A mechanistic model of tree competition and facilitation for Mediterranean forests: Scaling from leaf physiology to stand dynamics

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Abstract

Mechanistic theories of plant competition developed to explain changes in community structure and dynamics along resource availability gradients have been mostly applied to temperate forests and grasslands where light and nutrients are the two main limiting resources. In contrast, the mechanisms underlying the structure and dynamics of water-limited plant communities have been little explored. Also previous mechanistic models rely either on complex simulators, which are difficult to interpret or on simple conceptual models, which ignore too many critical details. In this study, we develop a model of stand dynamics for light and water-limited forests of intermediate complexity and we provide an analytical framework for its analyses. The model is an individual-based simulator that describes the feedback between transpiration, stomatal function and soil water dynamics with asymmetrical competition for light and water. Trees allocate carbon to three main compartments: shoot, stem and roots. We use the model to explore general patterns that may emerge across levels of biological organization from the leaf to the stand. Model predictions are consistent with a number of features of Mediterranean forests structure and dynamics. At the plant-level the leaf-based tradeoff between carbon gain and water loss expresses as a tradeoff between mortality and growth. This tradeoff explains plant morphological changes in above-ground biomass and root to shoot allocation along a water availability gradient. At the community-level, tradeoffs among carbon acquisition and water loss govern the sign of plant interactions along the gradient. Coexistence among morphological types was not observed for the range of parameters and environmental conditions explored. Overall the model provides an unifying explanation for the observed changes in the sign of plant to plant interactions along environmental gradients as well as a process-based formulation that can be linked to empirical studies.
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1. Introduction

A central goal of plant ecology is to understand the mechanisms controlling the structure and dynamics of

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plant communities (e.g., Crawley, 1986; Tilman, 1988). It is generally accepted that community structure is an emergent property of species responses to resource gradients and interactions, such as competition. Gradient analyses have shown spatial and temporal regularities in community structure across sites with respect to resource variation, suggesting the existence of a few common underlying ecological mechanisms for all plant communities (Whittaker, 1975). Over the last decades, the development of mechanistic theories of plant communities have allowed us to identify critical ecological processes for explaining and predicting changes in community structure along environmental and disturbance gradients (Tilman, 1982; Smith and Huston, 1989). Chiefly, the mechanistic theory of plant competition developed by Tilman (1988) is based on an individual-based model (ALLOCATE) that describes community structure as a feedback between individual plant responses to resource availability and resource depletion by plants. In the model, species ability to gather above- and below-ground resources is governed by an inevitable tradeoff between shoot-stem and root allocations. According to ALLOCATE predictions, this tradeoff explains species relative positions along environmental gradients and a large number of successional and segregation patterns along productivity gradients. The mechanisms controlling successional dynamics in plant communities have been explored only in a few systems, mainly in temperate regions, where light and nutrients are the main limiting resource. The constrains and tradeoffs associated with water availability, however, have not been explicitly incorporated in plant mechanistic theory despite the fact that water is along light and nutrients a critical resource influencing the productivity and composition of plant communities worldwide (Woodward, 1986; Stephenson, 1990).

The development of a mechanistic model for any plant system requires understanding two separate processes (e.g., Goldberg, 1990). First, we need to describe how plants respond to resource heterogeneity and the interspecific tradeoffs implied (plant performance submodel). Secondly, we need to understand how biotic and abiotic processes interact dynamically to control resource supply rates (resource sub-model). Both individual responses and resource variation interact dynamically to determine the nature of the interspecific mechanisms driving successional change in plant communities; e.g., competition, facilitation or neutral

interactions. A large number of studies have focused on plant functional responses and tradeoffs in response to light and nutrient limitations (e.g., Shugart, 1984; Brokaw, 1985; Chazdon, 1988; Tilman, 1988; Canham, 1989; Grubb et al., 1996; Kobe et al., 1995). In contrast, whole-plant responses to combined gradients in light and water availability are poorly understood and studies on plant–water relations have typically focused on leaf-level ecophysiological processes (e.g., Tenhunen et al., 1990). Shade and drought effects do not act independently on plant performance (Holmgren et al., 1997; Sack, 2004) but rather show interactive effects, which are qualitatively different from those described for light and nutrient limitations. Similarly, as a result of the interaction between irradiance and soil moisture, spatial and temporal distribution of soil moisture can be qualitatively from temperate forests (e.g., Joffre and Rambal, 1993; Kitzberger et al., 2000). All these evidences suggest that water shortage results in qualitatively different mechanisms of community assembly than nutrient limitations. Finally, another difficulty in developing mechanistic models of forest dynamics is the existing compromise between model complexity and mathematical tractability. Mechanistic theories developed so far rely either on simple analytical or heuristic models that omit too many critical biological details (e.g., Tilman, 1982; Smith and Huston, 1989) or on size-structured numerical models (e.g., Shugart, 1984; Tilman, 1988; Mouillot et al., 2001) that are difficult to analyze and interpret from a biological point of view. Asymmetric resource competition in forest size-structured populations, however, can be described through partial differential equation systems (Kohyama, 1991), which have been shown to emerge from approximate aggregations of individual-based models (e.g., Pacala and Deutschman, 1995; Lischke et al., 1998). Thus, the development of analytical models of stand dynamics seems a feasible goal.

In this study, we develop a simulator of stand dynamics that incorporates the main constrains and tradeoffs experienced by plants in water-limited forests. The model is specifically suited to describe stand structure and dynamics of Mediterranean evergreen forests, which represent a transition stage between northern more humid temperate forests and semi-arid vegetation (Archibold, 1995). The model is a size-structured individual-based simulator of forest stand dynamics coupled to a stochastic soil water

balance. Individual tree performance is described by a physiologically-based big-leaf model which describes carbon gain and transpiration as a function of climatic and edaphic conditions. Differences among species are based on morphological (size and allocation patterns) rather than on physiological differences. All plants sharing the same morphology and germinating at the same time define a cohort of individuals. Trees compete for light and water, with shorter trees being shaded by taller trees and soil water is depleted through cumulative transpiration. Competition for water is asymmetrical with trees with a higher root density experiencing a higher water supply. We use the simulator to explore general patterns that may emerge at different levels of biological organization. First we explore how the leaf-level tradeoff between carbon gain and water loss expresses at the whole-plant-level and the influence of allocation strategy on plant performance along a water availability gradient. Secondly, we ask whether plant competitive mechanisms may change along annual rainfall and rainfall frequency gradients and, in particular whether shifts from competitive to positive interactions are observed. Third, we investigate how stand structure and composition are modified by changes in the rainfall regime and disturbances. Specifically, we investigate how annual rainfall and rainfall stochasticity influence standing crop and coexistence of species differing in their allocation strategy. Finally, we propose a general analytical framework to describe stand dynamics in light and water-limited size-structured populations.

2. The forest stand model

The simulator is a size-structured individual-based model that describes the temporal dynamics of overlapping tree cohorts structured by light and water competition (Fig. 1). It results from coupling of two different models: a model of tree growth and mortality, and a resource dynamics model (light and soil water availability). Both models are interconnected, as tree performance is a function of resource availability, which depends in turn on tree transpiration and light interception by canopy trees. Individual tree growth and mortality are functions of both climatic conditions and light and water availability. Carbon assimilation and transpiration are described through a physiolog-
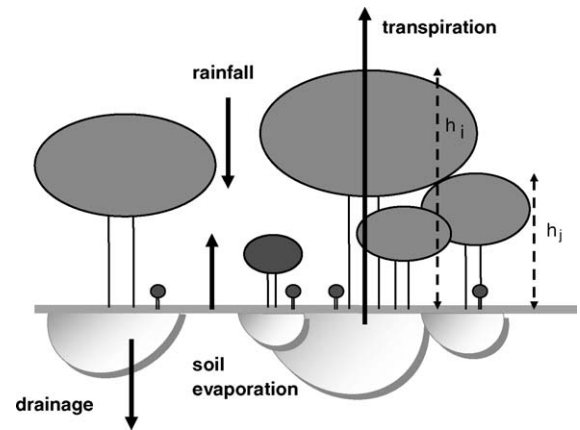

Fig. 1. Diagram of model flows. Light competition is asymmetric with trees of a given height (h_j) being shaded by taller individuals ($h_i > h_j$). Soil moisture is determined as the balance of water inputs (rainfall) and outputs (tree transpiration, drainage and soil evaporation). Trees with larger root systems have a larger water supply. Water demand and supply for each individual tree are adjusted thorough a physiological model which maximizes carbon tree growth while prevents the tree from reaching the cavitation threshold.

ical big-leaf model. Light at a given height is computed through a light extinction model (Beer's Law). Water availability is estimated through a soil water balance model, which considers both climatic conditions and the cumulative effects of transpiration by individual trees. All model state variables are updated at an hourly scale. Trees of the same height receive the same radiation and soil moisture is assumed to be homogeneously distributed in the stand. We do not include explicitly spatial heterogeneity (neither vertical or horizontal) nor neighbourhood competitive effects, thus, the results from this model are only valid in the context of stand-level processes and cannot be extrapolated to heterogeneous forest landscapes.

2.1. Individual tree growth, carbon allocation and mortality

Tree growth and mortality are based on a physiological model that describes carbon and water balance individually for each tree. The environment is characterized by air temperature, dew point, radiation, and frequency and intensity of storm events. The physiological model is a big-leaf approximation that predicts hourly values of carbon assimilation, transpiration, leaf temperature and stomatal conductance (see Appendix

for details; Zavala, 2004). The soil–plant–atmosphere continuum is represented by a simplified water potential circuit in which tree canopy, stem and root system are represented by a single resistance (Sellers et al., 1995). A system of four non-linear equations and five unknowns is derived based on assumptions of equilibrium in canopy latent heat fluxes and energy, carbon and plant water balances. To solve the system, we use Ball et al. (1987) equation, which links stomatal conductance to carbon assimilation rates. In this equation, however, the parameter g_F that determines the level of conductance attained for a given assimilation rate is unknown. To estimate g_F over the course of the drought we use a negative feedback algorithm via leaf water potential that ensures the plant performs a strategy of long-term carbon gain optimization and avoidance of mortality. This algorithm (see Zavala, 2004) has been shown to result in realistic gas exchange rates during the dry period (Tenhunen et al., 1990; Sala and Tenhunen, 1996).

Individuals start as seedlings and undergo continuous vegetative growth. The plant allocates carbon to four different compartments: shoot, stem, roots and reproduction. Growth for each allocation compartment is evaluated at an hourly scale after discounting maintenance respiration from carbon gain. Shoot allocation is described by leaf area per unit ground area (LAI). Physiological canopy conductance per unit ground area is estimated as the product of mean leaf conductance per unit LAI (equivalent to the parallel sum of individual leaves' conductance, Woodward, 1986). Trees differ in their competitive advantage for water according to their differential allocation to fine root density. A larger investment decreases soil–root resistance, which is estimated as the parallel sum of individual fine roots conductance. Allocation to deep roots (serial resistance) that would confer competitive advantage in soils with a vertical gradient in soil moisture availability is not considered here. We estimate LAI, stem height and diameter and root density from carbon concentration in shoot, stem and root allocation through allometric equations (Woodward, 1986; Tilman, 1988). Once the plant has reached reproductive age a fraction of carbon is allocated to reproduction. The number of seeds produced annually by each individual tree is a function of seed size (constant in this study) and are dispersed uniformly in the stand.

Tree mortality can result both from exogenous (e.g., disturbances) or endogenous causes: water stress or negative carbon balance. Plant water stress is evaluated through the parameter g_F, which integrates plant endogenous processes that can induce stomatal closure in response to drought. Specifically, "plant water stress" (PWS) is estimated through the number of days in which g_F reached its minimum value. The parameter g_F is computed through a negative feedback via leaf water potential, therefore its minimum value is reached when leaf water potential approaches the cavitation threshold. Tree probability of mortality as a result of drought stress is described as a logistic function of PWS. Trees also die when their integrated annual carbon balance is negative. Exogenous mortality rate is a free parameter, which allows us to simulate the effect of changes in the disturbance regime.

2.2. Resource dynamics and tree interactions

Light competition is asymmetric with taller trees shading shorter trees. It decreases exponentially throughout the canopy at a rate that depends on LAI of taller trees (Tilman, 1988). Soil water dynamics is modelled through a discrete time water bucket model with water inputs taking place in a fixed instant of the day (evening). Daily variation is described through an stochastic model with rainfall events being Poisson distributed and rainfall depth following an exponential distribution (Rodríguez-Iturbe et al., 1990; Appendix). Soil water reserves are depleted by tree transpiration, soil evaporation and drainage. Tree water supply is variable across individuals with trees with a larger root surface being able to tap more water. Trees adjust their transpirational demand to their individual water supply as to maximize carbon uptake and avoid mortality during the dry season. For this purpose g_F is iteratively adjusted as to result in the maximal growth rates for which plant survival is ensured (Zavala, 2004). Demand and water supply are adjusted simultaneously for all trees so we do not account for competitive strategies associated with faster water uptake after storm events. Neither we consider neighbourhood nor vertical effects in water competition and assume that both individual root systems and soil moisture are evenly distributed throughout the soil profile.

2.3. Model solution and simulations performed

To evaluate plant performance in relation to LAI and R:S ratio we estimated annual net carbon assimilation and mortality for a range of trees differing in their LAI and R:S growing under two water availability environments: dry (400 mm annual rainfall) and humid (1200 mm annual rainfall). Stem and reproductive allocations were fixed and plants were considered to grow in isolation (no competitive interactions). We also explored the existence of an optimal LAI and R:S allocation along the rainfall gradient by gradually increasing LAI or R:S until the benefit of increasing LAI or R:S with respect to annual carbon gain approached to zero.

To evaluate plants responses to combined gradients in light and water availability and to explore shifts in plant interactions from competition to facilitation, we explored plant performance along two axes of variation. The first axis is a water availability gradient defined by four environments: 400 and 1200 mm of annual rainfall combined with a high and a low storm frequency. The second axis is a continuous variation in light suppression estimated as percentage of photosynthetic available radiation (PAR) at full sunlight. Two possible cases were considered: (1) radiation was changed as an independent factor (e.g., seedling influenced by changes in understory radiation), and (2) we explicitly simulated neighbour competition thus reduced radiation was inevitable associated with lower soil moisture because of increased transpiration (e.g., juvenile influenced by both lower soil moisture and radiation).

To investigate how stand production, dynamics and composition change along gradients of water availability we performed several runs with individuals sharing the same allocation pattern and both deterministic and stochastic environments. By deterministic, we mean a model in which daily precipitation input is estimated as a constant fraction, while in the stochastic regime daily precipitation is given by a probability distribution of rainfall frequency and intensity (Fig. 2, Appendix). We investigated the existence of equilibrium solutions in standing crop for three different precipitation regimes (xeric, 200 mm; dry, 400 mm and humid, 1200 mm) and evaluated its stability from different initial conditions and perturbations, such as biomass extraction or episodic droughts. To evaluate coexistence condi-
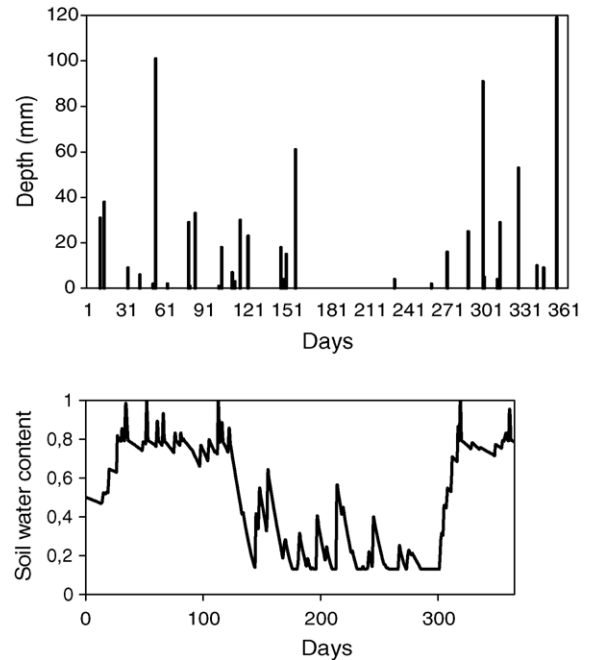

Fig. 2. Temporal variation in daily rainfall inputs (mm) and soil water content (fraction of one) dynamics in the stochastic soil water balance model.

tions among species differing in their root to shoot allocation strategy we performed more than one hundred runs along different combinations of rainfall and disturbance regimes.

A complete account of model equations and parameters are given, respectively, in Appendix and in Table 1. Structural and functional parameters hydraulic resistance (R_s), leaf area index (LAI), Root to shoot (R/S), cavitation threshold (Ψ_c) and light extinction coefficient (α) were set to describe standard values for a typical Mediterranean sclerophyll (*Quercus ilex* L.) (Jones, 1992). Monthly and hourly values of photosynthetic available radiation, air temperature and dew point for this location were obtained by interpolating the 6-h ISLSPC global climate database for a location in Northeastern Iberian Peninsula, 42°N–1°W (Sellers et al., 1995). The stochastic rainfall model was parameterized to reproduce local rainfall patterns. Prior to each simulation the model was iterated one hundred times to prevent soil moisture content being dependent on initial conditions.

Table 1
Main parameter values used in the simulations

Sub-model	Parameter	Value	Units	Source
Stomatal conductance	D_o	0.010	mol mol^{-1}	Leuning (1995)
	Cuticular transpiration (b_o)	0.020	mol m^{-2} s^{-1}	
Plant and stand structure	Hydraulic resistance (R_s)	15×10^6	MPa s m^{-1}	Jones (1992)
	Leaf area index (LAI)	1.0		
	Root to shoot ratio (R/S)	1.0		
	Cavitation threshold (Ψ_c)	-2.5	MPa	
	Light extinction coefficient (β)	0.0045		Tilman (1988)
	Height (h)/biomass (B) allometry	$h = 4 \times 2500 B^{0.5}$		
Soil water balance	Soil depth (Z_r)	400	mm	Rodríguez-Iturbe et al. (1990)
	Saturated hydraulic conductance (K_s)	400	mm day^{-1}	
	Drainage constant (c)	4.0		
	Soil type curve (k_1)	-0.04		
	Soil type curve (k_2)	1.5		
	Soil porosity (n)	0.425		

2.4. General analytical framework

Even under computing intensive simulations only a small number of parameter combinations can be explored. Also understanding the causes of model behaviour can be cumbersome: e.g., mechanisms leading to stable coexistence among species, identification of switches from competitive to positive interactions or the influence of rainfall frequency gradients on density dependence processes. In this section, we propose a general multi-species model of a size-structured tree population, which takes into account the effects of competition for light and water. We justify the construction of this general framework to show evidence of convergence between forest simulators and analytical models, and leave analytical qualitative and numerical analysis (e.g., as in Angulo and López-Marcos, 2002) for further studies.

The framework introduced is a multi-species size-structured model describing tree growth, mortality and recruitment (sensu Lischke, 2001). The resource dynamics model (light and soil water availability) included in the simulator will be implicitly taken into account in the general form of functions describing growth, mortality and recruitment rates. Both independent variables size (x) and time (t) are considered to be continuous. The size variable x represents, following Kohyama (1992), the dbh (trunk diameter of breast height). Let N_i (t, x) ($i = 1, \ldots, p$) be the population density of trees of species i in the stand with respect to dbh, i.e., $\int_{x_1}^{x_2} N_i(t, x)\,dx$ represents the number of trees of species i in the stand with dbh $x \in [x_1, x_2]$ at time t.

We choose a weighted cumulative basal area of taller trees as the light index to express the shading effect and, therefore, asymmetric light competition. We suppose different ratio height/dbh for each species, denoting α_i the one corresponding to species i. This index for x-sized trees of species i is defined by,

$$I_L^i(t, x) = \sum_{j=1}^{p} \beta_j \left(\int_{x(\alpha_i/\alpha_j)}^{\infty} \frac{\pi}{4} s^2 N_j(t, s)\,ds \right)$$

and measures the basal area of all the trees, of any species that are taller than trees of species i with dbh equal to x. Coefficients β_j represent the differences in light suppression due to trees of the same height of different species.

We also define a water index through weighted total basal area to reflect competition for water, which is chosen to be the following assuming that water uptake is proportional to root surface and, therefore, to basal area:

$$I_W(t) = \sum_{i=1}^{p} \gamma_i \left(\int_{x_0}^{\infty} \frac{\pi}{4} s^2 N_i(t, s)\,ds \right)$$

where coefficients γ_i represent possible differences among species in the ratio basal area to root surface. The size x_0 is the minimum dbh for a seedling to be considered a new recruited individual.

The changes in size distribution depend on the rates of size growth, mortality and recruitment.

The species i growth rate:

$$G_i(t, x) = g_i(x, I_L^i(t, x), I_W(t))$$

depends on the individual size x, the size and species specific light index and the water index. In general, $g_i(u, v, w)$ can be described as an unimodal function on variable u reflecting that, under the same environmental conditions, growth rate increases to attain its maximum at a certain size and then decreases to cero; with respect to v, $g_i(u, v, w)$ is a decreasing function due to the negative effect on the growth rate produced by the light index which is a measure of shading; finally the dependence on variable v is difficult to be generally specified because, as argued in the introduction, an increase in global density could have either positive or negative effects on water availability in a Mediterranean climate depending on annual rainfall and rainfall frequency gradients.

Mortality rate for species i, $M_i(t, x)$, must take into account exogenous and endogenous causes as well as relative size differences. Thus, we propose a general mortality rate depending on size and light and water indexes:

$$M_i(t, x) = m_i(x, I_L^i(t, x), I_W(t))$$

Recruitment rate for species i, $R_i(t)$, is considered to be proportional to the basal area of trees of this species which have reached the minimum reproduction age, a_r^i, with a proportionality coefficient which includes the effects of light and water competition on seed germination and seedling establishment (e.g., until the minimum size x_0 is attained). So a proposed general form for the recruitment rate is:

$$R_i(t) = r_i(I_L^i(t, x_0), I_W(t)) \int_{x_r^i}^{\infty} \frac{\pi}{4} s^2 N_i(t, s) \, \mathrm{d}s,$$

where $r_i(u, v)$ is a decreasing function on both variables, and x_r^i is the dbh at the minimum reproduction rate, i.e., $x_r^i = x(a_r^i)$ with $x(t)$ being the solution of the initial value problem $\mathrm{d}x/\mathrm{d}t = G_i(t, x)$, $x(0) = x_0$.

The model based upon the classical model for a state-structured population, see Metz and Diekmann (1986) and de Roos (1997), reads as follows ($i = 1, \ldots, p$):

Balance law

$$\frac{\partial N_i}{\partial t} + \frac{\partial[g_i(x, I_L^i(t, x), I_W(t))N_i]}{\partial x}$$
$$= -m_i(x, I_L^i(t, x), I_W(t))N_i, \quad (t > 0, x > x_0)$$

Birth law

$$g_i(x_0, I_L^i(t, x_0), I_W(t))N_i(t, x_0)$$
$$= r_i(I_L^i(t, x_0), I_W(t)) \int_{x_r^i}^{\infty} \frac{\pi}{4} s^2 N_i(t, s) \, \mathrm{d}s, \quad (t > 0)$$

Initial dbh distribution

$$N_i(0, x) = \phi_i(x), \quad (x > x_0)$$

Particular cases of this model has been discussed by Kohyama (1991, 1992) where no water competition nor interspecific differences in allometry are considered. Calsina and Saldaña (1997) performed an analytical study (asymptotic behaviour of the solutions) of the particular case for which growth, mortality and recruitment rates of a single species depend on a linear combination of resource availability but it is size-independent. Similar non-local terms as the one used in our model have been developed and applied by Angulo and López-Marcos (1999, 2000, 2002) to solve numerically monospecific size-structured population models.

3. Results

3.1. Resource allocation and whole-plant performance

Leaf area index (LAI) had a strong effect on both mortality and annual carbon gain. A larger LAI implies a larger photosynthetic apparatus and larger light interception but also higher water loss and reductions in stomatal conductance (see reduction in g_F in Fig. 3). Diminishing payoffs in terms of carbon gain result in hyperbolic increments of annual net carbon assimilation per unit of ground with respect to LAI and in a decrease of net assimilation per unit of leaf (Fig. 3). This effect was found both in a dry (400 mm annual rainfall) and in a humid site (annual rainfall 1200 mm) although differences among the two climates were rather small. Plant probability of mortality increased sharply with respect to LAI in both environments fol-
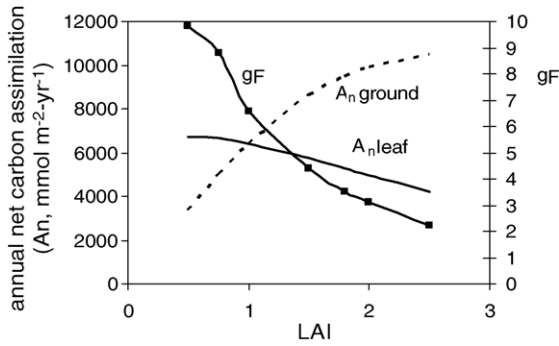
Fig. 3. Variation in plant net carbon assimilation per unit of leaf (solid line, left axis), per unit of ground (dashed line, left axis) and in the parameter g_F (dotted solid line, right axis). Results apply to a single *Quercus ilex* individual.

lowing a logistic function (Fig. 4). The risk of mortality started to increase after LAI values around 1.5 in dry and 2.0 in humid environments. For values larger than 2.5 the probability of mortality approached 1.0 and 0.69 in dry and humid environments, respectively.

Root to shoot allocation (R:S) had also a relatively larger impact on mortality than on annual net carbon assimilation (Fig. 5). Plant mortality increased after R:S allocations around 1 and 0.5 in dry and mesic sites, respectively increasing according a logistic function. For R:S values around 0.5 plant probability of mortality in mesic sites was close to zero, reaching 0.7 in xeric sites. Optimal leaf area index increased linearly with increasing values of annual precipitation (Fig. 6) with values around 1 in sites receiving less than 400 mm and reaching up to 2.5 when annual rainfall exceeded 1000 mm. Optimal root to shoot allocation decreased along the rainfall gradient to reach a minimum of 0.25 at localities receiving annually more than 1000 mm and reached its maximum value around 200 mm (Fig. 6).

3.2. Shade effects, plant interactions and stand structure and dynamics

Plant water stress was strongly modified by light suppression, annual rainfall and frequency of rainfall events (Fig. 7). In humid climates plant water stress reached 27 and 18 days under low and high rainfall frequencies regimes, respectively. A threshold respond was observed for a reduction of 70%, which resulted in dramatic improvement of plant water status. As expected plant water stress was much higher in the dry
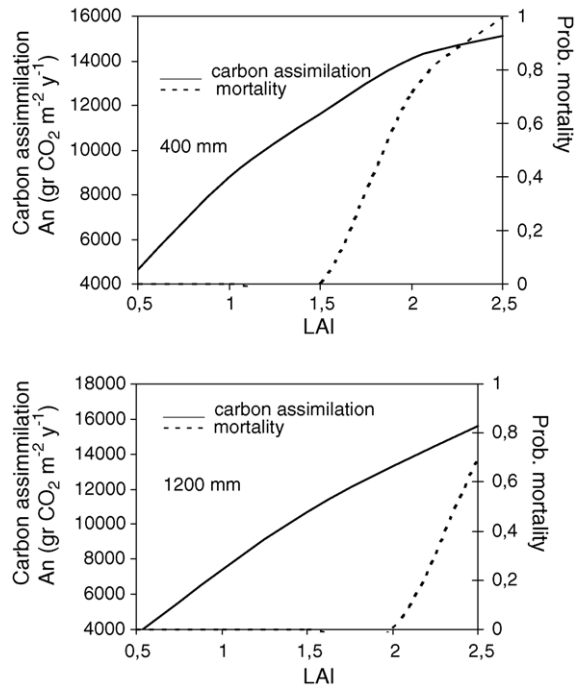

Fig. 4. Effects of increasing LAI (leaf area index) on plant annual net carbon assimilation (left-handed axis, solid line) and plant probability of mortality (right-handed axis, dashed lines) for dry (400 mm annual rainfall, upper figure) and humid (1200 mm annual rainfall, lower figure) environments ($R/S = 0.5$). Results apply to an isolated *Quercus ilex* individual.

than in the humid climate (Fig. 7). Unlike the humid climate, water stress was significantly lower in the low than in the high frequency rainfall regime. Also the decrease in stress resulting from light suppression was hyperbolic (as opposed to logistic). These trends can also be documented through the variability in the risk of mortality with respect to light, which also showed a dramatic effect (Fig. 8). In the drier climate (400 mm of annual rainfall) and low rainfall frequency, probability of mortality reduced with shade according to a logistic function with maximum values around 0.75 under full sunlight, down to 0 for a shade reduction of 0.65. A high rainfall frequency resulted in higher plant mortality across the light suppression gradient. In moister climates (1200 mm) shade reduced mortality both under high and low frequency rainfall regimes. The risk of mortality was more elevated in the high frequency regime where it remained close to one and decreased sharply for light suppression values lower
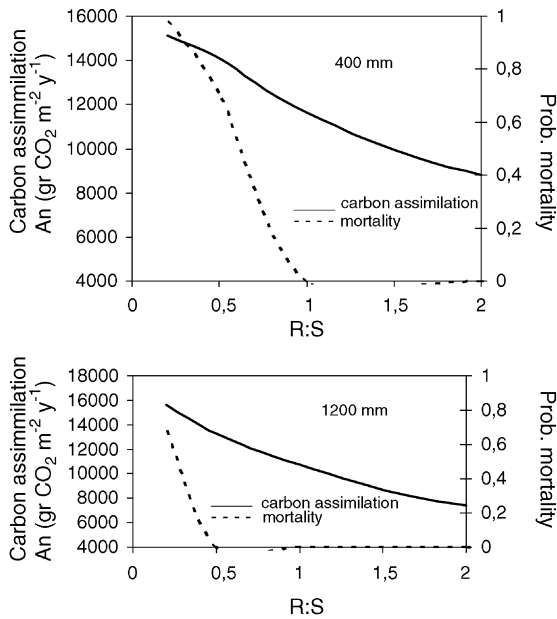
Fig. 5. Effects of increasing R/S (root to shoot) allocation on plant annual net carbon assimilation (left-handed axis, solid line) and plant probability of mortality (right-handed axis, dashed lines) for dry (400 mm annual rainfall, upper figure) and humid (1200 mm annual rainfall, lower figure) environments (LAI = 1). Results apply to a single *Quercus ilex* individual.

than 0.72. Probability of mortality was lower for the low frequency treatment, reaching maximum values at full sunlight, to decrease smoothly afterwards following a logistic function. Water competition intensified considerably plant probability of mortality by pushing the whole curve to the left and the plant becoming more sensitive to radiation (data not shown).

Rainfall regime had a dramatic impact. Stand biomass followed cyclic dynamics without reaching an equilibrium and with cycle amplitude decreasing with annual precipitation. Standing crop was highly resilient to initial conditions, disturbances and episodic droughts. Rainfall stochasticity had a major influence on stand biomass by increasing considerably stand production. For the range of climatic conditions explored we did not observe coexistence among species differing in their $R:S$ allocation. Along the precipitation gradient "rooty" species excluded leafy species in the lower dry end of the gradient while "leafy" species eliminated "rooty" ones in the long run in mesic and humid sites (Fig. 9). We did not observe a coexis-
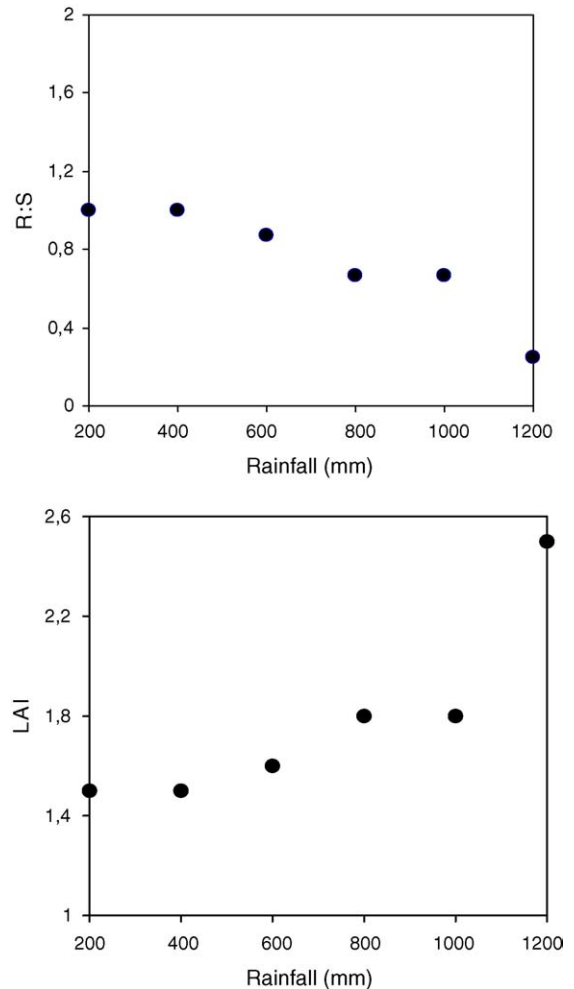

Fig. 6. Predicted optimal R/S (root to shoot) allocation (upper figure) and LAI (lower figure) along a rainfall gradient. Results apply to an isolated *Quercus ilex* individual.

tence region for intermediate rainfall values but rather a threshold response with shifting dominance of one phenotype over the other. These simulations however only included a few combinations of model parameters.

4. Discussion

4.1. Resources and biomass invested by plants

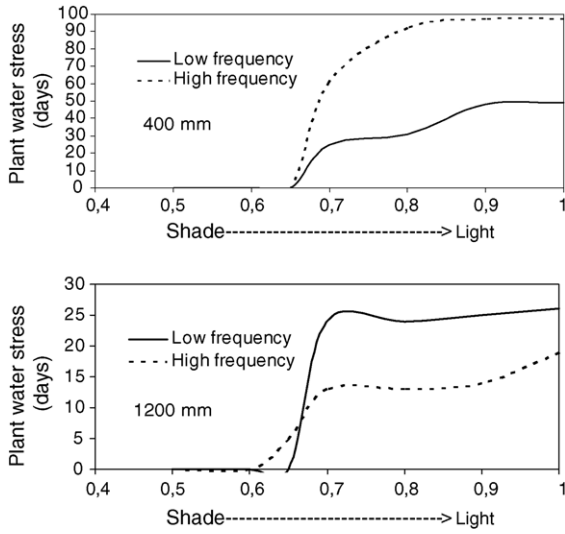According to the classical tradeoff between above- and below-ground resource uptake (Tilman, 1988) a

Fig. 7. Plant water stress at the two extremes of an annual rainfall gradient: humid Mediterranean (1200 mm, lower figure) and semi-arid (400 mm, upper figure). The vertical axis shows number of days in which plant stress reaches critical values. The horizontal axis indicates the percentage of light reduction. The two lines indicate respectively low (solid lines) and high (dashed lines) rainfall frequencies (LAI = 1, R/S = 0.5). Results apply to a *Quercus ilex* individual within a forest stand.
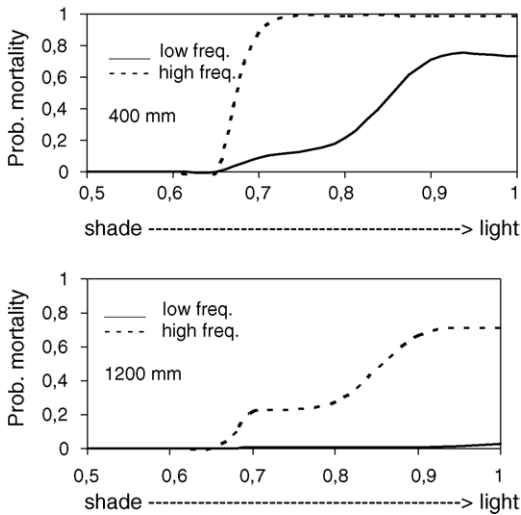

Fig. 8. Effects of rainfall regime and light suppression on plant probability of mortality (LAI = 1, R/S = 0.5). The horizontal axis indicates the percentage of light reduction. Two annual rainfall regimes are contrasted: 400 mm (upper figure) and 1200 mm (lower figure). Two rainfall frequencies are shown: low frequency (solid line) and high frequency (dashed line).
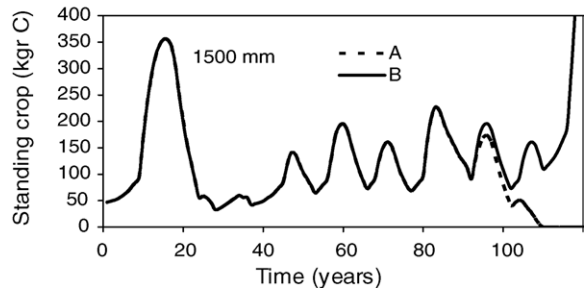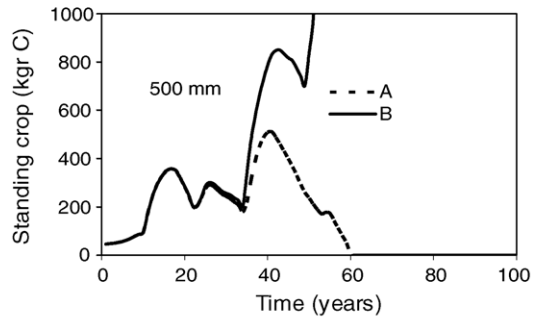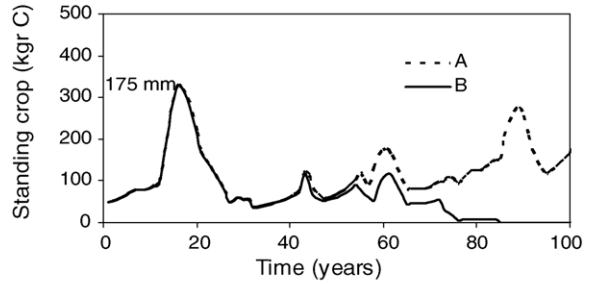

Fig. 9. Outcome of competition among "rooty" (dashed line) and a "leafy" (solid line) allocation strategies in arid (upper graph), Mediterranean (middle graph) and temperate environments (lower graph). Simulations are performed in a 1000 m^2 plot and with a disturbance rate of 10% of annual biomass removal. Simulation and results apply to a stand of interacting individual trees.

larger allocation to photosynthetic apparatus results in higher rates of light interception while a larger investment in roots increases below-ground resources uptake rates. Our results imply however that tradeoffs associated with light and water competition express across functional levels in a qualitatively different manner than tradeoffs associated with nutrient competition. Water use in Mediterranean sclerophylls seems governed by a series of mechanisms that operate hierarchical to maximize long-term carbon gain and escape

summer mortality (Rambal, 1993; Tenhunen et al., 1990; Sala and Tenhunen, 1996). At the leaf level stomatal adjustments allow the plant to perform a suboptimal strategy in which leaves optimize water use efficiency under rapidly changing atmospheric conditions and a fixed level of soil potential. As water availability changes, whole plant carbon gain and water use optimization requires that the plant reaches a new functional equilibrium in which daily patterns of water expenditure are readjusted in terms of soil water availability (Rambal, 1993; Zavala, 2004). Plants with a larger photosynthetic apparatus experience higher transpiration rates and deplete water in the soil at a faster rate than plants with a relatively lower leaf investment. Thus, plant carbon gain per unit of ground area increases but so does transpiration per unit ground area. This increase in transpiration translates into longer periods of stomatal closure. Thus, the payoff of LAI investment diminishes, explaining why the relationship between assimilation rate per unit of ground and LAI follow a hyperbolic relationship as opposed to linear. Moreover, the risk of mortality increases with LAI at a faster rate than plant growth suggesting that the energetic leaf-level constrain between carbon acquisition and water loss expresses as a tradeoff between growth and survival at the plant-level (Cowan, 1982).

A number of experimental studies have shown that plant optimal allocation may result from a compromise among selective forces acting in opposite directions (Tilman, 1988). A high shoot allocation will have a positive effect on survivorship in light limited environments where mortality is mainly the result of a negative carbon balance. In contrast, water-limited environments the benefits of shoot allocation (e.g., specific leaf area) do not compensate the costs of root construction and maintenance. More likely mortality induced by drought results from a collapse in water potential. Seedlings grown under well watered regimes may perform worse during the summer (higher mortality rates) than plants grown under water limiting conditions because they develop larger shoots that increase water losses and mortality (van den Driessche, 1991). According to our model predictions allocation to fine roots can improve plant survivorship (see Canham et al., 1999 for temperate forest tree species and Villar-Salvador et al., 2000 for a Mediterranean evergreen). There is some conflicting evidence on how root to shoot allocation and drought tolerance interrelate.

This disagreement is often the result of lumping in the same pool roots devoted to structural support and storage with fine roots which are seemingly linked to resource uptake (Canham et al., 1999; Zavala et al., 2000). Therefore our theoretical results suggest that root storage/ support components must be separated from fine root biomass in order to effectively test for allocational tradeoffs associated with shade and drought tolerance.

4.2. Shifts in plant interactions along environmental gradient and species coexistence

Our results suggest that under a Mediterranean climate plant interactions can be qualitatively different than those observed in temperate forests where light and nutrients are the main limiting resources (Tilman, 1988; Smith and Huston, 1989; Pacala et al., 1996). According to classical plant competition theory an increase in population size will result in poorer performance of new recruiting individuals because of reduced light and nutrient availability. As predicted by our model; however, in a Mediterranean climate detrimental effects of canopy cover (mainly increased light and water competition) can be offset by the benefits. Thus, neighbouring individuals may facilitate rather than difficult the establishment and growth of new individuals (Callaway, 1992; Maestre et al., 2003). A number of processes haven been shown to ameliorate water stress or to improve resource availability under plant cover (see Fig. 10). Irradiance in Mediterranean climates can be very intense resulting in photoinhibition that can increase the risk of mortality and decrease carbon gain (Valladares and Pearcy, 1997). Thus, partial shade can facilitate seedling survival (Rey Benayas, 1998). Also water availability can be relatively larger in the shade than in the open because of the predominant role of soil evaporation with respect to canopy interception and tree transpiration (Joffre and Rambal, 1993). Other positive effects of neighbouring trees not included in our model include wind protection (Wilson and Agnew, 1992), hydraulic lift (Richards and Caldwell, 1987), herbivore protection (Castro et al., 2002), canopy interception and patchy distribution of soil moisture or nutrients through stem flow (Schlesinger et al., 1996). Finally, shade can have indirect positive effects on seedling performance through a reduction in herbaceous cover and water depletion
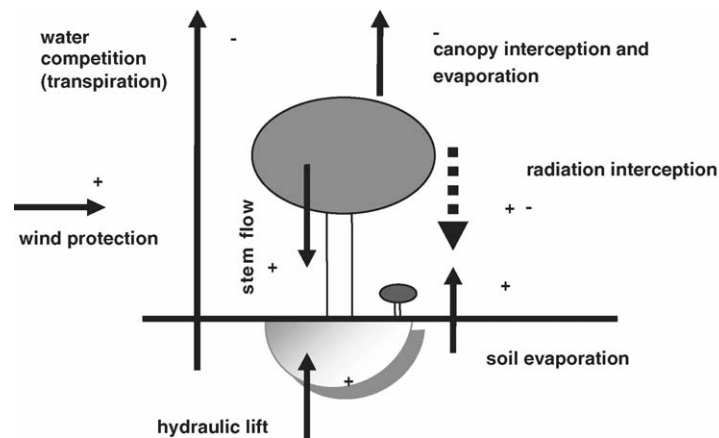
Fig. 10. Positive (+) and negative (−) effects of a competing established individual on a seedling during the establishment process. Radiation attenuation by the canopy decreases photosynthesis rates but also ameliorates negative radiation effects. Canopy interception and tree transpiration are major negative effects which decrease soil water available for the seedling. Hydraulic lift, wind and temperature oscillation protection, stem flow and a reduction in soil evaporation tend to improve seedling water status and soil water availability. Also indirect effects through reduction of herbaceous cover have been reported.

rates (Maestre et al., 2004). In agreement with previous empirical studies, the net outcome of plant interactions can change along environmental spatial (slope aspect, Gómez-Aparicio et al., 2004, edaphic, Pugnaire et al., 2004) or temporal gradients associated with the availability of water (Tielborger and Kadmon, 2000; Kitzberger et al., 2000). Unlike previous simpler graphical models (Holmgren et al., 1997) our model provides both an unifying explanation for the variety of cases in which the sign of plant to plant interactions in Mediterranean environments can shift, and for the first time a mechanistic description that can be linked to data from current empirical studies.

According to our model the outcome of the interaction among two species does not lead to stable coexistence but rather to dominance of the best competitor for each environmental condition. A number of studies (e.g., Hacker and Gaines, 1997) have suggested that positive interactions can enhance diversity by creating new opportunities for some species. In contrast for the range of simulations performed we did not find evidence of light and water-partitioning strategies leading to stable coexistence as described in light and nutrient limited ecosystems. This can be due to the fact that we did explore only a portion of the possible parameter combinations that can emerge in a complex simulator highlighting the importance of formulating

or aggregating analytically tractable models. Nevertheless coexistence in spatial models is often the result of partitioning of spatial heterogeneity with each species becoming dominant in a given part of the gradient but without long-term coexistence within resource patches (Pacala and Tilman, 1994). Also previous analytical studies of stand dynamics under water-limited conditions show the existence of multiple stable states (changes between founder control and competitive exclusion driven by shifts from facilitation to competition), and absence of stable coexistence (Zavala, 1999).

4.3. Perspectives on scaling ecological processes in Mediterranean forests

The structure and physiognomy of Mediterranean vegetation is strongly linked to moisture patterns (Miller, 1981). Stand production is very variable from site to site depending on slope aspect and other topographic variables, which influence plant water balance. Also gradients in water availability modify community physiognomy by inducing changes in above- or below-ground biomass. In previous studies (Specht, 1981; Woodward, 1986), leaf area index is estimated through an optimization process in which it is iteratively adjusted to maintaining soil water potential

beyond wilting point. However, community level optimization processes are not supported by evolutionary theory and identification of the rules from which collective behaviour emerges from individual level interactions (the unit of natural selection) is required (Maynard Smith, 1982).

Maximization of water use efficiency (Cowan and Farquhar, 1977) may be a valid strategy for established individuals of tree species that can have good access to soil water. For this species, carbon gain maximization may be achieved by operating at the safety limits imposed by cavitation and embolism risk. Implementation of such a strategy in a model of Mediterranean gas exchange simulator resulted in realistic water use patterns (Zavala, 2004) and it is also in agreement with empirical studies of hydraulic performance (Tyree and Sperry, 1989). In contrast, water use efficiency maximization is not likely to be selected in competitive environments where saving water is of little use. Both conservative and wasteful water use strategies have been reported in Mediterranean chaparral species (Miller, 1981). Also, in addition to stomatal control plant phenology (Heilmeier et al., 2002) or resource temporal partitioning (Chesson, 1983) may be more relevant for explaining niche differentiation in these communities.

The scaling of physiological processes directly from the leaf to the stand or to the ecosystem ("Green Slime models") may be of little relevance to ecological systems in which demographic processes interact disturbances, history and chance to shape vegetation dynamics. Mechanistic theories developed so far rely either on simple analytical or heuristic models that omit too many critical biological details (Holmgren et al., 1997; Smith and Huston, 1989) or on size-structured numerical models (Shugart, 1984; Tilman, 1988; Mouillot et al., 2001). Simulation studies are a useful first approximation to explore the main processes at work in any ecosystem but a full understanding of model dynamical behaviour in relation to biologically interpretable mechanisms is best achieved through analytical models. Advances in aaggregation techniques in which collective properties of the modelled system are described as emergent properties of biological phenomena at lower levels of organization (e.g., Auger and Roussarie, 1994; Moorcroft et al., 2001) suggests that scaling of ecological processes may be a feasible goal.

Appendix A. Whole-tree physiological model

Tree growth is based on a big-leaf model (see Zavala, 2004 for details) described by a system of non-linear equations that simulates the following variables: leaf temperature (T_1), leaf water potential (ψ_1), leaf latent heat flux (φE), leaf conductance (g_s) and plant net carbon assimilation (A_n). To estimate T_1 we assume that net canopy energy balance equals the rate of storage, which is considered negligible in relation to the other terms in the energy balance (Jones, 1992). Net sensible heat loss from the leaf (C) is proportional to the difference between leaf and air temperature ($T_1 - T_a$), air heat capacity (C_p) and the parameter g_a, which describes plants boundary layer conductance (Jones, 1992). Transpiration rates are assumed to equilibrate instantaneously with incoming water flux. The former is driven by the difference in water potential between leaves and roots ($\psi_L - \psi_c$) divided by hydraulic resistance to water flow from the soil to leaves mesophyll (R_s) (Rambal, 1993). Leaf transpiration (E) is proportional to D_1 (vapour mole fraction difference between the leaf and the air), and to leaf conductance (Jarvis and McNaughton, 1986). We assume a fully turbulent regime in which the series sum of plant boundary layer conductance and canopy conductance converge to the latter. Plant net carbon assimilation (A_n) is computed as the difference between gross assimilation rate and respiratory losses (both due to CO_2 production and maintenance of woody structures).

Gross assimilation rate is estimated with a simplified version of a photosynthesis model (Farquhar et al.,

1980) in which leaf photosynthesis is described as a minimum of two potential capacities limited respectively by radiation (J_e) and Rubisco (J_c) (Collatz et al., 1991; Foley et al., 1996). The light limited rate of photosynthesis (J_e) is given as:

$$J_e = \alpha \, \mathrm{PAR} \frac{C_i - \gamma}{C_i + 2\gamma} \tag{A.1}$$

where PAR is flux of photosynthetically active photons absorbed by the leaf, α is the intrinsic quantum efficiency for CO_2 uptake in C_3 plants, C_i is CO_2 concentration in the intercellular air spaces of the leaf and γ is gross photosynthesis compensation point. The parameter γ is estimated as half the ratio of the atmospheric oxygen concentration $[O_2]$ and χ (the ratio of kinetic parameters describing the partitioning of enzyme activity to carboxylase or oxygenase function). The Rubisco limited rate of photosynthesis is estimated as:

$$J_c = V_m \frac{(C_i - \gamma)}{C_i + K_c(1 + [O_2]/K_o)} \tag{A.2}$$

where V_m is Rubisco maximum capacity to perform the carboxylase function and K_c and K_o are the Michaelis–Menten constants for CO_2 and O_2, respectively. Concentration in the intercellular air spaces of the leaf (C_i) is estimated iteratively through the following equation:

$$C_i = C_a - A_n(1.6 \, g_a + 1.4 \, g_s) \tag{A.3}$$

where C_a atmospheric CO_2 concentration.

Respiratory leaf CO_2 production (R_d) was assumed equal to $0.015 V_m$ (Farquhar et al., 1980). Maintenance respiration for woody structures (R_{wood}) is given by:

$$R_{wood} = \beta_{wood} \, C_{wood} \, f(T_a) \tag{A.4}$$

where β_{wood} is a maintenance respiration coefficient defined at $15\,\mathrm{C}°$ ($0.20\,\mathrm{year}^{-1}$ for fine root biomass), C_{wood} describes carbon invested in stem, branches and roots, and $f(T_a)$ is the Arrenhius ambient temperature function. The kinetic parameters of the model: χ, K_c, K_o, V_m and respiratory leaf CO_2 production (R_d) also change with temperature according to the Arrenhius function (see Foley et al., 1996 for exact parameter values). Net leaf assimilation rate is obtained after discounting leaf and wood maintenance respiration.

The resulting system of four equations and five unknowns (φE, ψ_l, T_l, g_s and A_n) requires another

equation relating g_s to other state variables. We use a BWB-type of model in which the parameter that controls stomatal conductance for a given net CO_2 assimilation rate (g_F), is unknown for water limiting conditions (Ball et al., 1987). We use the formulation developed by Leuning (1995), stated as:

$$g_s = g_F \frac{A_n}{(c_s - \gamma)(1 + (D_l/D_o))} + b_o \tag{A.5}$$

where c_s is CO_2 concentration at the leaf surface (approximately equal to c_a under fully turbulent regime), D_l is the water vapour mole fraction difference between the leaf and the air D_o is a reference value expressed in the same units than D_l and b_o is leaf cuticular conductance.

A.1. Stochastic soil water balance

Soil water balance dynamics is described by a discrete-time version of Rodríguez-Iturbe et al., 1990 stochastic model, coupled to the whole-plant model through transpiration:

$$\begin{aligned} \Delta s_t &= s_{t+1} - s_t \\ &= \left(\frac{1}{n\,Z_r}\right)[P_t - E_t\,(s_t) - T_t(s_t) - D_t(s_t)] \end{aligned} \tag{A.6}$$

where s_{t+1} and s_t are relative soil moisture in two consecutive hours, Z_r is soil depth, and P_t, $T(s_t)$ and $D(s_t)$ describe respectively daily precipitation, transpiration and drainage. Soil volume is estimated as the volume sum of air, water and mineral components,

$$V_s = V_a + V_w + V_m \tag{A.7}$$

Soil porosity is estimated as:

$$n = \frac{V_a + V_m}{V_s} \tag{A.8}$$

It follows that soil volumetric water content (θ) is the ratio of water volume to soil volume and relative soil moisture becomes,

$$s = \frac{V_w}{V_a + V_m} = \frac{\theta}{n} \tag{A.9}$$

Water inputs (P_t) take place daily at a fixed instant (evening) with rainfall events Poisson distributed with

rate τ (average number of day between two successive rainfall arrivals). The probability of a storm event within t days is given by:

$$P(t) = 1 - e^{-t/\tau} \tag{A.10}$$

Every storm event is characterized by a certain depth or magnitude (r), described by an exponential distribution:

$$f_r(r) = \alpha\, e^{-\alpha r} \tag{A.11}$$

where f_r is the probability distribution of rainfall events of r intensity, and α is a parameter linked with mean depth. For simplicity canopy interception and evaporation are not considered.

Soil evaporation, $E_t(s_t)$, is estimated from potential transpiration (PT) and corrected by an exponential Michaelis–Menten function of soil moisture:

$$PT = \eta \frac{\delta R}{\varphi(\delta + j)} \tag{A.12}$$

where δ is the rate of change of saturation vapour pressure with temperature, φ is the latent heat of water vaporization, j is the psychometric constant, R is canopy net heat gain estimated from PAR and η is a parameter that describes R attenuation throughout the canopy as:

$$\eta = e^{-\beta\, LAI} \tag{A.13}$$

where β is the extinction coefficient of net radiation through the canopy and LAI is the leaf area index (see Rambal, 1993).

The transpiration term, $T_t(s_t)$, is described by the biological feedback established between soil moisture and stomatal conductance and it is adjusted through changes in the parameter g_F (see text for details).

Losses from deep drainage, $D(s_t)$ equal soil saturated hydraulic conductivity of the soil, k_s, when this is saturated ($s_t = 1$), and decrease according to a power function of relative soil moisture content in unsaturated soil. This is,

$$D(s_t) = \begin{cases} K_s\, s_t^c & s_t < 1 \\ K_s & s_t = 1 \end{cases} \tag{A.14}$$

where c is an empirical parameter which depends on soil type. The relationship between soil water potential and relative soil moisture content follows a power law:

$$\psi_s = k_1(n\, s)^{-k_2} \tag{A.15}$$

where n is soil porosity and k_1 and k_2 are constants linked to soil-type (see parameter values in Rodríguez-Iturbe et al., 1990 and Rambal, 1993).

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