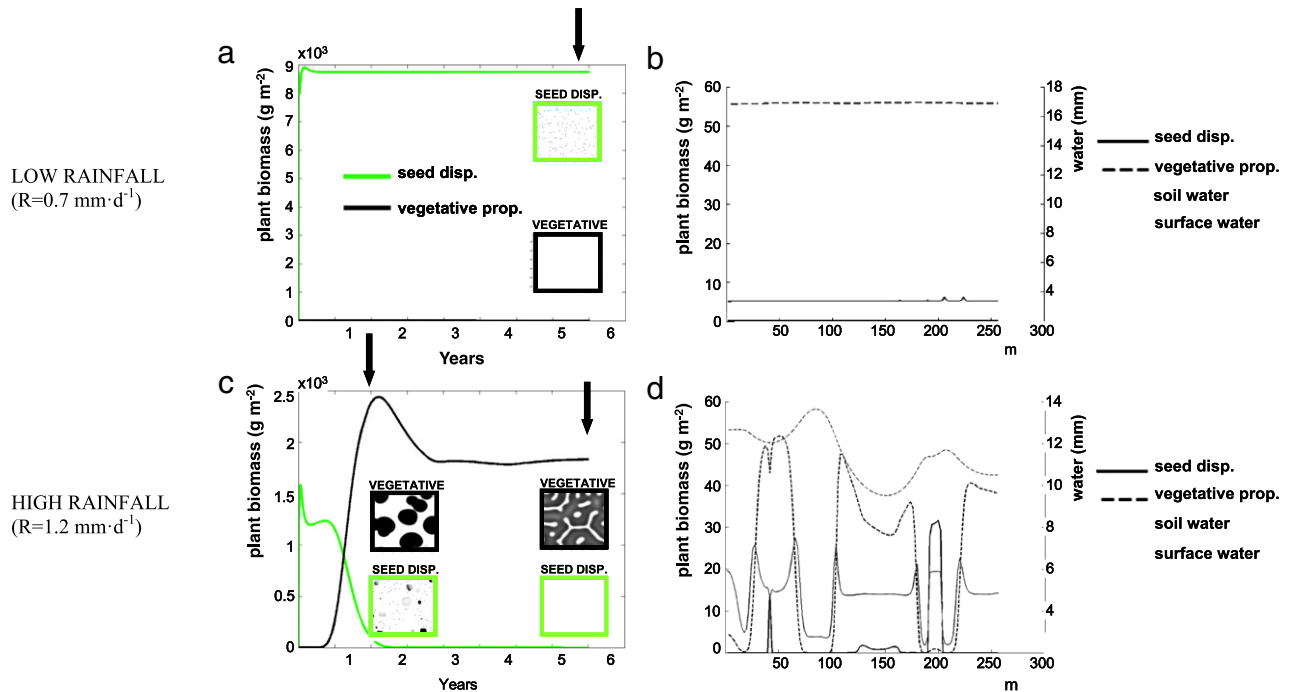


Fig. 5. Plant with vegetative propagation as an invader of an established seed dispersed plant population with low and high rainfall. (a) Plant biomass along with time and spatial patterns of the two plant types with low rainfall ($R = 0.7$); (b) profile showing the invasion process with low rainfall ($R = 0.7$); (c) plant biomass along with time and spatial patterns of the two plant types with high rainfall ($R = 1.2$); (d) profile showing the invasion process with high rainfall. Arrows indicate the time step of the spatial patterns and profiles shown. The profile shown in (d) corresponds to the left arrow in (c). $W_0 = 0.2$; $\alpha = 0.2$; $r_w = 0.2$; $c_V = 10$; $c_S = 9$; $g_{S \max} = 0.05$; $g_{V \max} = 0.05$; $d_S = 0.25$; $d_V = 0.25$; $k_1 = 5$; $k_2 = 5$; $k_3 = 5$; $D_V = 0.1$; $D_W = 0.1$; $D_0 = 100$; $Rc = 0.6$; $D = 10$; $g_S = 1$; $f = 0.001$. $\bar{W}_V = 5$; $\bar{W}_S = 6.2875$. Initial biomass of the invader: 0.1 g m^{-2} .

$\bar{W}_V \ll \bar{W}_S$ and rainfall was low ($R = 0.7$), the seed disperser population had a very low biomass and plants with vegetative propagation could not invade (Fig. 5(a) and (b)). However, under

higher rainfall conditions and when $\bar{W}_V \ll \bar{W}_S$, plants with vegetative propagation could invade the seed disperser population (Fig. 5(c) and (d)).

4. Discussion

Using a modelling approach, we explored the consequences of biotic interactions between plants with different reproductive traits for succession, desertification and invasion processes. Previous approaches addressed the modelling of local facilitation in arid ecosystems through bare soil colonization (Kéfi et al., 2007a,b) and plant-water feedbacks (Gilad et al., 2007), the role of biomass spread in the vegetation spatial organization (Pueyo et al., 2008; Thompson and Katul, 2009; Thompson et al., 2008), and the dynamics of plant communities composed by plants with vegetative growth and seed dispersal (Harada and Iwasa, 1994). However, to our knowledge, this is the first attempt to incorporate interactions between plants with different reproductive traits in a mechanistic model of plant and water dynamics in arid and semi-arid environments. Until now only a few modelling studies about trade-offs in plant traits took facilitative interactions between plants into account, since usually mostly competitive interactions are considered (Gilad et al., 2007), but see (Brooker et al., 2007; Chen et al., 2009; Travis et al., 2005). These studies ignoring facilitation are not applicable to arid and semi-arid environments, where facilitative interactions are well-known to play a crucial role (Callaway, 1998; Pugnaire et al., 1996). Our approach brought together facilitation and competition between plant types for one limiting resource mechanistically, acting simultaneously at different spatial scales and plant life stages.

First, we could understand the role of reproductive traits on population survival and productivity along a rainfall gradient through the dynamics of monospecific plant communities with different reproductive traits. The plant-water feedback is an important mechanism increasing plant biomass and survival in arid and semi-arid environments (Gilad et al., 2004; Rietkerk et al., 2004, 2000). Our results showed that the dispersal traits that optimized the ability to create and maintain the plant-water feedback (and thus pattern formation) changed along a rainfall gradient.

Under very dry conditions, the maintenance of biomass locally was a key property in our model to create vegetation patches that would quickly activate the plant-water feedback leading to a redistribution of water in space. Thus, reproduction close to the nurse plant was more efficient than long-distance seed dispersal in water-limited ecosystems dominated by plant-water feedbacks. When rainfall was low, bare soil was an unsuitable place for seed establishment, due to its low water content. Under these conditions, the population dispersed by seeds could only sustain a low amount of biomass, corresponding to the seeds dispersed close to the vegetated patches. The plants dispersed by vegetative propagation were able to build up vegetation patches, as the water available around the vegetation patches could favour vegetative reproduction close to the patch. This could be the explanation for the large dominance of steppes of clonal perennial grasses, like *Stipa tenacissima* L. and *Lygeum spartum* L. in arid and semi-arid environments (Le Houerou, 2001). This would also explain why short-distance dispersal strategies, such as attelechory and antithelechory, which keep seeds close to the parental plant, are common in arid regions (van Rheede van Oudtshoorn and van Rooyen, 1999).

Considering species characterized by long-distance seed dispersal, the ability in the establishment would need to be high enough to allow seedling establishing, growing and forming patches quickly. This could be the case of annual plants, abundant and successful in arid environments (Guterman, 2002). At an intermediate rainfall, the ability of colonizing bare soil (and not only the reproduction close to the nurse plant) was an efficient trait for the population, as showed by the good establishment of seed dispersers from a low biomass.

Interestingly, in our model seed dispersers with low ability in the establishment could sustain more biomass than the other two vegetation types simulated under intermediate rainfall (namely, semi-arid conditions between rainfall 0.9 and 1.3 mm d⁻¹), even having the worst efficiency in water acquisition, (the largest \bar{W}_ϕ). When establishment ability was high, seedling establishment was less dependent on soil water availability, and thus, less dependent on the spatial aggregation of pre-existing vegetation. This in turn promoted less spatially structured populations, with a weak scale-dependent feedback (i.e. plant biomass and water less spatially aggregated), which is less productive for the whole population (Pueyo et al., 2008).

When communities composed of two plant types were simulated, competition was the dominant biotic interaction between plant types. In arid and semi-arid environments, the efficiency in water acquisition is a key property for plant survival (Noy-Meir, 1973). There are several traits involved in the competitive ability for water acquisition, but trade-offs between plant traits constrain the possible combinations (Suding et al., 2003). The competitiveness of different dispersal strategies in a spatial context has been extensively investigated in the context of the competition-colonization trade-off (Bolker and Pacala, 1999; Bolker et al., 2003). This trade-off predicts that plants can invest either in local competitiveness or in high reproductive efforts and both strategies can be equally competitive independently of the environmental conditions. However, this was not what we found in our model for arid and semi-arid plant communities with plant-water feedbacks. We found that the investment in fecundity reduced the local competitiveness, giving advantage to the plant that invested biomass in vegetative growth, and thus took more water resources per unit time. The colonization strategy would only be successful combined with the adaptation to establish under stressful conditions.

We mainly found facilitation occurring in the establishment stage, acting as a driver of succession and invasion processes. Our results are in agreement with previous modelling approaches predicting the presence of facilitation in the harshest environmental conditions when the positive interaction is at the reproductive stage (Travis et al., 2006, 2005). During old-field succession in steppes, seed-dispersed shrubs often predominate initially and are then replaced by perennial clonal grasses at the end of succession in absence of perturbations. This indicates that the competition-facilitation net effect is more favourable for perennial grasses than for shrubs during establishment and seedling stages (Aguilar and Sala, 1994; Soriano et al., 1994). Our model showed that the effect of reproductive strategies on the balance between facilitation and competition could be the underlying mechanism behind the observed steppes dynamics. In Patagonian steppes, where shrubs and perennial grasses coexist, shrubs are colonizers or initiators of vegetation patches (Bisigato and Bertiller, 2004). Small and young shrubs facilitate tussock until the shrubs disappear locally from the patch (Aguilar and Sala, 1994; Soriano et al., 1994). Adult grasses exert a strong below-ground competition for space to seedlings of both perennial grasses and shrubs (Aguilar et al., 1992; Alados et al., 2006; Jurena and Archer, 2003). Due to the competitive process with seedlings, shrubs would need to colonize new bare areas by seeds to remain in the community. In environments where harsh conditions on bare soil hamper scrub recruitment and under strong plant-soil feedbacks, vegetative propagation could have benefits for exploitation of limited resources (Pennings and Callaway, 2000) favouring stable grassland communities.

On the other hand, we found that the invasive process can be very fast when plants with long-distance seed dispersal were involved. Seed dispersers can take advantage of the already well established plant-soil feedback. This mechanism could contribute to explain the shrub encroachment frequently found in some arid

$$\bar{S} = 0, \quad \bar{V} = 0, \quad \bar{O} = \frac{R}{\alpha \cdot w_0}, \quad \bar{W} = \frac{R}{r_w} \quad (\text{A.1})$$

$$\bar{S} = 0, \quad \bar{V} = \frac{c_V \cdot R}{d_V} - \frac{c_V \cdot r_w \cdot k_2}{c_V \cdot g_{V \max} - d_V}, \quad \bar{O} = \frac{R}{\alpha \left(\frac{\bar{V} + k_3 \cdot w_0}{\bar{V} + k_3} \right)}, \quad \bar{W} = \frac{k_2 \cdot d_V}{c_V \cdot g_{V \max} - d_V} \quad (\text{A.2})$$

$$\bar{S} = \frac{(c_S \cdot g_{S \max} + Rc \cdot g_S \cdot f) \cdot (R \cdot (c_S \cdot g_{S \max} + Rc \cdot g_S \cdot f) - (d_S + f) \cdot (R + k_1 \cdot r_w))}{g_{S \max} \cdot (c_S \cdot g_{S \max} - d_S - f + Rc \cdot g_S \cdot f) \cdot (d_S + f)}, \quad \bar{V} = 0, \quad (\text{A.3})$$

$$\bar{O} = \frac{R}{\alpha \left(\frac{\bar{S} + k_3 \cdot w_0}{\bar{S} + k_3} \right)}, \quad \bar{W} = \frac{k_1(d_S + f)}{c_S \cdot g_{S \max} - d_S - f + Rc \cdot g_S \cdot f}.$$

Box 1. Equilibrium points of the model.

and semi-arid areas. Shrub encroachment is a big economic and ecological problem in many areas of the world (Schlesinger et al., 1990), but the underlying mechanisms are still not completely understood, potentially including overgrazing, fire regimes, plant biological traits, soil conditions, climatic factors and atmospheric CO₂ levels (Archer et al., 1995; Brown and Archer, 1999; Grover and Musick, 1990; Van Auken, 2000). Our results point out the biological traits of the invasive shrubs that could be involved in the encroachment. First, the shrub species would need to be more efficient in water acquisition than the grasses. Second, since the invasion by seed dispersers occurs from the border of the patch, a high patch perimeter/patch area ratio would favour the invasion, by increasing the number of suitable places for seed germination of the invader. Thus, our results suggest that the invasion would be faster along an increasing aridity gradient. However, it is noteworthy that we used a continuous representation of seeds in our model, which implied that fraction of seeds were able to spread and germinate. This introduces a bias in the estimation of long-distance dispersal and has a tendency to overestimate the migration rate (Clark et al., 2003). For that reason, we should consider cautiously the conclusions about invasion spread.

Recent modelling studies have stressed the importance of rainfall seasonality (Guttal and Jayaprakash, 2007) and stochasticity (D'Odorico et al., 2005) for vegetation growth and survival under low rainfall. Many seeds have adaptations to germinate only when environment conditions are optimal, remaining until then in the seed bank and giving an evolutionary advantage to the plants dispersed by seeds. In addition, net biotic interactions change with environmental conditions, especially when reproductive fitness is measured (Tielborger and Kadmon, 2000). Some authors even argued that competition for growth is not relevant in arid environments because resource uptake takes place in short pulse periods (Goldberg and Novoplansky, 1997). This would decrease the relevance of competition for water as a driving force of ecosystem dynamics. Thus, an interesting improvement to our model would be to incorporate more realistic rainfall conditions to investigate the reproductive traits best adapted.

Concluding, this study contributed to the understanding of the relationship between plant reproductive traits and biotic interactions in semi-arid environments, giving insights into the role of several plant strategies in plant community dynamics (i.e. successional and invasive processes). We showed that biological plant traits (and more specifically, reproductive plant traits) can be responsible for the simultaneous positive and negative interactions found in semi-arid environments. In a further study, it would be interesting to incorporate other important biological traits, besides reproductive traits, in our model, such as root layering in the soil or allelopathic compounds. These other traits, together with rainfall stochasticity, can play an important role in biotic interactions among plants. An integrative approach would allow us to disentangle the relative importance of each plant trait on plant community dynamics in arid and semi-arid environments.

Acknowledgments

This study was supported by the projects CGL2008-00655/BOS (from the Ministry of Science and Innovation of Spain), GA-LC-010/2008 and GA-LC-020/2010 (from the Aragón Regional Government and “La Caixa”) and PIE-2009301145 (from CSIC). The research of YP was partially supported by a “Juan de la Cierva” contract from the Spanish government. The research of S.K. and M.R. was supported by a personal VIDI grant of the Netherlands Organization of Scientific Research/Earth and Life Sciences (NWO-ALW) to M.R. Part of SK's research was also funded by a Humboldt fellowship from the Alexander von Humboldt foundation to S. K. RDS's research was supported by the INTERBOS3 project (CGL2008-04503-C03-03, Ministry of Science and Innovation of Spain).

Appendix. Equilibrium points and stability analysis

There are 3 equilibrium points that can be computed analytically (see equations in Box 1):

The equilibrium points are always stable. In the text, we refer to \bar{W}_V as the soil water content at equilibrium (A.2) as given in Box 1, when the seed disperser biomass, \bar{S} , is zero, and the biomass of the plant with vegetative propagation, \bar{V} , is larger than 0. Similarly, in the text we refer to \bar{W}_S as the soil water content at equilibrium (A.3) as given in Box 1, when the biomass of the plant with vegetative propagation, \bar{V} , is zero, and the seed disperser biomass, \bar{S} , is larger than 0.

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